

Running headline: plant interactions and restoration

**The role of plant interactions in the restoration of degraded ecosystems: a
meta-analysis**

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1 **Summary**

- 2 **1.** Traditionally, techniques of plant manipulation during restoration have focused on the reduction of
3 competition by “problematic” existing vegetation. However, the recent revitalization of facilitation in
4 mainstream ecology has brought a change in the practice of restoration towards a better awareness
5 of the benefits inherent to conserving neighboring vegetation.
- 6 **2.** Here I provide the results of a meta-analysis of published studies that have manipulated
7 interactions among plants with the objective of restoring degraded terrestrial systems. I created four
8 different datasets corresponding to the variables most commonly used to measure plant performance
9 (i.e. emergence, survival, growth and density), and asked whether the benefits of facilitation as a
10 restoration tool vary depending on the study duration, the life form of the neighbor and target species,
11 and the ecosystem type.
- 12 **3.** Neighbor effects varied strongly among performance estimators, larger and positive effects found in
13 general for emergence and survival, and smaller negative effects for growth and density.
- 14 **4.** No clear support existed for a relationship between study duration and neighbor effect.
- 15 **5.** The life form of the interacting species, particularly of neighbors, largely influenced the interaction
16 outcome. Herbs had strong negative effects, especially on other herb species, whereas shrubs had
17 large facilitative effects, especially on trees.
- 18 **6.** Semiarid and tropical systems showed in general more positive neighbor effects than wetlands and
19 particularly temperate systems. However, these results were largely influenced by the over-
20 representation of herb species in wetlands and temperate habitats, survival facilitation being found in
21 all systems when only woody species were considered.
- 22 **7. *Synthesis.*** Pre-existing vegetation can have large impacts on species establishment in degraded
23 habitats. Inhibition predominates in herbaceous communities typical of early-successional stages,
24 whereas facilitation prevails in communities dominated by shrubs and trees. Even productive
25 systems appear suitable for the application of facilitation as a restoration tool of woody communities.
26 These results differ in principle from predictions of current theoretical models, and warn about the
27 direct application to degraded habitats of the ecological understanding developed for natural systems.
28 Whereas restoring herbaceous communities seems largely reliable on removal techniques,
29 augmenting populations of nurse shrubs and trees should be considered a promising strategy for
30 restoring late-successional communities.

1

2 **Key-words:** competition; degraded systems; establishment; facilitation; growth; life-forms; nurse
3 plants; plant-plant interactions; restoration; succession.

4

5 **Introduction**

6 As human impacts on ecosystems worldwide intensify, the restoration of degraded habitats
7 increasingly becomes an urgent task and a difficult challenge (Choi *et al.* 2008; Hobbs & Cramer
8 2008). Stimulated by this need, the science of restoration ecology has experienced a major advance
9 in the last 20 years, and numerous restoration techniques have been proposed as tools to recover the
10 physical, chemical and biological properties of degraded systems (Perrow & Davy 2002; van Andel &
11 Aronson 2006). Among these techniques, the manipulation of the plant community appears as one of
12 the most promising and effective ways to simultaneously overcome the abiotic and biotic barriers that
13 usually limit the recovery of degraded areas. Plants alter surface wind and fluvial flows, ameliorate
14 stressful microenvironmental conditions, and are a source of organic matter that improves soil fertility,
15 therefore serving as a natural, self-sustaining way to restore the abiotic environment (Davy 2002;
16 Whisenant 2002). As a result of this modifying activity, established vegetation can facilitate the
17 incorporation of new individuals into the community, according to a model of succession by facilitation
18 (Connell & Slatyer 1977). However, it can also occur that once earlier colonists are established and
19 have secured space and resources, they arrest the incorporation of new individuals according to a
20 model of succession by inhibition (Connell & Slatyer 1977). The balance between these positive and
21 negative plant interactions will condition the rate and direction of successional change, and therefore
22 its manipulation can be used to influence the development or regression of a degraded system
23 towards the target plant community (Siles *et al.* 2008).

24 Traditionally, the most popular techniques of plant manipulation during restoration have
25 focused on the reduction of competition by “problematic” existing vegetation. Thus, before seeding or
26 planting desired species, neighbors were eliminated with different treatments such as fire, herbicides,
27 grazing, or hand/mechanical removal (Jordan 1988; Clewell & Lea 1990; Savill *et al.* 1997). However,
28 the recent revitalization of positive plant interactions in mainstream ecology, and the accumulating
29 evidence of facilitation as the dominant interaction in many situations (Callaway 2007; Brooker *et al.*
30 2008), has initiated a change in the practice of restoration towards a better awareness of the benefits

1 inherent to conserving neighboring vegetation (Byers *et al.* 2006; Padilla & Pugnaire 2006; Halpern *et*
2 *al.* 2007). Thus, in Mediterranean post-fire shrublands pioneer shrubs have been shown to act as
3 nurse plants that benefit the establishment of late-successional woody species (Gómez-Aparicio *et al.*
4 2004; Castro *et al.* 2006; Siles *et al.* 2008). In semiarid rangelands, where typical restoration
5 approaches included shrub removal to promote herbaceous forage production for livestock grazing,
6 more recent studies have focused on using established shrubs to enhance herbaceous production
7 and diversity (Pyke & Archer 1991; Huber-Sannwald & Pyke 2005). Similarly, whereas weed
8 suppression has been usually considered necessary in wetland restoration, some doubts have started
9 to rise about the need of weed control in all situations (McLeod *et al.* 2001).

10 Despite the increasing number of facilitation examples in restoration practice, it is still not
11 clear when and where existing vegetation should be removed or promoted. For example, in tropical
12 abandoned pastures, grasses and shrubs have been found to compete with trees for resources in
13 some situations (Sun & Dickinson 1996; Holl 1998; Griscom *et al.* 2005), but to buffer harsh abiotic
14 conditions and facilitate tree recruitment in others (Aide & Cavelier 1994; Vieira *et al.* 1994; Holl 1999).
15 The consequence of such conflicting results are passive management recommendations such as
16 “being cautious about assuming that removing non-tree vegetation will benefit forest regrowth until
17 more is known” (Duncan & Chapman 2003a,b) or the need of “more research before shrubs are
18 introduced on a wide-scale to help restore abandoned pastures” (Holl 1998). Clearly, being passive
19 implies not exploiting the large potential that managing plant interactions has to accelerate the
20 recovery of degraded systems. The outcome of plant interactions is highly variable because it implies
21 a balance of positive and negative effects that may change depending on several factors such as the
22 characteristics of the species interacting or the environmental conditions (Callaway & Walker 1997;
23 Armas & Pugnaire 2005; Maestre *et al.* 2009). Therefore, if we are to take an active restoration
24 approach, efforts should be directed to improve our understanding of which species and habitats are
25 more prone to benefit from a management based on releasing competition, and which from a
26 management based on promoting facilitation.

27 In this study I provide the results of a meta-analysis that aims to synthesize the results obtain
28 to date by studies that have manipulated interactions among vascular plants with the objective of
29 restoring degraded terrestrial systems. Meta-analysis (Gurevitch & Hedges 2001) provides a useful
30 tool for extracting general results from a suite of individual studies, and therefore is used here to

1 explore whether the experience accumulated over the past few decades can be used to formulate
2 general recommendations about the use of facilitation as a restoration tool in degraded systems.
3 Although different words with somewhat different meanings are frequently used in ecological
4 restoration (i.e. restoration, rehabilitation, reclamation, remediation), here I followed Hobbs & Norton
5 (1996) and used the term “restoration” to refer broadly to all activities that seek to repair damaged
6 ecosystems and restore their biological potential. I focused the meta-analysis on 4 main questions.
7 First, I asked whether the benefits of facilitation as a restoration tool vary depending on the plant
8 performance estimator (i.e. emergence, survival, growth, density). Understanding how restoration
9 practices can differentially affect demographic parameters is important to appropriately weigh the
10 costs and benefits of the restoration (Gillespie & Allen 2004). Second, I asked whether the benefits of
11 facilitation vary depending on the duration of the study. Because competition has been shown to
12 increase with ontogeny (Miriti 2006; Quero *et al.* 2008; Armas & Pugnaire *in press*), I would expect the
13 net effect of established neighbors to become increasingly negative as study duration increases. Third,
14 I asked whether the benefits of facilitation vary depending on the life form (i.e. herb, shrub, tree) of the
15 neighbor and target species. If so, I further explored the existence of interdependence between
16 neighbor and target life forms, looking for particular pair combinations that were more likely to render
17 positive interactions. Knowledge of the extent to which a certain species group may facilitate the
18 establishment of another group would be valuable in formulating assembly rules for ordering the
19 introduction of species into a site (Gómez-Aparicio *et al.* 2004; Siles 2008). Finally, I asked whether
20 the benefits of using established vegetation as nurse plants vary among ecosystem types (i.e.
21 semiarid, tropical, wetland, temperate). Because positive plant interactions are expected to be
22 especially common under high abiotic stress (Bertness & Callaway 1994, see discussion in Maestre *et*
23 *al.* 2005, 2006a; Lortie & Callaway 2006), facilitation could be a more useful restoration tool in
24 stressful systems such as water-limited habitats than in more productive ones such as wetlands or
25 temperate habitats.

26

27 **Material and methods**

28 DATABASE

29 I focused on published studies that explicitly explored the role of plant interactions (both positive and
30 negative) in the restoration of degraded terrestrial ecosystems. Studies were located by searching

1 keywords in an electronic database (ISI Web of Science 1945-2008) for combinations of two groups
2 of terms: 1) "facilitation", "competition", "positive interaction", "negative interaction", "interference" or
3 "nurse", and 2) "restoration", "rehabilitation", "reclamation", "remediation", "revegetation",
4 "reforestation" or "afforestation". More studies were found within the reference lists of the gathered
5 papers. A study was considered valid for the meta-analysis if it met the following criteria: 1) the study
6 had to be quantitative and the data reported in a usable form; 2) the study had to be conducted under
7 natural conditions in the field (greenhouse experiments were excluded); and 3) the study had to
8 evaluate the effect of neighbors on the performance of target species or group of species.
9 Performance of the target species growing in the vicinity of a neighbor was compared with that of
10 plants growing in open areas (without neighbors) or in areas where neighbors had been removed.
11 Studies where the influence of neighbors was reduced (e.g. canopy thinning) but not eliminated (i.e.
12 no pure "open treatment" existed) were not considered. When several removal methods were tested
13 (e.g. mowing vs. herbicide), only the data from the most effective method was considered. Studies
14 that used burning as a removal method were not included due to the several side-effects of fire (e.g.
15 on soil structure and nutrient content; Certini 2005). Studies that simulated the presence of neighbors
16 (i.e. artificial shade) instead of using real plants were not included.

17 Suitable studies were grouped in 4 different data sets, depending on the plant performance
18 estimator quantified: emergence, survival, growth (measured as biomass or height), and density
19 (measured as number of individuals or cover per a given area). If repeated measures were taken in a
20 study, only the results obtained at the end of the experiment were used. If more than one publication
21 presented results from the same field plots (e.g. Castro *et al.* 2002 and 2004), I relied upon data from
22 the most recent paper. In cases in which the neighbor treatment was crossed with additional
23 treatments that implied explicit manipulation of the environment (i.e. fertilizer addition), I included only
24 the ambient treatment. In cases in which articles involved several combinations of nurse and target
25 species, or conducted the same experiment in several sites or years, each combination was treated
26 as a separate study. I decided to include several studies from the same paper because, although it
27 tends to reduce the overall heterogeneity in effect sizes, excluding multiple results from a paper can
28 underestimate effect sizes (Gurevitch & Hedges 1999; Karst *et al.* 2008). When data were only
29 reported in graphical form, I used the data-grabbing software TechDig v2.0 (Jones 1998).

30

1 META-ANALYSIS

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

7 Emergence and survival data were summarized in 2×2 contingency tables, with columns
8 representing treatments (with vs. without neighbors) and rows the possible outcomes (emerged vs.
9 not emerged, alive vs. dead). An odds ratio (OR) metric was obtained for each study, calculated as
10 the ratio of the odds of emergence/survival in the presence of neighbors (experimental treatment) to
11 the odds of emergence/survival in their absence (control treatment). Because there were some
12 studies where all individuals emerged/survived or not emerged/survived, and this could produce odds
13 ratio values that require division by 0, the odds ratio were calculated adding 1 to the number of
14 individuals in each category for every study (Hyatt *et al.* 2003; Maestre *et al.* 2005). Values of the
15 natural log of the odds ratio [$\ln(\text{OR})$] higher than 0 indicate a positive effect of neighbors on
16 performance (facilitation), whereas values lower than 0 indicate a negative effect of neighbors
17 (competition). Magnitudes of effect sizes were interpreted *sensu* Cohen (1969).

18 The effect size of neighbors for growth and density data was calculated using the natural log
19 of the response ratio [$\ln(\text{RR})$] and its associated variance ($v_{\ln\text{RR}}$). The response ratio (RR) is the ratio
20 of the mean outcome in the experimental group to that of the control group. The response ratio was
21 preferred over the more traditional Hedge's d because it better estimates the actual difference in
22 mean performance among treatments, whereas the Hedge's d (based on standard deviation units)
23 can yield large effect sizes even when the absolute difference among means is small (Morris *et al.*
24 2007). The estimate of $\ln(\text{RR})$ and $v_{\ln\text{RR}}$ for each study is based on means, SDs, and replicate
25 numbers for control and treatments (Hedges *et al.* 1999). If standard errors (SEs) were reported, they
26 were transformed according to the equation: $\text{SD} = \text{SE} (n^{1/2})$. Unidentified error bars were assumed to
27 represent SE. As for odds ratios, positive $\ln(\text{RR})$ values indicate facilitation and negative values
28 competition.

29 The effect of neighbors was first assessed for each of the four entire datasets. The total
30 heterogeneity of each meta-analysis, Q_T , was calculated to analyse whether the variance among

1 effect sizes was greater than expected by sampling error (Rosenberg *et al.* 2000). Q_T is a weighted
2 summed of squares comparable to the total sum of squares in ANOVAs, and it is tested against a χ^2
3 distribution with $n-1$ degrees of freedom. Then, I evaluated the homogeneity of results among groups
4 (Q_M , variance explained by the model) created to respond to the specific questions posed in the study.
5 The percentage of variation in effect sizes explained by each grouping variable was estimated as
6 Q_M/Q_T (Rosenberg *et al.* 2000). One continuous and 4 categorical grouping variables were selected.
7 The continuous variable was “study duration”, and its effect was explored using weighted least
8 squares regression adjusted for meta-analysis (Rosenberg *et al.* 2000). The duration effect was only
9 assessed for survival and growth (variables measured mainly in experimental seedlings, and rarely in
10 natural vegetation) because emergence was always assessed a few months after sowing, and density
11 was in many cases a one-time estimation of cover or abundance of natural vegetation. The 4
12 categorical grouping variables were: 1) neighbor life-form (i.e. herb, shrub and tree). Herbaceous
13 species were further subdivided into grasses vs. forbs, and annuals vs. perennials; 2) target life-form
14 (i.e. herb, shrub and tree). As for neighbors, herbaceous species were subdivided into grasses vs.
15 forbs, and annuals vs. perennials; 3) neighbor-target combination (i.e. herb-herb, herb-shrub, herb-
16 tree, shrub-herb, shrub-shrub, shrub-tree, tree-herb, tree-shrub, and tree-tree); and 4) ecosystem type
17 (i.e. semiarid, tropical, wetland and temperate). The semiarid category was used in broad sense to
18 include different types of water-limited ecosystems (arid, semiarid, Mediterranean), since preliminary
19 analysis did not show differences among them. Also based on a preliminary data exploration, wet and
20 dry tropical systems were merged into a single tropical category. To control for possible correlation
21 among grouping variables (e.g. woody species were more common in semiarid and tropical studies
22 than in wetland and temperate ones, and the opposite was true for herbs), I also examined ecosystem
23 effects considering only woody species. Differences in mean effect sizes among groups were
24 calculated using random-effects models, which allows for the possibility that studies differ not only by
25 sampling error (as fixed-effects models do), but also by a random component in effect sizes between
26 studies (Gurevitch & Hedges 2001). Bias-corrected bootstrap 95% confidence intervals (CIs) were
27 calculated for each effect size (Rosenberg *et al.* 2000). If the 95% CI did not overlap with zero, then
28 effects were significant at $P < 0.05$.

29 Sensitivity analyses were used to control dependence between data and confirm that the
30 trends detected were not affected by a few large studies (Gates 2002; Lortie & Callaway 2006). For

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

11

12 **Results**

13 EMERGENCE

14 A total of 14 studies met the selection criteria, yielding 62 suitable cases (see Appendix S1 in
15 Supplementary Material). On average, neighbors had a neutral effect on emergence (i.e. 95% CI
16 crossed zero; Fig. 1a). The test of the overall heterogeneity was not significant ($Q_T = 43.09$, $df = 61$, P
17 $= 0.95$). However, significant among-group differences appeared for the 4 categorical grouping
18 variables ($P < 0.05$ in all cases; Table 1). Among neighbor life forms, herbs had a neutral effect on
19 emergence, whereas the effect of shrubs was positive (there were not enough cases available to
20 calculate a tree effect; Fig.1a). Among target groups, herbs showed a neutral response, whereas the
21 response of shrubs and trees was largely positive (Fig. 1a). However, when herbs were subdivided
22 into grasses and forbs, the response varied from positive in grasses to negative in forbs (Fig. 2a).
23 When neighbor and target groups were analyzed in pairs to explore interdependence, herbs were
24 found to have a negative effect on themselves but a positive effect on shrubs and trees, whereas
25 shrubs had positive effects on the 3 groups, especially on trees (Fig. 3a). Among ecosystem types,
26 the effect of neighbors was significantly positive in semiarid and tropical habitats, whereas no
27 significant effect was found for wetlands or temperate systems (Fig. 1a). The small sample size
28 precluded exploring differences among ecosystem types considering only woody species.

29

30 SURVIVAL

1 A total of 57 studies met the selection criteria, yielding 287 suitable cases (see Appendix S2 in
2 Supplementary Material). Across all studies, the presence of neighbors had a neutral effect on
3 survival (Fig. 1b). The test of the overall heterogeneity was not significant ($Q_T = 250.11$, $df = 286$, $P =$
4 0.95). However, large significant differences in neighbor effects appeared for all continuous and
5 categorical grouping variables ($P < 0.05$ in all cases; Fig 4a, Table 1). There was a significant
6 negative relationship between the duration of the study and the effect size (Fig. 4a). Regarding the
7 neighbor life form, herbs had a large negative effect on survival, whereas trees and particularly shrubs
8 had a positive effect (Fig. 1b). Within herbs, grasses had a much larger negative effect than forbs,
9 whereas only marginal differences appeared among annuals and perennials (Table 2; Fig. 2b).
10 Among target groups, herbs and shrubs showed a neutral response to neighbors, whereas the
11 response of trees was positive (Fig. 1b). No differences appeared among the different target
12 subgroups of herbs (Table 2; Fig. 2b). When neighbor and target groups were analyzed in pairs,
13 herbs were found to have a significant large negative effect on themselves and on trees, but not on
14 shrubs. Shrubs had a positive effect on the 3 groups, especially on trees, and trees had a positive
15 effect only on themselves (Fig. 3b). The neighbor effect was positive in semiarid and tropical systems,
16 and negative in wetland and temperate habitats (Fig. 1b). However, when analyses were repeated
17 considering only woody species, differences among ecosystem types disappeared ($Q_M = 2.65$, $df = 3$,
18 158 , $P = 0.44$), and positive neighbor effects were found in all systems (lnOR [95%CI] semiarid = 0.75
19 [0.50-0.98]; tropical = 0.40 [0.09-0.73]; wetland = 0.69 [0.41-1.07]; temperate = 0.61 [0.13-1.30]).

20

21 GROWTH

22 A total of 54 studies met the selection criteria, yielding 202 suitable cases (see Appendix S3 in
23 Supplementary Material). Across all studies, the presence of neighbors had a small negative effect on
24 the growth of target species (Fig. 1c) and the dataset showed significant internal heterogeneity ($Q_T =$
25 257.57 , $df = 201$, $P = 0.006$). There was not a significant relationship between the effect size and the
26 duration of the study (Fig. 4b). Among neighbor groups, although the effect size was small in all cases,
27 it varied from negative for herbs, through neutral for trees, to positive for shrubs (Fig. 1c). Within herbs,
28 annual neighbors had a larger negative effect than perennials (Fig. 2c). Among target species, only
29 herbs showed a significant negative response to neighbors (Fig. 1c). When neighbor and target
30 groups were analyzed in pairs, herbs had the largest negative effects on themselves, followed by

1 trees, whereas the effects on shrubs were not significant. Shrubs had a neutral effect on herbs, and a
2 positive effect on themselves and especially on trees. Contrary to shrubs, trees had a negative effect
3 on herbs, and a neutral effect on themselves (Fig. 3c). Among ecosystem types, the neighbor effect
4 varied from not significant for semiarid and tropical systems, to negative for wetland and particularly
5 temperate systems (Fig.1c). Differences among ecosystems remained when only woody species were
6 considered ($Q_M = 12.64$, $df = 3$, 71 , $P = 0.005$).

7

8 DENSITY

9 A total of 40 studies met the selection criteria, yielding 123 suitable cases (see Appendix S4 in
10 Supplementary Material). Across all studies, the presence of neighbors had a moderate negative
11 effect on the density of target species (Fig. 1d). The dataset presented significant internal
12 heterogeneity ($Q_T = 157.87$, $df = 122$, $P = 0.008$). Among neighbor groups, herbs and trees had a
13 negative effect on target density, whereas the effect of shrubs was neutral (Fig. 1d). However, the
14 statistical differences among the three groups were only marginally different (Table 1). There were no
15 differences among herbaceous subgroups in their neighbor effects (Table 2; Fig. 2d). The response of
16 target groups to the presence of neighbors was negative for herbs and shrubs and neutral for tree
17 species (Fig 1d). No differences appeared in the response of the different herb subgroups considered
18 (Table 2; Fig. 2d). When neighbor and target groups were analyzed in pairs, herbs had large negative
19 effects on shrubs and on themselves, but positive effects on trees. Shrub effects were not significant
20 for any of the three groups, and trees had significant (negative) effects only on herbs (Fig. 3d). Among
21 ecosystems, the effect of neighbors was significantly different from zero only in temperate systems,
22 where they had a large negative effect on target density (Fig. 1d). These differences among systems
23 remained when only woody species were considered in the analysis ($Q_M = 19.06$, $df = 3$, 45 , $P =$
24 0.0003).

25

26 ASSESMENT OF INDEPENDENCE AND PUBLICATION BIAS

27 At the study level, results for the overall meta-analysis and the comparisons among neighbor and
28 target life forms were similar to those obtained when considering each experimental case separately.
29 The smaller sample size resulted though in generally lower significance of the tests (see Appendixes
30 S5, S6 and S7 in Supplementary Material). Differences among ecosystem types, on the contrary,

1 disappeared at the study level, indicating the existence of bias due to interdependence. The negative
2 relationship between study duration and the survival effect size also disappeared at the study level
3 ($Q_M = 1.76$, $df = 56$, $P = 0.18$), indicating the existence of bias probably induced by a few larger
4 studies that found strong positive short-term neighbor effects.

5 Fail-safe numbers tended to be large compared to the number of cases included in the meta-
6 analyses. Rosenthal (1979) suggested that if the fail-safe number was larger than 5 times the sample
7 size plus 10, it was safe to conclude that results were robust regarding publication bias. This was true
8 for all response variables (emergence fail-safe number = 667.4; survival fail-safe number = 679.6;
9 growth fail-safe number = 9759.4; density fail-safe number = 7360.9). Scatter plots of effect size
10 against sample size of the four data sets (not shown) exhibited a typical funnel shape, indicating that
11 studies with small sample sizes (and generally low precision) showed a larger scatter around the true
12 effect value than studies with larger sample sizes (and higher precision). Accordingly, the Spearman's
13 rank correlation tests between effect size and variance were not significant for any of the four
14 performance estimators ($R_s = -0.04$, $P = 0.74$ for emergence; $R_s = 0.01$, $P = 0.82$ for survival; $R_s = -$
15 0.11 , $P = 0.10$ for growth; $R_s = 0.03$, $P = 0.78$ for density), Overall, these results suggest that there
16 was little publication bias in the studies included in the review and that the meta-analyses outputs
17 were robust.

18

19 Discussion

20 Restoration strategies of degraded terrestrial systems usually center on accelerating changes in
21 species composition (Pyke & Archer 1991; Whisenant 1999; Walker *et al.* 2007). One of the most
22 popular tools to accelerate successional dynamics is the deliberate introduction of the desired species
23 into the system, overcoming in this way a major constraint in the restoration of degraded habitats
24 represented by the lack of seed dispersal (van Wieren 2002; Howe & Miriti 2004). Accordingly, the
25 large majority of the studies included in this meta-analysis involved the seeding or planting of target
26 species. Results shown here indicate that understanding the complexity of how these introduced
27 target species will interact with the pre-established neighboring vegetation can largely influence the
28 success of restoration. Thus, although low-magnitude or non-significant neighbor effects were found
29 when all studies were pooled together, strong significant patterns emerged when interaction
30 outcomes were explored among different life forms of neighbors and targets that represent differential

1 successional stages in diverse ecosystem types.

2

3 THE IMPORTANCE OF THE PERFORMANCE ESTIMATOR

4 A first important result of this review is that the effect of neighbors was clearly dependent on the
5 variable used to estimate target performance, a conclusion in agreement with previous studies on
6 plant interactions (Goldberg *et al.* 1999, 2001; Hastwell & Facelli 2003; Maestre *et al.* 2005).
7 Neighboring vegetation had in general a stronger effect on emergence and survival of introduced
8 species than on their growth. Thus, the effect of neighbors on target emergence and survival varied
9 from largely negative ($\ln OR \sim -1$) to largely positive ($\ln OR \sim 1$), whereas the effect on growth was
10 always of small magnitude ($-0.5 < \ln RR < 0.5$; Fig. 1). Although neighbor effects in terms of density
11 were also sometimes of large magnitude ($-1.2 < \ln RR < 0.5$), their interpretation should be taken
12 cautiously, since they are clearly affected by other factors beyond the neighbor-target interaction,
13 such as dispersal patterns or predator activity (Maestre *et al.* 2005).

14 The large effect of neighbors on emergence and survival reflects the well-known vulnerability
15 of seeds and seedlings to the abiotic environment during early establishment (Harper 1977; Kitajima
16 2007). Most studies targeted on small 1-2 year old seedlings, whereas a very low percentage focused
17 on older life stages (i.e. saplings, adults). The small effect of neighbors on growth was probably also
18 influenced by the focus on small seedlings during short periods of time. More than half of the 54
19 papers that analysed neighbor effects on growth lasted 2 years or less, and only 3 studies lasted
20 longer than 5 years. Because growth rates and resource demand are usually low in seedlings and
21 increase with plant size/age (Kitajima & Fenner 2000; Coomes & Allen 2007), a stronger neighbor
22 effect on growth might have been detected if older age classes or long-term studies were better
23 represented in the review. Specifically, a relative increase of competition with ontogeny could be
24 expected, as it is consistently found by studies that compare neighbor effects on early (i.e. seedling,
25 sapling) vs. late (i.e. adult) life-history stages (Miriti 2006; Schiffers & Tielbörger 2006; Armas &
26 Pugnaire *in press*). So far, the short-term nature of the dataset at hand precludes obtaining any
27 conclusion about long-term neighbor effects, but at least indicates that no strong evidence exists for
28 shifts in the neighbor-target interaction during the first 5-6 years of a restoration activity.

29 Not only the magnitude but also the sign of the interaction varied among performance
30 estimators. Thus, although the interaction outcome depended largely on the neighbor and target life

1 forms considered (see below), the probability of finding positive outcomes was much higher for
2 emergence and survival than for growth and density, for which negative interactions predominated.
3 Interestingly, this pattern of variation from strong positive neighbor effects on emergence and survival
4 to negative effects on growth has been repeatedly found in natural systems (De Steven 1991a,b;
5 Callaway *et al.* 1996; Suding & Goldberg 1999; Walker & Powell 1999; Foster 2002), indicating that
6 the environmental conditions that maximize early establishment are not necessarily those that
7 maximize biomass production. This type of life-stage conflicts (*sensu* Schupp 2007) adds complexity
8 to the restoration of vegetation, indicating that any given treatment will imply some cost in terms of
9 plant performance. However, because this review indicates much larger neighbor effects on
10 emergence and survival than on growth, and recruitment limitation is a key determinant of long-term
11 community composition and dynamics (Grubb 1977; Hurt & Pacala 1995; Hubbell *et al.* 1999),
12 vegetation management during the first 5-6 years of a restoration program should probably focus on
13 maximizing emergence and survival, despite the potential costs in terms of growth.

15 THE IMPORTANCE OF THE NEIGHBOR AND TARGET LIFE FORMS

16 A second main result of this review is that the neighbor life form strongly influenced the interaction
17 outcome, to a much larger extent than the life form of the target species. The neighbor effect varied
18 from very negative in herbs to strongly positive in shrubs (Fig.1). Moreover, among herb groups,
19 grasses had a larger negative effect than forbs, supporting previous studies that show grasses to be
20 better competitors and have higher establishment and growth rates than forbs (Goldberg *et al.* 2001;
21 Pywell *et al.* 2003). Grasses have fibrous roots and a large root:shoot ratio that allow them to compete
22 efficiently for soil resources (Caldwell & Richards 1986), especially against short woody plants such
23 as seedlings (Davis *et al.* 2005; Picon-Cochard *et al.* 2006). This is probably a main reason why the
24 few restoration studies that have found benefits in using grasses as nurse plants are either conducted
25 in systems where facilitation is largely non-resource mediated (e.g. reduced salinity or structural
26 support in wetlands; Egerova *et al.* 2003; McKee *et al.* 2007) or under extreme low-resource
27 conditions that prevent rapid grass growth (e.g. mine tailings [Choi & Wali 1995], chalk marl spoil
28 [Mitchley *et al.* 1996], or semiarid steppes [Maestre *et al.* 2001]).

29 Shrubs appeared by large as the most promising life form to use as nurse plants in restoration
30 activities. Their effect on target performance was never negative, varying from neutral for density to

1 increasingly positive for growth, emergence and survival (Fig. 1). On the one hand, shrubs are not as
2 strong competitors as early-successional grasses for belowground resources due to differences in
3 allocation patterns (e.g. lower root:shoot ratio, higher inversion in unproductive tissues as stems) and
4 in architecture (e.g. higher rooting depth that promotes niche partitioning with seedlings; Aerts *et al.*
5 1991; Jackson *et al.* 1996; Köchy & Wilson 2000). On the other hand, they are not as strong
6 competitors as trees for aboveground resources due to their general smaller size, providing frequently
7 a moderate shade intermediate between the too high irradiance levels of open habitats and the
8 limiting deep shade of closed forests (Harrington & Johns 1990; Puerta-Piñero *et al.* 2007). As a
9 result, shrubs offer the benefits of proximity (e.g. microclimate amelioration, increased soil fertility) at
10 minimum costs in terms of competitive effects.

11 Although the role of the target life form was not as determinant of the interaction outcome as
12 that of the neighbor, results indicated a differential response of herbs, shrubs and trees to the
13 presence of established vegetation in degraded habitats. Thus, whereas the overall response of herbs
14 was not positive for any of the performance estimators analysed, it was always facilitative in the case
15 of trees (though not significantly for growth and density), shrubs showing an intermediate response
16 (Fig.1). These differences are related to the way the two main components of the facilitative response
17 of a target species -competitive-response ability and stress tolerance- may vary among life forms with
18 different successional role. The facilitative response is expected to increase with increasing
19 competitive-response ability and decreasing stress tolerance (Brooker & Callaghan 1998; Liancourt *et*
20 *al.* 2005). Herbs are generally light-demanding species typical of early-successional open habitats,
21 with high growth and resource consumption rates that make them highly sensitive to competition by
22 neighbors (i.e. poor competitive-response ability). Comparatively, trees are late-successional life
23 forms with a conservative use of resources and therefore stronger competitive-response ability
24 (Tilman 1988; Wilson 1999). They could also be considered more stress-intolerant than herbs and
25 shrubs, with higher seedling mortality rates and a regeneration niche more frequently linked to nurse
26 species (Gómez-Aparicio *et al.* 2004; Valiente-Banuet *et al.* 2006; Mendoza *et al.* 2009; Padilla *et al.*
27 *in press*). Therefore, the use of pre-established vegetation as nurse plants will be a more efficient
28 restoration tool when the target species are woody plants, particularly trees (with strong facilitative
29 response), than when they are herbaceous species.

30

1 RESTORATION MANAGEMENT BASED ON KEY NEIGHBOR-TARGET COMBINATIONS

2 Beyond the general trends in the effects and responses of the different life forms, results shown here
3 also indicate that taking into account the interdependence among neighbor and target life-forms would
4 benefit the design of restoration activities. For example, the restoration of late-successional forest
5 communities could benefit from the finding of herb species having much weaker negative effects on
6 shrubs than on trees (Fig. 3). Most revegetation initiatives that aim to recover a forest canopy directly
7 introduce the target tree species into the early-successional habitat to be restored. However, planting
8 trees directly into an herbaceous cover usually renders poor results in terms of survival and/or growth
9 (Rey Benayas *et al.* 2005; Devine *et al.* 2007). Herb removal is therefore needed before planting,
10 which implies intensive site preparation, can be prohibitively expensive especially at large scale, and
11 can destroy naturally regenerating plants (Hovick & Reinartz 2007; Sampaio *et al.* 2007). This meta-
12 analysis indicates that a two-phase restoration strategy, where shrubs are sown or planted into the
13 herb layer in a first stage, and tree species later introduced under the shrub cover, should be
14 considered as an alternative to the direct introduction of trees. It would not only overcome the problem
15 of the strong inhibition of tree species by herbs, but it would also take advantage of the large positive
16 effects of shrubs on trees. Reforestation schemes with a similar multi-phase approach have been
17 recently proposed for the restoration of Mediterranean (Gómez-Aparicio *et al.* 2004; Siles 2008) and
18 tropical forests (Cabin *et al.* 2002). Mimicking the sequential stages of the successional process (i.e.
19 herb-shrub-tree) and avoiding successional jumps is probably the most natural, cheap and secured
20 way to recover late-successional communities.

21 Moreover, the fact that tree species had an overall positive (survival) or neutral (growth,
22 density), but not negative, effect on other trees indicate that not only shrubs but also trees can be
23 considered as nurses in the restoration of forest communities. This result supports the benefits of one
24 of the most extensively applied methods to catalyze the restoration of degraded forests: the use of
25 nurse plantations. Fast-growing conifers have been used since the 19th century to promote the
26 establishment of more valuable late-successional hardwoods in the temperate zone (Vallauri *et al.*
27 2002; Pausas *et al.* 2004), and also more recently throughout the tropics (Ashton *et al.* 1997; Parrotta
28 *et al.* 1997; Feyera *et al.* 2002; McNamara *et al.* 2006). The most important drawback of nurse
29 plantations is that they require intensive post-planting management (e.g. thinning), since their
30 beneficial effects usually disappear as the tree stand develops (Otsamo 1998; Dulohery *et al.* 2000;

1 McNamara *et al.* 2006). Unfortunately, such post-planting management is not always conducted,
2 rendering large monospecific and dense extensions of even-aged stands that become more of a
3 problem than a solution (Gómez-Aparicio *et al.* in press). If managed actively, however, nurse
4 plantations can have the advantage of producing economic benefits (i.e. wood, fruits) that
5 compensate or even exceed restoration costs.

6 When the restoration objective is the maintenance or recovery of early-successional
7 communities, two important recommendations can be derived from the neighbor-target
8 interdependence found here. First, no support was found for an interference effect of shrubs on herb
9 species (Fig. 3). Although the number of studies analyzing shrub-herb interactions was too low to
10 reach definite conclusions ($n = 5$), they indicate that shrubs can facilitate herb establishment in
11 degraded systems without hampering their growth or abundance. This is an important result from the
12 perspective of the shrub-herb coexistence, since it suggests that traditional restoration techniques
13 applied in systems with encroachment “problems” and based on shrub removal (van Auken 2000)
14 could be not always justified. Facilitation should be considered as another possible outcome of shrub-
15 herb interactions in these systems, especially when shrub cover is only moderate (House *et al.* 2003).
16 A second advice for the restoration of early-successional communities is based on the fact that herb-
17 herb interactions were by far the most negative ones found among all the neighbor-target
18 combinations tested, and suggests that the concept of facilitation will be of little help when restoration
19 involves exclusively herbaceous species (e.g. Pywell *et al.* 2002).

20

21 FACILITATION: A RESTORATION TOOL FOR ALL SYSTEMS?

22 Current conceptual models about the effect of abiotic conditions on the facilitation-competition
23 balance suggest that positive interactions should be particularly common in harsh, limiting
24 environments, while competition dominates more fertile, mesic, and stable habitats (Bertness &
25 Callaway 1994; Callaway & Walker 1997). Accordingly, a recent review of 296 nurse-protégé
26 interactions conducted by Flores & Jurado (2003) found more than half of these interactions to occur
27 in arid and semiarid communities. Based on these results, I anticipated the benefits of facilitation to be
28 larger in the restoration of severe environments (i.e. water-limited systems) than on more productive
29 habitats (i.e. wetlands or temperate systems). The results of the meta-analysis, however, supported
30 this expectation only partially. After correcting for interdependence, no significant differences

1 appeared among ecosystems for any of the four performance estimators analysed (Appendix S5), still
2 effect sizes tended to be more positive for semiarid and tropical systems than for wetlands and
3 particularly temperate systems. Moreover, when analyses were run considering only woody species
4 (i.e. correcting for the over-representation of herb species in wetland and temperate studies),
5 neighbor effects on survival turned positive in all systems. These two results together indicate that
6 positive neighbor effects are not necessarily restricted to systems cataloged as “stressful” at a global
7 scale, and that the dominant interaction is not governed only by the severity of the abiotic
8 environment, but also (and very importantly) by other factors such as the life history of the interacting
9 species (see also Maestre *et al.* 2009).

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

21 Because restoration studies are usually manipulative but not mechanistic, studies included in
22 the meta-analysis rarely identified a single mechanism of facilitation, but just discussed the many
23 potential mechanisms involved. Some mechanisms were highly system-specific, such as salinity
24 reduction, structural support or hydrodynamics alteration in wetlands (Dulohery *et al.* 2000; Egerova
25 *et al.* 2003; McKee *et al.* 2007). However, the majority of the mechanisms advocated were extensive
26 to all systems. Thus, woody species (and sometimes also herbs) were suggested to ameliorate
27 stressful abiotic conditions (i.e. increase soil fertility and water availability, reduce extreme
28 temperatures and high-light levels) in successional grasslands and shrublands (e.g. Maestre *et al.*
29 2001 and Gómez-Aparicio *et al.* 2004 in semiarid systems; Vieira *et al.* 1994 and Holl *et al.* 2000 in
30 the tropics; Li & Ma 2003 in the temperate zone), as well as in second-growth forests and plantations

1 (e.g. Otsamo 2000 in the tropics; Rodríguez-Trejo *et al.* 2003 in temperate systems). Regarding
2 mechanisms of facilitation involving other trophic levels, the most repeatedly invoked one was
3 attraction of seed dispersers, particularly in the tropics, where a large fraction of the species are
4 animal-dispersed (Aide & Cavelier 1994; Duncan & Chapman 1999; Zamora & Montagnini 2007).
5 Protection from herbivores was surprisingly poorly explored in the context of restoration, partly
6 because many restoration studies were conducted within exclosures in order to maximize their
7 probability of success. Although the few examples available support the importance of herbivory
8 protection in very different systems such as semiarid shrublands (Aerts *et al.* 2007), tropical old-fields
9 (Zanini *et al.* 2006) or temperate pastures (Smit *et al.* 2006), more work is needed to assess its role
10 during restoration efforts at a general scale. Finally, facilitation mediated by soil organisms (e.g.
11 mycorrhizae, N-fixing bacteria) was hardly ever mentioned in the studies reviewed. However, because
12 some authors have found higher mycorrhizal inoculum under nurse species than in open spaces in
13 degraded systems (Carrillo-García *et al.* 1999; Azcón-Aguilar *et al.* 2003), plant-soil biota interactions
14 could be also involved in the process of establishment facilitation during restoration. Again, much
15 more work is required to fully understand the relative importance of nurse effects mediated by soil
16 organisms in degraded habitats.

17

18 CONCLUDING REMARKS: CAVEATS AND OPPORTUNITIES OF MANAGING PLANT 19 INTERACTIONS IN DEGRADED SYSTEMS

20 An important challenge in restoration ecology is to find rules that are general enough to be widely
21 applicable and easily transferred to managers, but specific enough not to be useless (Temperton &
22 Hobbs 2004). This meta-analysis represents an effort to learn from the accumulated experience to
23 identify general rules that can be used by restorationists for the management of plant interactions
24 involving different types of species and degraded systems. However, because meta-analyses are
25 conditional on the set of studies included, the analyses presented here had some clear limitations to
26 assess this aim. First, the quantity of data available was only moderate in most cases, and rather low
27 for some performance estimators (e.g. emergence) and among-group comparisons. For example, the
28 number of independent papers that analysed the effect of woody neighbors on target species was
29 relatively high (>10) only in the semiarid, and as low as 3 in wetlands. Therefore, more studies would
30 be desirable before conclusions could be considered definitive. A second important drawback was the

1 short duration of most studies, which force the conclusions of this review to be applicable only in the
2 short-term. Thus, although we can discuss on the benefits of using facilitation to maximize early
3 establishment in degraded systems, not enough data are available to fully understand its long-term
4 contribution to vegetation dynamics. More long-term research is urgently required, either by promoting
5 long-term monitoring (despite its logistical problems), or by using promising alternatives such as
6 modeling (e.g. Siles *et al.* 2008).

7 Despite these limitations, results shown here clearly indicate that pre-existing vegetation can
8 have large impacts on the success of species establishment in degraded systems, inhibition
9 predominating in herbaceous communities typical of early-successional stages and facilitation in
10 communities dominated by shrubs and trees. These results in principle differ from the expectations of
11 successional theory, which predicts facilitation to predominate during primary succession or early
12 stages of colonization, and competition to increase along secondary succession as biomass
13 increases (Connell & Slatyer 1977; Callaway & Walker 1997; Wilson 1999; Grime 2001). Degraded
14 systems as those included in this review have, however, particular characteristics that could
15 contribute to explain these discrepancies. One the one hand, many early-successional habitats
16 subjected to restoration are invaded by very aggressive exotic grasses (Holl *et al.* 2000; Midoko-
17 Iponga *et al.* 2005) or have high residual soil fertility, which promotes competition with herbaceous
18 vegetation (Marrs 1993; Wall & Hytönen 2005). And on the other hand, canopy cover in degraded
19 woody communities is usually only moderate, rarely reaching the high densities typical of late-
20 successional natural forests where competition for light is a main driver of community dynamics
21 (Tilman 1988).

22 Whereas restoring early-successional herbaceous communities seems necessarily reliable on
23 removal techniques, augmenting populations of facilitator shrubs and trees should be considered as a
24 promising strategy for restoring degraded shrublands and forests (Holl *et al.* 2000; Su & Zhao 2003;
25 King 2008). Introduced nurses can nucleate forest recovery at several isolated points and promote
26 patch formation through both abiotic (e.g. resource trapping) and biotic (e.g. attraction of seed
27 dispersers) feedback dynamics (Aerts *et al.* 2006a). Probably, the cheapest and easiest way to trigger
28 this process of nucleation would be first introducing shrubs that catalyze natural succession, later
29 introducing under their canopies those tree species not able to colonize spontaneously. Shrubs have
30 the advantage of maturing and fruiting rapidly (quickly attracting dispersers) and require less intense

1 pre- and post-planting management than trees. Because they are more vigorous and stress-tolerant
 2 than trees, grass control does not seem an obligate requirement to assure their establishment, and
 3 because of their usual smaller size, the time required by seedlings and saplings to overgrow them will
 4 not be excessively long. This is an important point to take into account, since maximizing
 5 establishment will often come at a cost of reducing growth, this cost being minimal or inexistent in
 6 water-limited environments and much larger in productive systems such as temperate habitats.
 7 Restoration approaches that promote rapid revegetation and minimize cost and effort are urgently
 8 needed, especially for developing countries with few resources and incentives to restore degraded
 9 forests (Brown & Lugo 1994; Aerts *et al.* 2006b; McKee *et al.* 2007). Incorporating facilitation into the
 10 mainstream of practical ecology can clearly contribute to achieve this aim.

11

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18

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24

25 **Supplementary Material**

26 The following supplementary material is available for this article:

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

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

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

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

- 1 **Appendix S5.** Summary of random models analysing differences among groups in neighbor effects at
- 2 the study level.
- 3 **Appendix S6.** Mean effect sizes (calculated at the study level) by categorical grouping variable for
- 4 emergence (a), survival (b), growth (c), and density data (d).
- 5 **Appendix S7.** Diagram describing the magnitude of the interactions (calculated at the study level)
- 6 among different neighbor and target life forms that represent different successional stages.
- 7 **Appendix S8.** References included in Appendices S1–S4 and not cited in the main text.

Table 1. Summary of random models analysing differences among groups in neighbor effects for each of the four performance estimators (emergence, survival, growth and density). Data represent the degrees of freedom (df) 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	df	Q_M	Q_E	Q_M/Q_T	<i>P</i> -value among groups
Emergence					
Neighbor (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					
Neighbor (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					
Neighbor (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					
Neighbor (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

Table 2. Summary of random models analysing differences in neighbor 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) vs. forbs (F), and as annuals (A) vs. perennials (P). Data represent the degrees of freedom (df) 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 vs. forb comparison was conducted.

Comparison	df	Q_M	Q_E	Q_M/Q_T	<i>P</i> -value among groups
Emergence					
Target					
G-F	1, 37	11.17	37.55	0.23	0.0008
Survival					
Neighbor					
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					
Neighbor					
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					
Neighbor					
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

Figure legends

Fig 1. Mean effect sizes by categorical grouping variable (neighbor life form, target life form, neighbor-target combination, and ecosystem type) for emergence (a), survival (b), growth (c), and density data (d). Error bars are 95% bootstrapped confidence intervals. Number of cases is shown in parenthesis. Significant neighbor 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 neighbor trees on target emergence.

Fig. 2 Mean effect sizes by grouping variable of herbaceous species (grass vs forb, annual vs 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 parenthesis. Significant neighbor 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 neighbor 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 $\ln(\text{OR})$ for survival and emergence, and $\ln(\text{RR})$ for growth and density. Significant effect sizes (i.e. 95% bootstrapped confidence intervals did not overlap zero) are highlighted in bold. Only the neighbor-target interactions for which there were more than 2 experimental cases available are represented. Small sample sizes (i.e. effect sizes calculated using less than 5 experimental cases) are indicated with a cross (*).

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.

Fig. 1

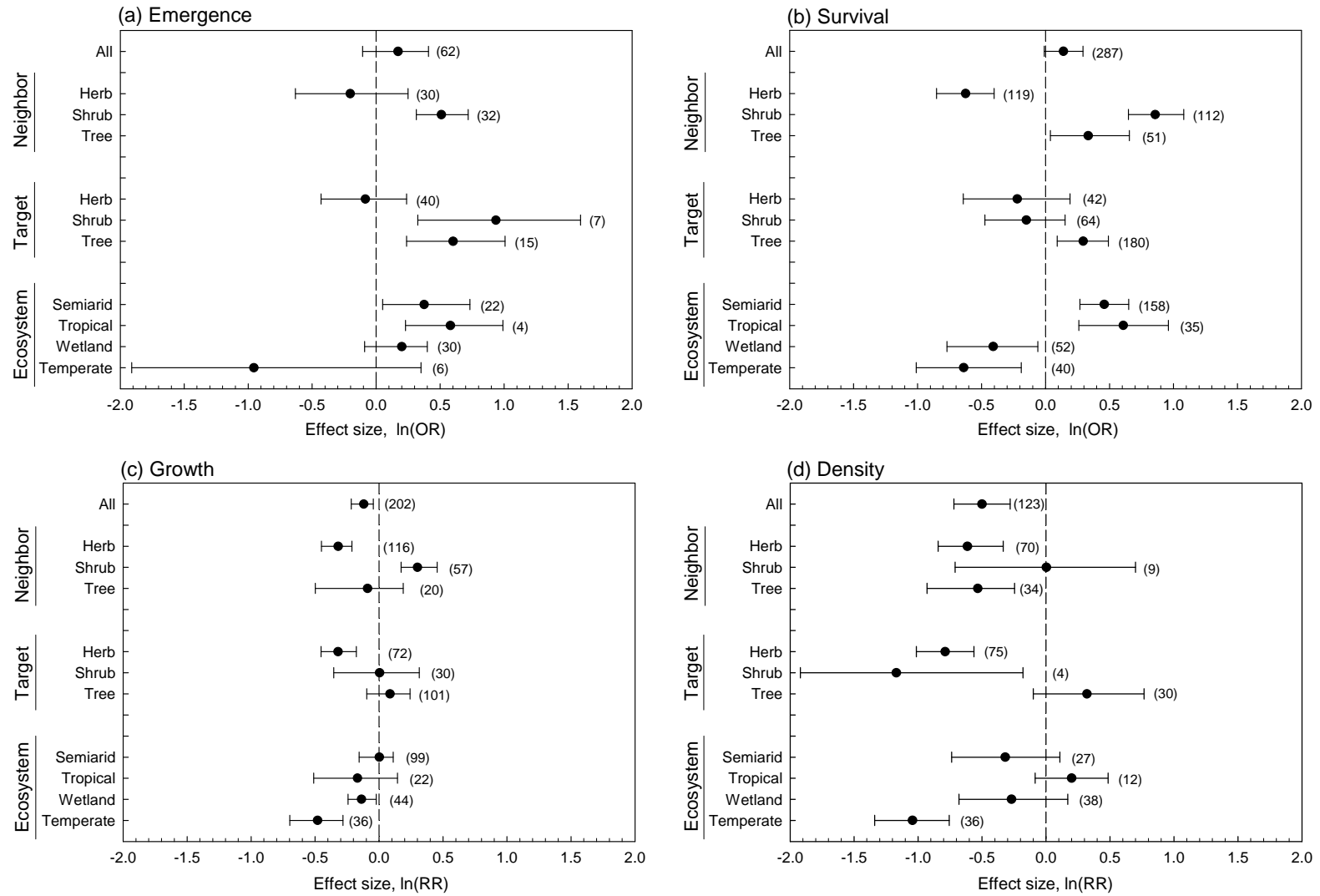


Fig. 2

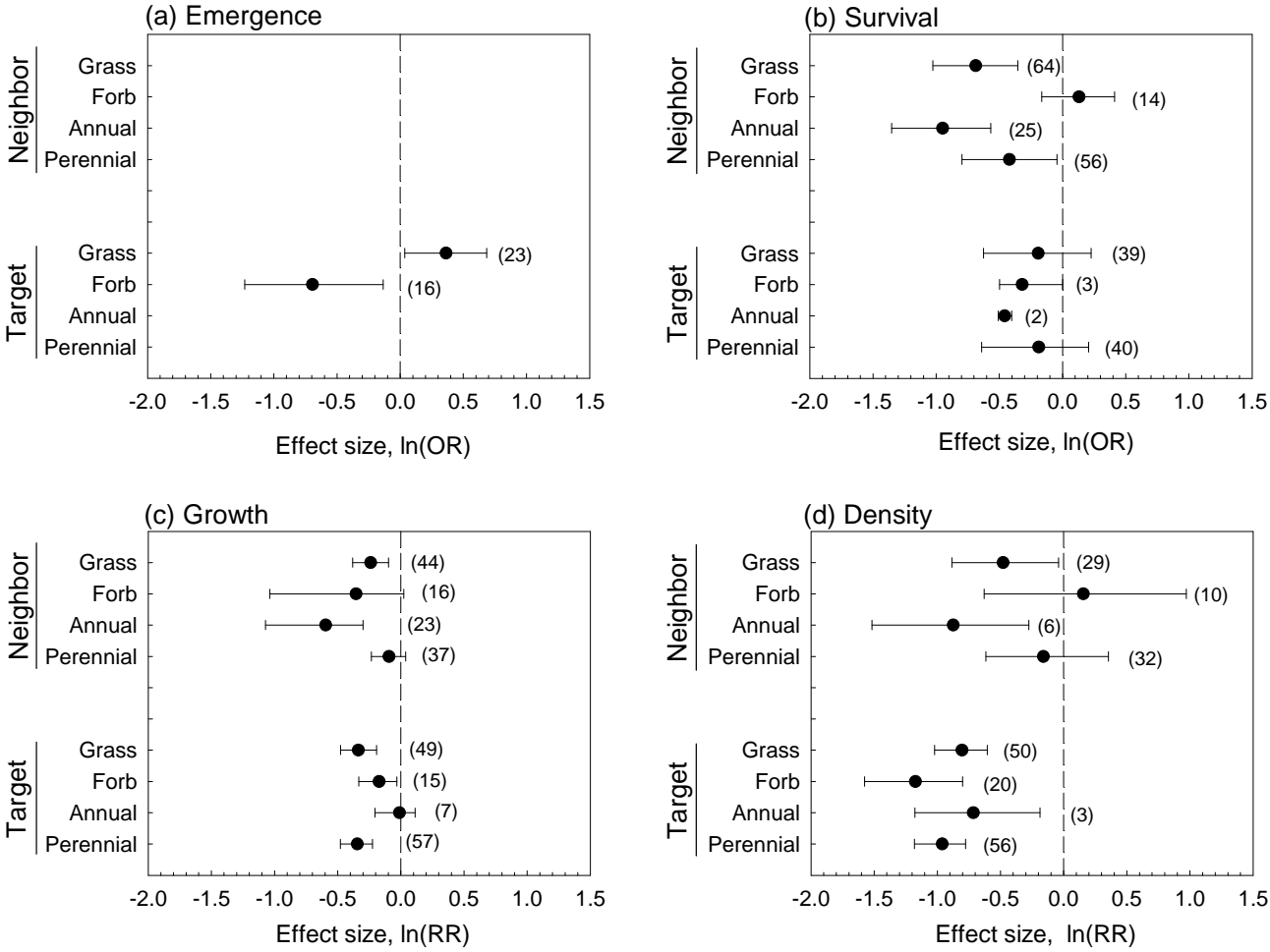
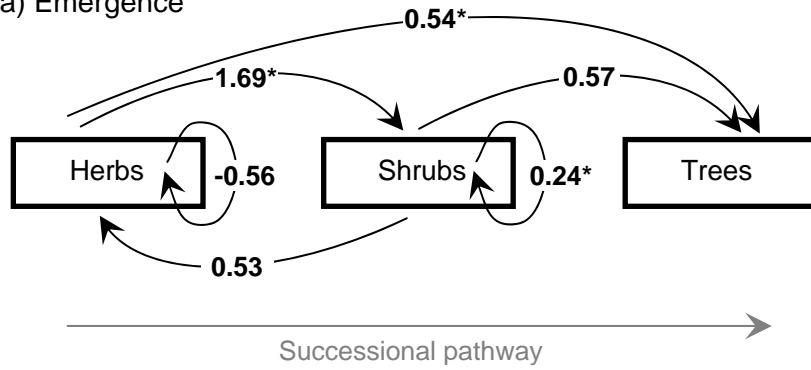
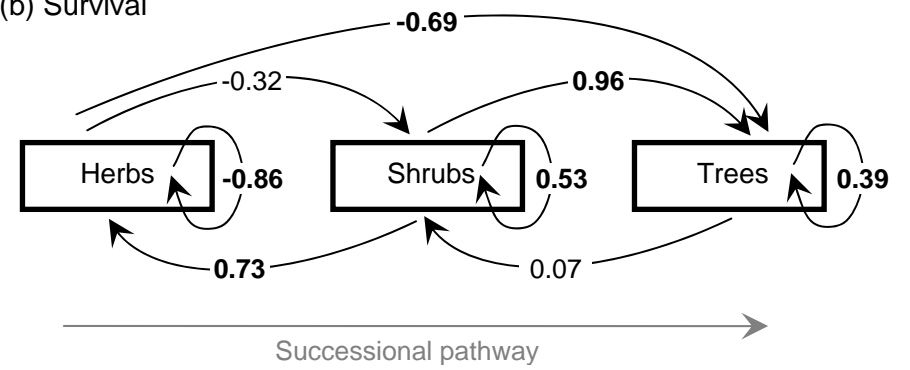


Fig. 3

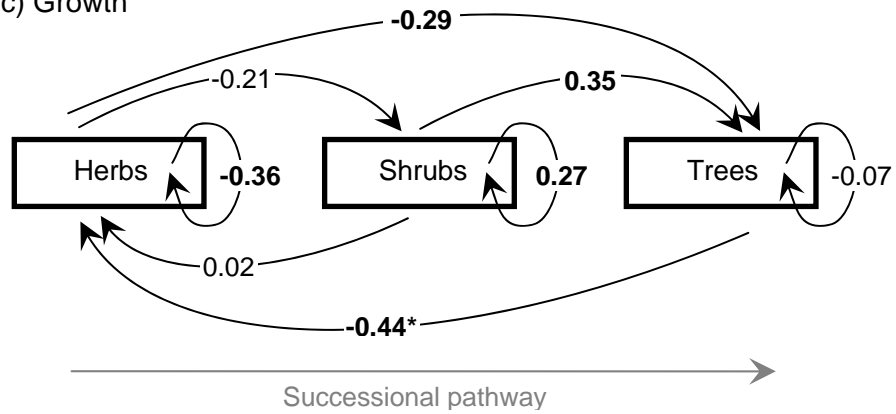
(a) Emergence



(b) Survival



(c) Growth



(d) Density

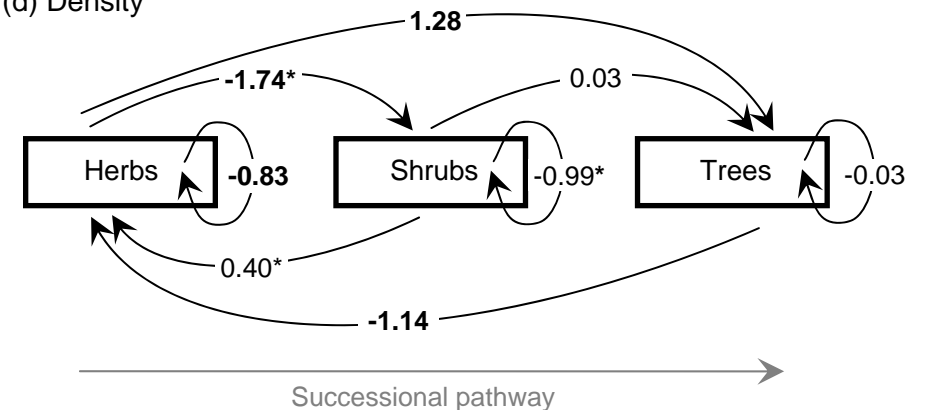


Fig. 4

