The role of nurse plants in the restoration of degraded environments

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Traditional ecological models have focused mainly on competition between plants, but recent research has shown that some plants benefit from closely associated neighbors, a phenomenon known as facilitation. There is increasing experimental evidence suggesting that facilitation has a place in mainstream ecological theory, but it also has a practical side when applied to the restoration of degraded environments, particularly drylands, alpine, or other limiting habitats. Where restoration fails because of harsh environmental conditions or intense herbivory, species that minimize these effects could be used to improve performance in nearby target species. Although there are few examples of the application of this "nursing" procedure worldwide, experimental data are promising, and show enhanced plant survival and growth in areas close to nurse plants. We discuss the potential for including nurse plants in restoration management procedures to improve the success rate of such projects.

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Plant interactions strongly influence community structure and dynamics, and are responsible for the presence or absence of particular species in a community. Traditionally, competition has been the most studied aspect of those relationships, so that ecological models have focused for decades on negative interactions, overlooking the existence of positive effects between plants. In the past 15 years, however, research has highlighted the role of positive plant interactions (facilitation) in almost all biomes (Bertness and Callaway 1994; Bertness and Hacker 1994; Callaway 1995; Brooker and Callaghan 1998; Callaway *et al.* 2002; Bruno *et al.* 2003; Lortie *et al.* 2004). Despite this increasing recognition, the inclusion of facilitation into mainstream ecological theory has been slow (Bruno *et al.* 2003). Facilitation appears to be an essential process, not only for survival, growth, and fitness in some plants (Callaway *et al.* 2002; Tirado and Pugnaire 2003; Cavieres *et al.* 2006), but also for diversity and community dynamics in many ecosystems (Pugnaire *et al.* 1996; Kikvidze *et al.* 2005). Examples are more evident in harsh, limiting environments, where some species are able to ameliorate the physical conditions in some way, or to prevent herbivory, thereby providing more suitable habitats for other species (Figure 1). This interaction has a practical side when applied to ecological restoration. In degraded habitats with extreme environmental conditions or large numbers of herbivores (Figure 2), the area near or under the canopy of certain species may provide refuge for the species being restored (target species), which otherwise may fail to establish. Here we review the potential of this procedure for ecological restoration.

In a nutshell:

- In limiting environments such as dryland, alpine, or unfertile habitats, some plants benefit from growing close to others that ameliorate extreme conditions, improve resource availability, or protect against herbivory
- The effect known as facilitation has implications for restoration where physical conditions or herbivores constrain plant performance
- The application of facilitation to restoration projects may improve the establishment of target plants, mimicking a natural process
- Species traits and site characteristics influence success rate and should be carefully considered

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Competition and facilitation

Plants growing close to each other influence their neighbors in many ways, resulting in a broad range of detrimental or beneficial outcomes. If negative effects prevail, the interaction results in competition or interference, a consequence of sharing limited resources (water, nutrients, light, space), or of a release of chemicals that will harm nearby plants (allelopathy). Conversely, nearby plants may exert a positive influence, termed facilitation, in which at least one neighboring species benefits from the interaction through improved survival, growth, or fitness.

Both positive and negative effects occur simultaneously, affect different variables, and change with time and location (Armas and Pugnaire 2005). The net balance between these effects represents the magnitude and sign (either positive or negative) of the interaction (Callaway and Walker 1997; Holmgren *et al.* 1997; Figure 3). Several factors affect this balance, including physiological and developmental traits (Callaway and Walker 1997;

Armas and Pugnaire 2005), but abiotic conditions seem to be the overriding factor, increasing the importance of positive effects in harsher environments (Brooker and Callaghan 1998; Pugnaire and Luque 2001; Callaway *et al.* 2002; but see Maestre *et al.* 2005 and Lortie and Callaway 2006 for discussion of the stress-gradient hypothesis).

The nurse effect

In some habitats, seedling establishment may be enhanced in the vicinity of adult plants that ameliorate extreme environmental factors (eg Cavieres *et al.* 2006). The positive influence of the adult plants on seedlings is called "nurse plant syndrome" (Niering *et al.* 1963), and is one of the first recorded examples of close spatial association between plants being more advantageous than detrimental. This effect is more common in environments where abiotic factors or herbivory limit plant performance, such as in arid (Flores and Jurado 2003) or alpine habitats (Cavieres *et al.* 2006). The underlying mechanisms relate mainly to the improvement of microclimatic conditions, increased water and nutrient availability, and protection against herbivory (Panel 1; also see Callaway 1995; Callaway and Pugnaire 1999).

Although some authors have suggested that this nurse effect could potentially play a role in restoration (Bradshaw and Chadwick 1980), by the mid-1990s only a few anecdotal reports on this topic were available (eg Mitchley *et al.* 1996). However, experimental evidence addressing the role of nurse plants in restoration has increased in the past few years (Table 1). Here we review restoration experiments in which seeds or seedlings of restored species were placed both near adult plants that acted as nurses and in control gaps (Figure 4), and provide suggestions for management. We have not included examples from natural or planted forest systems or from nurse crops (ie when nurse plants are cultivated, either in advance or simultaneously, with restored plants).

Figure 1. *Fertile area under the canopy of the leguminous shrub* Retama sphaerocarpa *in the Tabernas desert (Almería, Spain).* Retama *facilitates the growth of understory plants, leading to the development of a community consisting of numerous small shrubs and herbaceous species.*

Panel 1. The advantages of growing close to nurse plants

- Nurse plants may buffer non-optimal environmental conditions. Shade reduces soil water evaporation, lowers soil and air temperature, and decreases the amount of radiation reaching the plants, thus protecting seedlings from the damaging effects of extreme temperatures and low humidity in arid environments. Canopy protection also prevents salt enrichment in soil marshes and wetlands, and may reduce frost injuries in cold areas.
- Nurse plants may improve the availability of soil resources. Through the process known as "hydraulic lift", roots of certain species lift water stored in deep soil layers and release it near the soil surface. Once in the surface layers, the water can be used by understory plants, and improves their water status and growth rate. Nutrients in the understory are enhanced through litter and sediment accumulation, higher mineralization rates, and larger microorganism populations. Positive root interactions between facilitator and facilitated plants allow nitrogen transfer between legumes and non-leguminous plants, increase ectomycorrhizal infection, and make possible the exchange of nutrients and carbon via mycorrhizal fungi.
- Nurse plants may protect against grazing. In heavily grazed areas, plants growing beneath non-palatable or thorny plants have an advantage, as compared to unprotected plants.
- Nurse plants that are highly attractive to pollinators may increase pollinator visits to the target plants.

Role of facilitation in restoration

The first published research looking at the use of natural nurse plants for restoration purposes was carried out at the end of the 1990s in southeast Spain (Castro *et al.* 2002; Gasque and García-Fayos 2004). Since then several experiments have been conducted in alpine areas, semiarid steppes, arid shrublands, coastal wetlands, and degraded and burnt sites.

In the Sierra Nevada range (Spain), at an elevation of 1800 m, Castro *et al.* (2002) found that nurse shrubs decreased mortality in two mountain pines without inhibiting their growth. After two growing seasons, survival of Scots pine (*Pinus sylvestris*) and European black pine (*Pinus nigra*) was markedly better under sage (*Salvia lavandulifolia*) than in control gaps (55 versus 22% and 82 versus 57%, respectively). Differences were still present after four growing seasons (Castro *et al.* 2004); survival rates were 1.8 to 2.6 times higher under sage than in gaps. When the nurse plants were thorny shrubs such as *Prunus ramburii*, establishment differed between the north and south aspects of the plant; while results in the north were similar to survival levels seen under sage, in the south the results were similar to those seen in open areas.

In the same Sierra Nevada range, but including a wider

Figure 2. *In past centuries, intense pressure from human activities, including agriculture, overgrazing, burning, and logging, has resulted in the deforestation of most mountainous areas in SE Spain, such as the Sierra Alhamilla foothills shown here. Woodland restoration at such sites is frequently impeded by drought and grazing; using nurse plants may improve the success of restoration projects.*

altitudinal range (500–2000 m elevation), Gómez-Aparicio *et al*. (2004) conducted a series of experiments to test the effect of 16 native shrub species over 11 shrub and tree species. One year after planting, establishment success under shrubs was more than double that seen in the gaps, reaching fourfold higher numbers in some cases. However, the outcome differed, depending on the target species, type of nurse plant, and year. The observed nurse effect of shrubs was considerable for evergreen Mediterranean species, such as Holm oak (*Quercus ilex*), shrubs such as prickly juniper (*Juniperus oxycedrus*), and deciduous species like maple (*Acer opalus*), but was not significant for pines (Scots and black pine). The most successful nurse plant species were native brooms (such as *Genista* spp), and small and thorny shrubs. In contrast, a significant negative influence was seen with rockroses (*Cistus* spp), probably the result of allelopathy. In fact, the harsher the ecological conditions, the stronger the facilitative effect of the nurse plants.

A large number of experiments have been carried out to test the potential of esparto grass (*Stipa tenacissima*), a widespread perennial tussock-forming grass, as a nurse plant on degraded semiarid steppes in southeast Spain. However, the results differed depending on site, year, and target species involved. Gasque and García-Fayos (2004) found that the favorable conditions near esparto grass tussocks increased germination rate of Aleppo pine (*Pinus halepensis*; 43% under *Stipa* versus 8% in control gaps) as well as early establishment (19% under *Stipa* versus 3% in control gaps); after the summer drought, however, all the plants died. Similar results were obtained by Navarro-Cano *et al*. (pers comm) with seedlings of Kermes oak (*Quercus coccifera*) and *Rhamnus lycioides*, and by Maestre *et al*. (2002) with Kermes oak. Esparto grass increased germination and survival before the drought period, but again no plants survived beyond the summer. In other experiments using seedlings of moon trefoil (*Medicago arborea*), lentisc (*Pistacea lentiscus*),

Table 1. Experimental reports in which facilitation by nurse plants was used in restoration projects

Environment	*Nurses*	*Targets*	*Reference*
Mediterranean mountain	Shrubs, legumes (*Salvia, Genista*)	Shrubs, trees (*Pinus, Acer*)	Castro *et al*. (2002); Gómez-Aparicio *et al*. (2004)
Semiarid steppes	Perennial grass (*Stipa*)	Shrubs, trees (*Quercus, Pinus*)	Maestre *et al*. (2001, 2002); Gasque and García-Fayos (2004); Navarro-Cano *et al*. (pers comm)
Marshes	Perennial grass (*Spartina*)	Deciduous shrub (*Baccharis*)	Egerova *et al*. (2003)
Tropical sub-humid forest	Trees (*Acacia, Acalypha*)	Tree (*Brosimum*)	Sánchez-Velásquez *et al*. (2004)
Arid shrubland	Succulent shrubs (*Drosanthemum*)	Succulent shrubs (*Drosanthemum*)	Blignaut and Milton (2005)
Arid rangelands	Shrub (*Artemisia*)	Grasses (*Agropyron*)	Huber-Sannwald and Pyke (2005)
Semiarid abandoned fields	Leguminous shrub (*Retama*)	Shrubs (*Olea, Ziziphus*)	Padilla and Pugnaire (unpublished)

This is not an exhaustive list of the species used

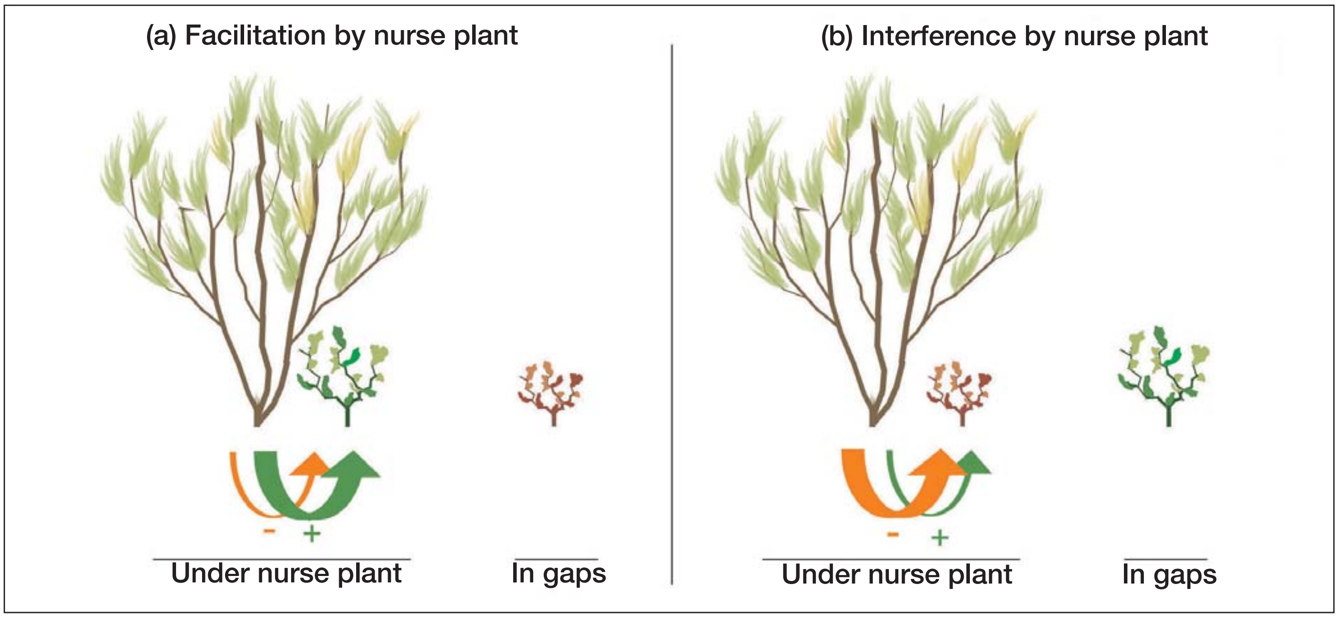

Figure 3. *Facilitation and interference under nurse plants. The balance between positive and negative effects of closely placed species determines the net outcome of the interaction. (a) When positive effects outweigh negative ones, seedling survival or growth is enhanced as compared to survival of individuals in gaps; (b) opposite results are found when negative effects outweigh the positive ones.*

and Kermes oak, *Stipa* did improve survival after the drought period, and did not affect plant growth (Maestre *et al.* 2001).

Nurse plants have also helped in the restoration of coastal marshes in Louisiana. Egerova *et al.* (2003) found higher survival and growth rates in groundsel trees (*Baccharis halimifolia*) growing among clones of the perennial smooth cordgrass (*Spartina alternifolia*) than in gaps (45 versus 11%, respectively), as a result of the more favorable microclimate and soils.

In a secondary tropical dry forest, Sánchez-Velásquez *et al.* (2004) looked at four different types of nurse plants for breadnut seedlings (*Brosimum alicastrum*). Breadnut establishment after one year differed depending on the type of species of nurse tree. It was higher under *Acalypha cincta* and guayabillo (*Thouinia serrata*; 55 versus 40%) and much lower (< 5%) under thin acacia (*Acacia macilenta*), trumpet tree (*Tabebuia chrysantha*), and on open ground.

Blignaut and Milton (2005) looked at survival of adult plants of three succulent Karoo shrubs (*Aridaria noctiflora*, *Drosanthemum deciduum*, and *Psilocaulon dinteri*) after transplanting. They moved plants of each species either close to or away from each other, in an arid shrubland in the Cape Province (South Africa). Overall, survival of translocated plants over the first 17 months was poorer for clumped than for isolated plants.

The potential for seeding of native bluebunch wheatgrass (*Pseudoroegneria spicata*) and the introduced crested wheatgrass (*Agropyron desertorum*) in the vicinity of big sagebrush (*Artemisia tridentata*) was examined by Huber-Sannwald and Pyke (2005), as a means of thinning woody shrubs in the Great Basin (USA) rangelands. Sagebrush did not affect final grass survival, but root interactions decreased seedling biomass. Since light reduction (70–90%) under sagebrush negatively affected grass establishment, the authors recommended seeding in gaps to minimize root interaction with sagebrush as well as light interception.

In semi-arid abandoned fields, the leguminous shrub *Retama sphaerocarpa* enhanced seedling survival of wild olive (*Olea europaea*) and lentisc in south-facing slopes, whereas the opposite effect was seen in wild jujube (*Ziziphus lotus*) in both south- and north-facing slopes. It is likely that understory herbs and *Retama* roots interfered with the jujube plants, since survival was much higher in irrigated gaps between plants than under *Retama* (Padilla *et al.* 2004).

■ Considerations for management

Successful tests in which seeds or seedlings are placed near nurse plants demonstrate the potential of this approach. There are, however, several caveats regarding species and site characteristics that could influence the outcome and should be carefully considered.

Ecological conditions

Using nurse plants is recommended for restoring degraded sites where physical conditions or grazing pressure seriously limit establishment, as spatial association with such plants might not provide any advantage where growing conditions are optimal, In such cases, the association could have negative rather than positive effects. Buckley (1984) found no positive effects using nurse crops in fertile sites, because their rapid growth depleted soil resources, whereas in less fertile fields crops grew less and the thinner cover improved the survival of sycamore maple seedlings. In research conducted by Marquez and Allen (1996), at a site

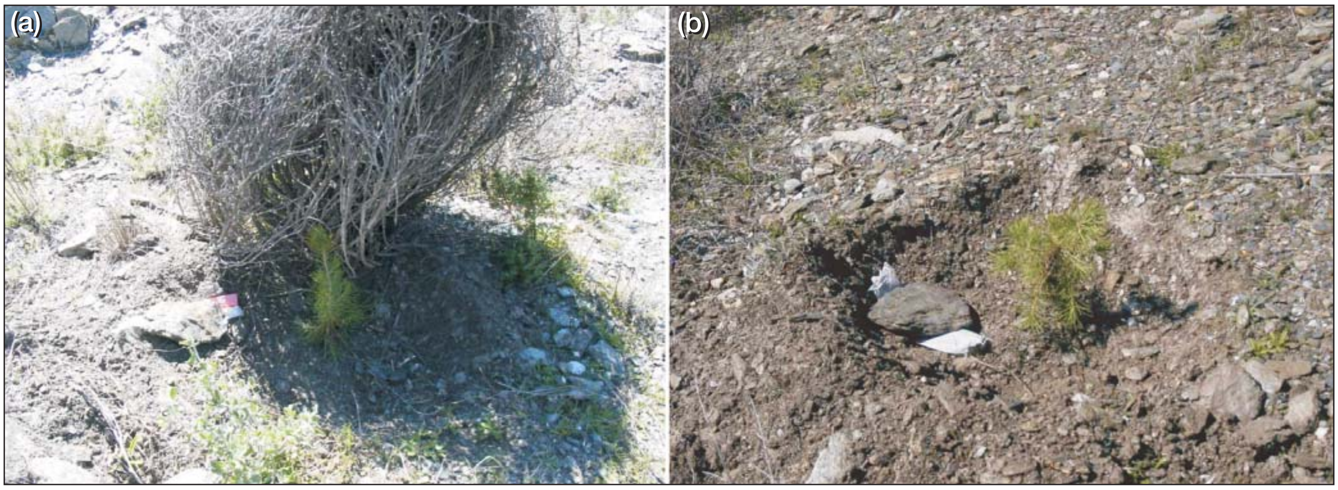

Figure 4. *(a) A planted Aleppo pine thrives under the canopy of the drought-deciduous shrub* Anthyllis cytisoides*, which provides shelter against (b) high radiation levels in experiments on nurse plants conducted in dry mountains in Almería (SE Spain).*

where soil resources and climatic conditions did not constrain establishment (reflected by 100% survival in control plots) sagebrush seedlings growing close to legumes were restricted rather than favored by nurse plants.

The importance of facilitation increases with increasing severity of the abiotic conditions (Pugnaire and Luque 2001; Callaway *et al.* 2002), and therefore the possibility of benefiting from nurse plants should also increase under such conditions. Gómez-Aparicio *et al.* (2004), for example, found that facilitation effects were stronger in dry locations and on the south-facing slopes of a dry Mediterranean mountain.

Rainfall variability

In dry areas, changes in water availability may make interactions among plants shift from competition to facilitation and vice versa, thereby increasing the importance of facilitation during drought (Holmgren *et al.* 1997). This shift between positive and negative effects may be relevant for nurse plant success, since different results could be obtained at the same site in different years, depending on rainfall. Furthermore, in wet years the nurse effect may not be as critical as in dry years, because establishment may occur without a nurse plant's protection (see Kitzberger *et al.* 2000). As described above, Gómez-Aparicio *et al.* (2004) found that shrubby nurse plants have considerable influence on seedling survival in dry years, but not in wet years. Similar results have been reported by Ibañez and Schupp (2001), in an experiment conducted in Logan Canyon, Utah, where they placed seedlings of curl-leaf mountain mahogany (*Cercocarpus ledifolius*) under big sagebrush; facilitation was apparent in a dry year whereas negative effects were seen during a wet year.

Nurse species

Selection of the best nurse species is an important decision in restoration projects, as this will determine the success of the project (Gómez-Aparicio *et al.* 2004; Sánchez-Velásquez *et al.* 2004). In extreme environments, the most suitable choices are native species that are able to improve environmental conditions for seedling establishment. Although some exotic species, such as black locust (*Robinia pseudoacacia*), have been used successfully as nurse crops in the south of England (Nimmo and Weatherell 1961), such options should be scrutinized carefully because of the risk of biological invasions. In heavily grazed sites, thorny, non-palatable species are recommended, although some herbivory and seed predation may still occur, since the nurse plants may provide refuge for small animals. Species that release allelopathic compounds should be avoided.

The nurse plant's canopy structure may also influence establishment success, in particular in relation to shade intensity and rainfall interception. The location of targets under the canopy also affects seedling survival (Castro *et al.* 2002), which is often higher in the shadier positions. In a tropical, sub-humid forest, the varying levels of shading created by the nurse plants appeared to be responsible for the variations in seedling establishment reported by Sánchez-Velásquez *et al.* (2004).

Many shrubs may limit water availability in their understories by intercepting rainwater during small precipitation events, making the soil under shrubs dryer than in open areas (Tielbörger and Kadmon 2000). Nonetheless, during moderate to heavy rainfall, some shrubs enhance water availability by directing water intercepted by the canopy to the understory through stemflow (García 2006). Distance from the nurse plant is another important factor; amelioration of negative conditions and improved availability of resources has been shown to decrease from the canopy center outwards (Moro *et al.* 1997; Dickie *et al.* 2005).

Factors such as competitive ability, use of resources by the nurse plants themselves, and the potential for root overlap between nurse plants and target plants (Blignaut and Milton 2005; Huber-Sanwald and Pyke 2005) must also be taken into account. Competition or interference caused by species that occur naturally under nurse plant canopies (eg understory herbaceous species) may also affect the outcome.

Target species

Interactions among plants depend upon species characteristics, so the selection of target species (ie those being restored) may influence the outcome of a restoration project. Furthermore, the balance of an interaction could be determined by the ecological requirements of the species involved and their ability to deal with unfavorable abiotic conditions (see Liancourt *et al.* 2005; Bertness and Hacker 1994).

Walker *et al.* (2001), for example, reported higher survival rates of *Ambrosia dumosa* in the open than under shrubs in an arid environment, because *Ambrosia* can successfully cope with the conditions that exist in open areas. *Ambrosia* was also subjected to competition from the nurse shrub. Gómez-Aparicio *et al.* (2004) reported that shade-tolerant species and late-successional shrubs showed a more positive effect in response to nurse plants than did pioneer shrubs and shade-intolerant pine trees (Castro *et al.* 2002, 2004). In spite of this positive influence, the nurse effect may be insufficient to increase plant establishment if target species have a low tolerance for the prevalent abiotic conditions, or if these are particularly severe. For example, Kitzberger *et al.* (2000) and Maestre *et al.* (2002) found no seedling establishment, either with or without nurse plant protection, during especially dry years.

The age and size of target species must also be considered, since several studies have shown that the balance between facilitation and competition varied with the life history of plants. Nurse plants had strong positive effects when the target species were relatively young, but predominantly competitive interactions were observed with older, larger individuals (Callaway and Walker 1997; Holmgren *et al.* 1997; Gasque and García-Fayos 2004; Armas and Pugnaire 2005). The use of plants of similar age and size, both as nurse plants and target species, could have exacerbated the negative effect of clumping reported by Blignaut and Milton (2005).

Positive and negative effects of nurse plants

High recruitment rates close to nurse plants do not preclude negative effects on target species, but do ensure that the positive effects outweigh the negatives ones. This may lead to higher survival rates under nurse plants than in gaps, but lower survival rates than those seen when using other procedures, such as artificial shading (Barchuk *et al.* 2005) or watering (Sánchez *et al.* 2004).

Conclusions

Published reports show that nurse plants improve seedling establishment in some systems, and that they may have potential for use in restoration projects. Restoration ecologists and land managers should take facilitation effects into account, not only because the role of facilitator species is key in restoring the characteristics and functions of the original system (Bruno *et al.* 2003), but also because facilitation is believed to drive succession in many habitats, particularly at disturbed sites (Walker and del Moral 2003).

Additional experiments, conducted under a variety of environmental conditions and using different nurse plant species, are needed to identify the potential of this process and to encourage long-term monitoring of target–nurse plant interactions. Research aimed at determining the nurse species' zones of influence and their effects on neighboring plants under differing conditions of resource availability, will provide us with a valuable technique for improving the success of restoration projects.

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