

1 **The role of nurse plants in the restoration of degraded environments**

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4

5 **RUNNING HEADS:**

6 Nurse plants in restoration

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

25

26

27 **In a nutshell**

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

37

38 Plant interactions strongly influence community structure and dynamics, and are
39 responsible for the presence or absence of particular species in a community.
40 Traditionally, competition has been the most studied aspect of those interactions, so that
41 ecological models have focused for decades on negative interactions, overlooking the
42 existence of positive effects between plants. In the past 15 years, however, research has
43 highlighted the role of positive plant interactions (facilitation) in almost all biomes
44 (Bertness and Callaway 1994; Bertness and Hacker 1994; Callaway 1995; Brooker and
45 Callaghan 1998; Callaway *et al.* 2002; Bruno *et al.* 2003; Lortie *et al.* 2004). Despite
46 this increasing recognition, the inclusion of facilitation into mainstream ecological
47 theory has been slow (Bruno *et al.* 2003). Facilitation appears to be essential process,
48 not only for survival, growth, and fitness in some plants (Callaway *et al.* 2002; Tirado
49 and Pugnaire 2003; Cavieres *et al.* 2006), but also for diversity and community
50 dynamics in many ecosystems (Pugnaire *et al.* 1996; Kikvidze *et al.* 2005). Examples of

51 facilitation are more evident in harsh, limiting environments, where some species are
52 able to ameliorate the physical conditions in some way, or prevent herbivory, thereby
53 providing more suitable habitats for other species (Figure 1). This interaction has a
54 practical side when applied to ecological restoration. In degraded habitats with extreme
55 environmental conditions or large numbers of herbivores (Figure 2), the area near or
56 under the canopy of certain species may be a safe site to place the seeds or plants of the
57 species being restored (target species), and which otherwise may fail to establish Here
58 we review the potential of this procedure for ecological restoration.

59

60 **Competition and facilitation**

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

68 Both positive and negative effects can be seen occurring at the same time, affect
69 different variables, and change with time and in different areas (Armas and Pugnaire
70 2005). The net balance between these effects represents the magnitude and sign (either
71 positive or negative) of the interaction (Callaway and Walker 1997; Holmgren *et al.*
72 1997; Figure 3). Several factors affect this balance, including physiological and
73 developmental traits (Callaway and Walker 1997; Armas and Pugnaire 2005), but
74 abiotic conditions seem to be the overriding factor, increasing the importance of
75 positive effects in harsher environments (Brooker and Callaghan 1998; Pugnaire and

76 Luque 2001; Callaway *et al.* 2002; but see Maestre *et al.* 2005 and Lortie and Callaway
77 2006 for discussion of the stress-gradient hypothesis).

78

79 **The nurse effect**

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

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

99

100 **Role of facilitation in restoration**

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

106 In the Sierra Nevada range (Spain), at an elevation of 1800 m, Castro *et al.*
107 (2002) found that nurse shrubs decreased mortality in two mountain pines without
108 inhibiting their growth. After two growing seasons, survival of Scots pine (*Pinus*
109 *sylvestris*) and European black pine (*Pinus nigra*) was markedly better under sage
110 (*Salvia lavandulifolia*) than in control gaps (55 versus 22% and 82 versus 57%,
111 respectively), and differences were still present after four growing seasons (Castro *et al.*
112 2004); survival was 1.8 to 2.6 times better under sage than in gaps. When the nurse
113 plants were thorny shrubs such as *Prunus ramburii*, establishment differed between the
114 north and south aspects of the plant; while results in the north were similar to survival
115 levels seen under sage, in the south the results were similar to those seen in open areas.

116 In the same Sierra Nevada range, but including a wider altitudinal range (500–
117 2000 m elevation), Gómez-Aparicio *et al.* (2004) conducted a series of experiments to
118 test the effect of 16 native shrub species over 11 shrub and tree species. One year after
119 planting, establishment success under shrubs was more than double that seen in the
120 gaps, reaching fourfold higher numbers in some cases. However, the outcome differed
121 depending on target species, type of nurse plant, and year. The observed nurse effect of
122 shrubs was considerable for evergreen Mediterranean species, such as Holm oak
123 (*Quercus ilex*), shrubs such as prickly juniper (*Juniperus oxycedrus*), and deciduous
124 species like maple (*Acer opalus*), but was not significant for pines (Scots and black
125 pine). The most successful nurse plant species were native brooms (such as *Genista*

126 *spp*), and small and thorny shrubs. In contrast, a significant negative influence was seen
127 with rockroses (*Cistus spp*), probably the result of allelopathy. In fact, the harsher the
128 ecological conditions, the stronger the facilitative effect of the nurse plants.

129 A large number of experiments have been carried out to test the potential of
130 esparto grass (*Stipa tenacissima*), a widespread perennial tussock-forming grass, as a
131 nurse plant on degraded semiarid steppes in southeast Spain. However, the results
132 differed depending on site, year, and target species involved. Gasque and García-Fayos
133 (2004) found that the favorable conditions near esparto grass tussocks increased
134 germination rate of Aleppo pine (*Pinus halepensis*; 43% under *Stipa* versus 8% in
135 control gaps) as well as early establishment (19% versus 3% in control gaps); after the
136 summer drought, however, all the plants died. Similar results were obtained by Navarro-
137 Cano *et al.* (pers comm) with seedlings of Kermes oak (*Quercus coccifera*) and
138 *Rhamnus lycioides*, and by Maestre *et al.* (2002) with Kermes oak. Esparto grass
139 increased germination and survival before the drought period, but again no plants
140 survived beyond the summer. In other experiments using seedlings of moon trefoil
141 (*Medicago arborea*), lentisc (*Pistacea lentiscus*), and Kermes oak, *Stipa* did improve
142 survival after the drought period, and did not affect plant growth (Maestre *et al.* 2001).

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

148 In a secondary tropical dry forest, Sánchez-Velásquez *et al.* (2004) looked at
149 four different types of nurse plants for breadnut seedlings (*Brosimum alicastrum*).
150 Breadnut establishment after one year differed depending on the type of species of nurse

151 tree. It was higher under *Acalypha cincta* and guayabillo (*Thouinia serrata*; 55–40%)
152 and much lower (<5%) under thin acacia (*Acacia macilenta*), trumpet tree (*Tabebuia*
153 *chrysantha*) and on open ground.

154 Blignaut and Milton (2005) looked at survival of adult plants of three succulent
155 Karoo shrubs (*Aridaria noctiflora*, *Drosanthemum deciduum* and *Psilocaulon dinteri*)
156 after transplanting. They moved all three species either together or separately in an arid
157 shrubland in the Cape Province (South Africa). Overall, survival of translocated plants
158 over the first 17 months was poorer for clumped than for isolated plants.

159 The potential for seeding of native bluebunch wheatgrass (*Pseudoroegneria*
160 *spicata*) and the introduced crested wheatgrass (*Agropyron desertorum*), in the vicinity
161 of big sagebrush (*Artemisia tridentata*) was examined by Huber-Sannwald and Pyke
162 (2005), as a means of thinning woody shrubs in the Great Basin (USA) rangelands.
163 Sagebrush did not affect final grass survival, but root interactions decreased seedling
164 biomass. Since light reduction (70–90%) under sagebrush negatively affected grass
165 establishment, the authors recommended seeding in gaps to minimize root interaction
166 with sagebrush as well as light interception.

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

173

174 **Considerations for management**

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

178

179 *Ecological conditions*

180 Using nurse plants is recommended for restoring degraded sites where physical
181 conditions or grazing pressure seriously limit establishment, since, where growing
182 conditions are optimal, spatial association with such plants might not provide any
183 advantage. In such cases, the association could have negative rather than positive
184 effects. Buckley (1984) found no positive effects using nurse crops in fertile sites,
185 because their rapid growth depleted soil resources, whereas in less fertile fields crops
186 grew less and the thinner cover improved the survival of sycamore maple seedlings. In
187 research conducted by Marquez and Allen (1996), at a site where soil resources and
188 climatic conditions did not constrain establishment (reflected by 100% survival in
189 control plots) sagebrush seedlings growing close to legumes were restricted rather than
190 favored by nurse plants.

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

196

197 *Rainfall variability*

198 In dry areas, changes in water availability may make interactions among plants shift
199 from competition to facilitation and vice versa, thereby increasing the importance of

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

211

212 *Nurse species*

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

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

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

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

243

244 ***Target species***

245 Interactions among plants depend upon species characteristics, and thereby the selection
246 of target species (ie those being restored) may influence the outcome of a restoration
247 project. Furthermore, the balance of an interaction could be determined by the

248 ecological requirements of the species involved and their ability to deal with
249 unfavorable abiotic conditions (see Liancourt *et al.* 2005); Bertness and Hacker 1994).
250 Walker *et al.* (2001), for example, reported higher survival rates of *Ambrosia*
251 *dumosa* in the open than under shrubs in an arid environment, because *Ambrosia* can
252 successfully cope with the conditions that exist in open areas. *Ambrosia* was also
253 subjected to competition from the nurse shrub. Gómez-Aparicio *et al.* (2004) reported
254 that shade-tolerant species and late-successional shrubs showed a more positive effect in
255 response to nurse plants than did pioneer shrubs and shade-intolerant pine trees (Castro
256 *et al.* 2002, 2004). In spite of this positive influence, the nurse effect may be insufficient
257 to increase plant establishment if target species have a low tolerance for the prevalent
258 abiotic conditions, or if these are particularly severe. For example, Kitzeberger *et al.*
259 (2000) and Maestre *et al.* (2002) found no seedling establishment, either with or without
260 nurse plant protection, during especially dry years.

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

269

270 ***Positive and negative effects of nurse plants***

271 High recruitment rates close to nurse plants do not preclude negative effects on target
272 species, but do ensure that the positive effects outweigh the negatives ones. This may

273 lead to higher survival rates under nurse plants than in gaps, but lower survival rates
274 than those seen when using other procedures, such as artificial shading (Barchuk *et al.*
275 2005) or watering (Sánchez *et al.* 2004).

276

277 **Conclusions**

278 Published reports show that nurse plants improve seedling establishment in some
279 systems, and that they may have potential for use in restoration projects. Restoration
280 ecologists and land managers should take facilitation effects into account, not only
281 because the role of facilitator species is key in restoring the characteristics and functions
282 of the original system (Bruno *et al.* 2003), but also because facilitation is believed to
283 drive succession in many habitats, particularly at disturbed sites (Walker and del Moral
284 2003).

285 We see the need for additional experiments, conducted under a variety of
286 environmental conditions and using different nurse plant species, to identify the
287 potential of this process, and to encourage long-term monitoring of target–nurse plant
288 interactions. Research aimed at determining the nurse species’ zones of influence and
289 their effects on neighboring plants under differing conditions of resource availability,
290 will provide us with a valuable technique for improving the success of restoration
291 projects.

292

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299

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416

417

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

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

420

421 This is not an exhaustive list of the species used

422

423 **Panel 1. The advantages of growing close to nurse plants**

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

444

445 **FIGURE CAPTIONS**

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

450

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

456

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

462

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

466

467 Figure 1



468

469

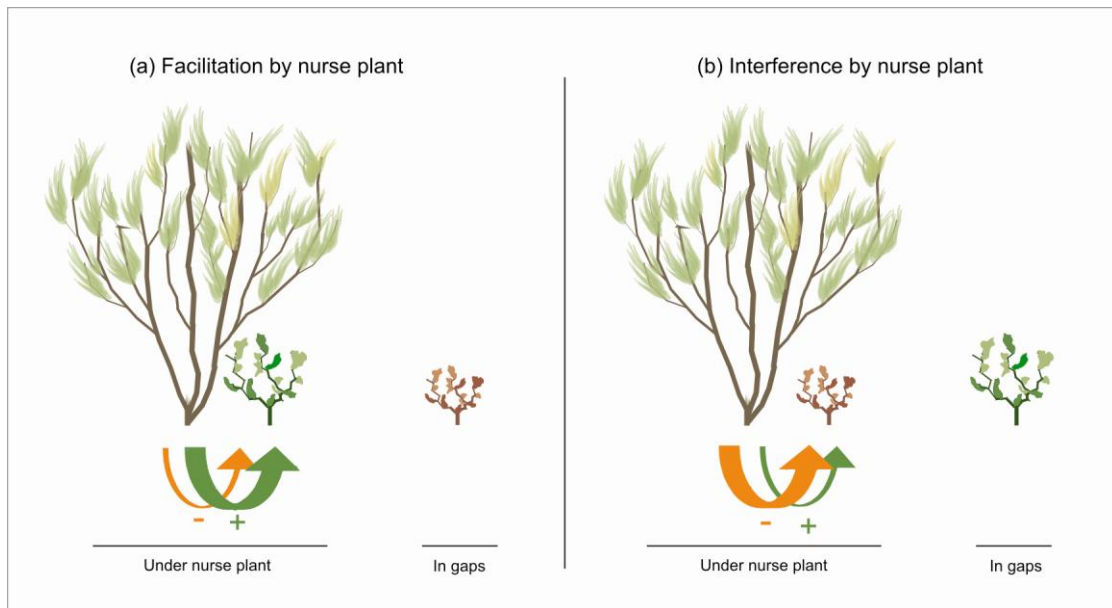
470 Figure 2



471

472

473 Figure 3



474

475

476 Figure 4



477