Chapter 7
Baccharis as Nurse Plants

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Abstract The genus *Baccharis* includes important shrub species that facilitate the regeneration and performance of other species that grow underneath. Some *Baccharis* species represent crucial nurse shrubs that provide shelter from abiotic or biotic stress to other "beneficiary" plants. Here, we uncover the role of *Baccharis* species as facilitators, particularly in stressful and herbivore-dominated environments. We highlight that the net facilitative effect of *Baccharis* strongly depended on multiple factors (its size and architectural form, the type and intensity of stress, the ontogenetic stage of beneficiary plants, the presence of conspecifics, etc.). We particularly focus on *Baccharis* as tree recruitment microsites that enhance both recruitment quantity and quality along many systems of the Americas (from California to Chile) and boost vegetation dynamics towards late successional stages and functioning systems. In addition, we highlight the roles of some *Baccharis* species in facilitating native vs. exotic herbaceous species and their possible role in reducing the colonization and expansion of invasive plants. Thus, the genus *Baccharis* includes extraordinary interesting species from an ecological, conservation, and restoration point of view due to their ability to work as nurse plants that favor the regeneration of keystone species and reduce the proliferation of invasive plants.

Keywords Plant facilitation · Plant-plant interactions · Regeneration microsites · Restoration ecology

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1 Plant Facilitation and the Nursing Phenomenon

Plant facilitation is a positive interaction where a nurse plant modifies the local abiotic and biotic conditions, improving the lifetime fitness of other, beneficiary plant species (Callaway 1995; Bertness and Leonard 1997; Bronstein 2009; Soliveres et al. 2011). Plant facilitation is, therefore, an important form of ecological nursing, where some plants (the "nurse" or "benefactors") facilitate seed arrival, germination, establishment, growth, or development of other plant species (the "beneficiary") by providing shelter from one or both sources of stress: (1) abiotic (e.g., drought, salinity, soil toxicity, frosts) or (2) biotic (e.g., herbivory, seed predation, pathogens; Franco and Nobel 1988; Valiente-Banuet and Ezcurra 1991; Brooker et al. 2008; Gómez-Aparicio et al. 2008; Perea and Gil 2014).

Plant facilitation has been mostly studied under abiotic stressful conditions, like those exerted in resource-limited or constraining environments (Stachowicz 2001; Tirado and Pugnaire 2005; but see Spadeto et al. 2017). As a result, some studies have shown strong evidence to support the stress gradient hypothesis (SGH), which predicts that the frequency of facilitation directly increases with abiotic stress (Bertness and Callaway 1994; Callaway 2007). However, other authors argue that the largest absolute facilitative effects will always occur under less abiotic stressful conditions (Holmgren and Scheffer 2010), leading to a strong debate on the predictions and extension of the SGH (Michalet et al. 2013; He et al. 2013; Soliveres and Maestre 2014; Soliveres et al. 2015).

A common consequence of plant facilitation is the formation of vegetation patches surrounded by open space (Prentice and Werger 1985; Castillo et al. 2010) or the proliferation of plant recruits (seedlings and saplings) under the cover of conspicuous nurse plants such as trees or shrubs (Callaway 1992; Gómez-Aparicio et al. 2008; Perea et al. 2016). Nurse shrubs are considered key elements on the facilitative process of plant-plant interactions as they are able to assemble ecological communities (Armas and Pugnaire 2005) and enhance the recruitment rates of many tree species that develop underneath (Castro et al. 2004; Smit et al. 2007; Perea et al. 2017; Spadeto et al. 2017). Among shrub species, the genus *Baccharis* L. is the largest genus in the family Asteraceae, with over 440 shrub species widely distributed throughout the Americas (Heiden et al. 2019). Their pioneer character (rapid growth, low longevity, high production of wind-dispersed seeds, and the capability to easily establish on disturbed sites; see Fernandes et al. 2014) stands for a strong potential to facilitate the progressive ecological shift towards later stages of plant succession where the nursing phenomenon plays an essential role.

This chapter synthesizes the nursing role of some shrub species in the genus *Baccharis* (Table 7.1) as they represent paradigmatic species within the plant facilitation process in the Americas (McBride 1974; Callaway and Davis 1998; Kitzberger et al. 2000; Duarte et al. 2006; Zavaleta and Kettley 2006; van Zonneveld et al. 2012; Perea et al. 2017, 2019; Macek et al. 2018; Peláez et al. 2019). We also highlight their ecological role as a key facilitator of native plant species over those invasive (Brennan et al. 2018; Perea et al. 2019), revealing a strong potential of *Baccharis*

Table 7.1 Summary of the different species of the genus *Baccharis* known to facilitate the regeneration and performance of different woody species along many systems of the Americas

Country	Habitat	Nurse plant *Baccharis* spp.	Beneficiary tree/ shrub species	References
United States	California grassland	*B. pilularis*	*Quercus agrifolia, Quercus douglasii, Q. lobata*	McBride (1974), Callaway and D'Antonio (1991), Zavaleta and Kettley (2006) and Perea et al. (2017)
United States	California coastal dunes	*B. pilularis*	*Lupinus arboreus*	Rudgers and Maron (2003)
Mexico	Fir forest clearings	*B. conferta*	*Abies religiosa*	Sánchez-Velásquez et al. (2011)
Mexico	Highlands of Chiapas	*B. vaccinioides*	*Quercus crassifolia Quercus rugosa*	Ramírez-Marcial et al. (1996)
Venezuela	Old fields in the tropical Andes	*B. prunifolia*	*Vallea stipularis Berberis discolor*	Bueno and Llambí (2015)
Brazil	*Pampa* grasslands	*B. uncinella*	*Araucaria angustifolia*	Duarte et al. (2006)
Brazil	*Pampa* grasslands	*B. mesoneura*	*Araucaria angustifolia*	Duarte et al. (2006)
Argentina	Patagonian xeric woodlands	*B. rhomboidalis*	*Austrocedrus chilensis*	Kitzberger et al. (2000)
Chile	Semiarid zone of the Chilean coast	*B. vernalis*	*Aextoxicon punctatum Myrceugenia correifolia*	Macek et al. (2018)
Chile	Temperate rain forest boundary	*B. vernalis*	*Myrceugenia correifolia Griselinia scandens*	van Zonneveld et al. (2012)

plants to prevent and control plant invasion. Finally, this chapter aims to provide ecologists and managers with new possible conservation practices based on the nursing ability of *Baccharis* shrubs to facilitate the recruitment of native species in harsh or degraded environments.

2 *Baccharis* as Tree Regeneration Microsite

The perpetuation of any natural ecosystem mainly depends on its regeneration ability. Those species unable to regenerate hamper their continuity in the ecosystem (Schemske et al. 1994). It is well known that the abundance, survival, and development of seedlings vary across microsites (Whittaker and Levin 1977; Collins and Good 1987; López-Sánchez et al. 2019). As a result, certain microsites increase the overall probability of plant recruitment by facilitating seed germination, seedling survival, or growth. These particularly favorable microsites for regeneration are known as "regeneration microsites" following the regeneration niche concept *sensu* Grubb (1977). Seedling establishment is indeed one of the most critical stages in the regeneration process of trees, with high mortality rates during this phase (Clark et al. 1999; Silvertown and Charlesworth 2001; Perea and Gil 2014). Multiple abiotic and biotic agents influence seedling survival and performance, among which are climatic conditions (Dreyer et al. 2001; Rodríguez-Calcerrada et al. 2008), soil resources (Baraloto et al. 2006), competition (Davis et al. 1998), and herbivory (Crawley 1983; Smit et al. 2006). However, all these factors might vary widely among microsites due to the great spatial and temporal heterogeneity of most ecosystems (González-Rodríguez et al. 2011; López-Sánchez et al. 2019).

Nevertheless, some particular microsites such as those underneath nurse shrubs have shown a significant advantage over other microsites (Callaway 1992; Pugnaire et al. 1996; Smit et al. 2007, 2008; Perea and Gil 2014). This is the paradigmatic case of *Baccharis* shrubs in open oak woodlands or savannas of North America (McBride 1974; Callaway and Davis 1998; Zavaleta and Kettley 2006; Perea et al. 2017) where there is a well-known facilitative relationship between the coyote brush (*Baccharis pilularis* DC) and the beneficiary coast live oak (*Quercus agrifolia* Neé), which strongly depends upon *Baccharis* cover to regenerate. Coyote brush is an evergreen, much-branched, and colonizer shrub that grows in shrub communities close to foothill woodlands of California (Steinberg 2002). These shrubs have shown a great ability to protect oak recruits from herbivory (Peláez et al. 2019) probably due to their low palatability and nutritious value (McBride and Heady 1968; Smither-Kopperl 2016; Fig. 7.1). In addition, shoot mortality attributed to water or temperature stress was 17% under shrubs and 63% in the open grassland (Callaway and D'Antonio 1991), suggesting a strong reduction of abiotic stress for those seedlings growing under shrub cover. Furthermore, abundances of all herbaceous species declined greatly after *Baccharis* formed a closed canopy at 2–3 years, and little seed of herbaceous species was either dispersed into shrub stands or stored in the soil (Hobbs and Mooney 1986).

Interestingly, Zavaleta and Kettley (2006) found that oaks established only under mature shrubs, suggesting that features of mature shrubs and their effects on site characteristics benefit establishing oaks. In fact, Peláez et al. (2019) found an interesting relationship between nurse plant size and the probability of facilitating oak recruitment, revealing that *Baccharis* started to be an efficient facilitator (probability of facilitation >0.5) when crown diameter was >2.5 m (age of 7 years) in heavily browsed areas and almost twice (> 5 m diameter; equivalent age of 15 years) at low herbivore stress levels (Fig. 7.2). This indicates that the herbivore pressure is a strong driver in determining plant facilitative effects, increasing overall plant facilitation at higher levels of biotic stress (herbivory).

Baccharis shrubs may not only contribute to increasing the number of recruits (regeneration abundance) but also to enhancing the recruit quality. Thus, the development of tree recruits may strongly depend on the protective effect of shrubs. In particular, *Baccharis* were proved to favor the growth and the adequate architecture

Fig. 7.1 *Baccharis pilularis* facilitating the establishment and growth of coast live oaks (*Quercus agrifolia*, left) and blue oaks (*Quercus douglasii*, right) in California oak woodlands. Oaks eventually surpass the shrub height and outcompete the *Baccharis* shrubs. At that stage, oak trees have grown sufficiently to avoid intense browsing damage aboveground and to reduce soil water deficit belowground. (Photos: Ramón Perea)

of oak saplings in herbivore-dominated environments by reducing the detrimental effect of browsers, which typically reduce the plant height/diameter ratio producing stunted individuals (Peláez et al. 2019; Fig. 7.3). The protective effect of *Baccharis* against browsers facilitates the advance of oak saplings to the next ontogenetic stages, ensuring the sexual reproduction of trees (production of flowers and fruits) and the plant community dynamics towards late successional stages (Fig. 7.3). The recruit quality was also affected by the *Baccharis* size, as sapling recruits under larger *Baccharis* shrubs had proportionally higher height/diameter ratios (Peláez et al. 2019). Another study in Mexico also showed that *Baccharis conferta* shrubs improved the growth of coniferous trees (*Abies religiosa* seedlings) growing underneath (Sánchez-Velásquez et al. 2011). Thus, *Baccharis conferta* shrubs were found to promote the seedling growth of commercial conifer plantations (Sánchez-Velásquez et al. 2011) as well as *Baccharis pilularis* has been shown useful for restoration purposes of the highly valuable oak woodlands (López-Sánchez et al. 2019). Similarly, other congeneric species such as *Baccharis uncinella* and *Baccharis mesoneura* have been argued to be facilitators of *Araucaria angustifolia* trees in the Brazilian Atlantic Forest (Duarte et al. 2006). In line with other studies, Duarte et al. (2006) found more forest species seedlings beneath the canopies of

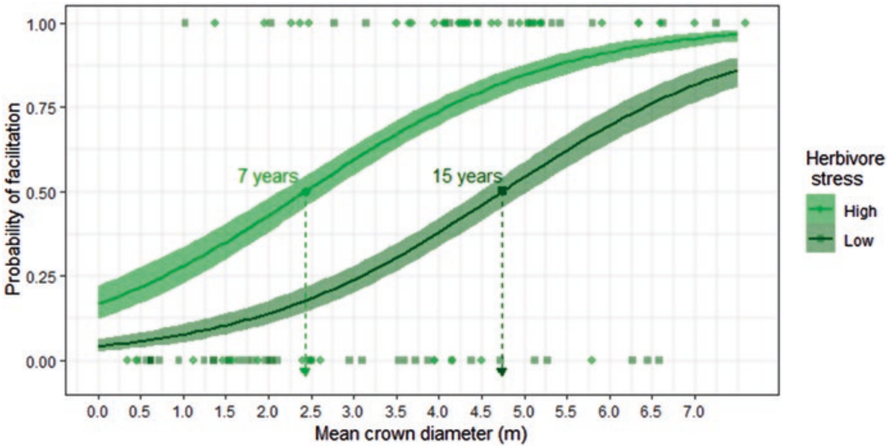

Fig. 7.2 Probability of plant facilitation in relation to nurse plant size (*Baccharis* mean crown diameter) and herbivory stress level (high or low deer densities). Arrows represent the threshold nurse plant size at which facilitation probability is 50%. Age of the nurse plant, in years, was annotated for both threshold values. (Adapted from Peláez et al. 2019)

Fig. 7.3 (**a**) Stunted individual of the coast live oak (*Quercus agrifolia*) growing in an open microsite, with low height/diameter ratio and modified architecture. (**b**) Oak juvenile of the same species growing under the protection of *Baccharis pilularis*, with adequate architecture and greater height/diameter ratio. (Photos: Ramón Perea)

nurse plants compared with open field grassland, creating new forest colonization sites in *Pampa* grasslands of Brazil. Other studies also point out shrub cover protection from direct sunlight as the main factor that enhanced the germination and survival of *Austrocedrus chilensis* in northern Patagonia (Argentina) where *Baccharis rhomboidalis* is a fairly common shrub that favorably influences tree regeneration (Kitzberger et al. 2000). Positive effects of *Baccharis prunifolia* shrubs were also found on the regeneration of old fields at the tropical Andean forest, where species richness, vegetation cover, and the density of dominant forest trees were higher under the shrub canopy than in the inter-shrub spaces (Bueno and Llambí 2015). Another study in semiarid Chile showed that tree species become established in a herbaceous matrix thanks to *Baccharis vernalis* patches, most likely due to a combination of fog-interception capacity, soil nutrient availability, and low competition (Macek et al. 2018).

Similarly, in the rain forest boundary of Chile, *Baccharis vernalis* was found to be the most successful nurse shrub along the arid scrubland-temperate rainforest, sheltering the most abundant and diverse seedling community (van Zonneveld et al. 2012). Interestingly, this study also highlights that dead shrubs also play an important role in facilitating tree seedling establishment although proportionally more seedlings were recruited under dead shrubs in the scrubland than in the forest borders, suggesting a stronger competition between living shrubs and establishing seedlings in drier (more stressed) environments (van Zonneveld et al. 2012). Previous studies demonstrated that dead nurse plants are able to ameliorate thermal stress without the negative cost of reducing soil water content (Anthelme et al. 2007). This occurs not only in dry and harsh environments but also after disturbances such as fires (Castro et al. 2011). Hence, dead shrubs may also play an important role in plant facilitation mostly through the abiotic mechanism of microsite amelioration and, thus, may represent key elements in the ecological restoration process after a fire or other disturbances.

Interestingly, *Baccharis* shrubs are also known to facilitate other shrubs. For instance, Rudgers and Maron (2003) recorded facilitative interactions between *Baccharis pilularis* and the coastal dune shrub *Lupinus arboreus*, an important nitrogen-fixer in California dunes. The relationship depended on the genotype of *B. pilularis*; only the prostrate architectural form of this species benefited seedling emergence, survival, and growth of *Lupinus arboreus* but had no effect on post-dispersal seed predation or adult establishment (Rudgers and Maron 2003). Importantly, by facilitating an important nitrogen-fixer, *Baccharis* shrubs also had effects that cascade to other members of the coastal plant community (Rudgers and Maron 2003), revealing a strong influence of *Baccharis* shrubs beyond pairwise interactions.

3 *Baccharis* as Facilitator of Native and Exotic Herbaceous Species

Many studies have documented the facilitative effect of *Baccharis* shrubs on native plant communities dominated by herbs, forbs, and grasses (van Zonneveld et al. 2012; Brennan et al. 2018; Perea et al. 2019). For instance, coyote brush (*Baccharis pilularis*) has been documented invading grasslands where non-native species were gradually replaced by not only coyote brush but also several other noteworthy native species (Brennan et al. 2018). This study finds that over the 37-year timeframe, exotic grasses gradually decline, while native plant cover increases in California grassy landscapes invaded by coyote brush (Brennan et al. 2018). Another recent study in two abandoned pasture areas of Brazil showed that plant diversity was significantly higher in the restored environment (after planting the nurse *Baccharis dracunculifolia* shrubs) compared to the degraded environment (Siqueira et al. in review). In addition, fewer ruderal and exotic species were recorded in the restored sites with *B. dracunculifolia*, concluding that restoration with *Baccharis* planting had a positive effect on the restructuring of the native plant community (Siqueira et al. in review, see also Fernandes et al. 2018).

Nevertheless, some studies have documented the opposite facilitative pattern, where neighbor grasses may act as facilitators of *Baccharis* shrubs by improving, for instance, water balance (Dechoum et al. 2018). Thus, facilitative interactions between herbaceous plants and *Baccharis* shrubs may be reciprocal and difficult to quantify when both groups coexist and, as a result, competition and facilitation are typically co-occurring. This has been documented in some field patterns where changes in resources (e.g., water) may shift from competitive to facilitative and vice versa (Holmgren et al. 1997). Although more rarely documented, few studies revealed that some invasive grasses may benefit from the *Baccharis* facilitative effect. For instance, the invasive South African grass, *Ehrharta calycina*, escaped herbivory by associating with *Baccharis pilularis*, showing greater performance (growth and aboveground biomass) than unassociated individuals of the California dune system (Cushman et al. 2011). Similarly, Perea et al. (2019) found that *Baccharis* facilitated the occurrence of the invasive *Hyparrhenia rufa* along the montane roads of Brazil although, overall, *Baccharis* favored the presence of native herbaceous plants over those exotic, with 61% greater probability of facilitation for native species than for exotic species (Fig. 7.4).

Some studies have shown that once *Baccharis* shrubs are established, they change the light and water availability under their canopy and provide cover for small mammals. These mammals, in turn, remove the grasses from under the shrub canopy and from its immediate ecotone (McBride and Heady 1968; Bartholomew 1970), thus preventing grasses from invading the shrubland. This mechanism may be behind the greater ability of *Baccharis* to facilitate native vs. exotic herbaceous plants although further studies are needed. Similarly, in Chile, the lower biomass of grasses under the canopy of *Baccharis linearis*, compared to where the shrubs are absent, also suggested inhibition of shrubs on the herbaceous stratum (Martínez and

Fig. 7.4 Adjacent areas without (left) and with (right) *Baccharis* shrubs along montane roads of rupestrian grasslands of Brazil. The establishment of transects allowed the evaluation of *Baccharis* as facilitator of invasive vs. native herbaceous plants (see Perea et al. 2019 for more details). Pioneer nurse shrubs such as a *Baccharis dracunculifolia* DC were found to alleviate the environmental shift generated by the construction and use of roads (e.g., disturbed soils with low nutrient content) (see Fernandes 2016) and represent an interesting alternative to mitigate exotic plant invasion along roadsides

Fuentes 1993). However, the interactive effects of invasive species and *Baccharis* plants may depend on the life-cycle stage at which the interactions occurred. For instance, in Chile, the early emergence of the invasive species *Centaurea solstitialis* L. enabled established plants to competitively displace the late-emerging *Baccharis linearis* and *B. paniculata* (Gómez-González et al. 2009). However, the presence of the invasive *C. solstitialis* (individuals or seeds) did not affect negatively the seed germination of the two abovementioned *Baccharis* species (Gómez-González et al. 2009). Interestingly, these authors also found that the biomass of both *Baccharis* species increased under conspecific competition compared to control (growing alone). Facilitation among conspecific plants of similar age or size is a kind of interaction that can be essential for seedling establishment in some arid and semiarid ecosystems (Goldberg et al. 2001; Franks 2003). Further studies should address whether seedling survival of *Baccharis* species is really being facilitated by conspecifics as they may better resist plant invasion at high densities (Gómez-González et al. 2009). This facilitative conspecific response may also contribute to explain the marked ecotones between *Baccharis* shrublands and annual grasslands in the California chaparral (McBride and Heady 1968; Hobbs and Mooney 1986) and central Chile (Martínez and Fuentes 1993).

Interestingly, *Baccharis* is a dioecious genus, i.e., with male and female individuals. Da Costa Fonseca et al. (2017) found that male and female *Baccharis platypoda* adults presented an aggregate pattern at smaller scales but random and uniform patterns for larger scales (>20 m). In addition, they found that male individuals preferred higher moisture soils probably due to distinct environmental preferences. Preliminary analysis (Perea et al. unpublished data) in the montane Neotropics showed that there were no significant differences in species richness between male and female *Baccharis* when facilitating herbaceous plants. However, there was

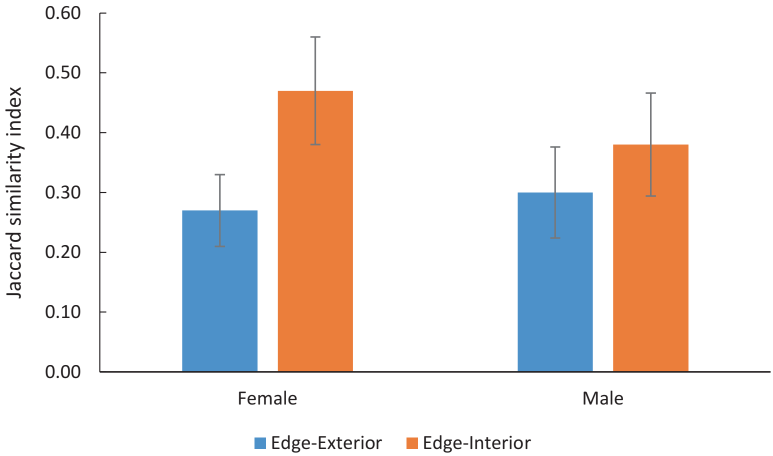

Fig. 7.5 Jaccard similarity index ± SE between communities located at the edge and the exterior and interior part of the nurse shrub for female and male *Baccharis* in Brazil. Notice how female individuals caused greater shifts in species turnover (Jaccard index) than male individuals. (Perea et al. unpublished results)

greater species turnover between exterior and edge position of the shrub than between interior and edge positions (Fig. 7.5), suggesting that female shrubs have a greater effect in species turnover with only 0.27 similarity between edge and exterior communities, 20% lower similarity than between interior and edge communities, whereas for males this turnover difference was only 8% (Fig. 7.5). These results reveal a possible differential pattern in species turnover for males and females which needs further analysis to corroborate a greater enhancement (facilitation) of plant community heterogeneity by female individuals as compared to male individuals (Perea et al. unpublished results). These sex-related differences in dioecious species tend to be associated with their distinct nutritional requirements (Marques et al. 2002), their sex-biased plant-animal interactions (Verdú and García-Fayos 2003), or their dissimilar physiology (Boecklen et al. 1990).

4 Conclusions

Overall, we summarize numerous facilitative interactions associated with the genus *Baccharis*, which are strongly dependent on multiple intrinsic and extrinsic factors (e.g., its size, sex and architectural form, the type and intensity of stress, the ontogenetic stage of beneficiary plants, the presence of conspecifics). Thus, the genus *Baccharis* includes extraordinary interesting species from an ecological, conservation, and restoration point of view due to their ability to work as nurse plants that favor the regeneration of keystone species and help reduce the proliferation of invasive plants in highly diverse systems. We encourage further research into the ecological and conservational role of *Baccharis* species as they are widespread and pioneer plants that are typically easy and inexpensive to propagate (Gomes and Fernandes 2002). As a result, plants in the genus *Baccharis* have an enormous potential to restore degraded and disturbed areas and to control plant invasion or recuperate areas already invaded by exotic plants. The facilitation process represents an incredible restoration mechanism that should be considered in future environmental and ecological projects where *Baccharis* species can play a prominent role in many areas of the Americas.

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