

# What are the impacts of terrestrial plant-plant interactions on evolutionary adaptations among the interacting plant species?

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**Abstract:** In this essay I look at the long term effects of plant-plant interactions and their potential as mechanisms for evolutionary adaptation. I first briefly discuss competition and allelopathy and then focus on facilitation. I found that both competition and allelopathy can act as mechanism for evolutionary adaptations and that facilitation can act as an ecological time machine and be a stabilizing force throughout ecological time. However it is not clear whether or not facilitation can lead to speciation, as current research on the topic is limited and contradicting. Thus, there is a clear need for experimental studies testing the potential of facilitation as a mechanism for evolutionary adaptations.

## Introduction

Plants interact in many different ways with their environment and with each other. They interact in a negative way and compete for resources (light, nutrients and water), space and pollinators (i.e. competition). But they can also interact in a positive way (i.e. facilitation) by protecting each other from the impacts of herbivores, other competitors or climatic extremes (Brooker et al. 2008). Over the years plant-plant interactions have receives more and more attention and our understanding of them has grown. Especially the importance of facilitation has been recognised more and more. However unlike the long term effects of interactions among plants and their consumers, pollinators and dispersers, which have been extensively studied by ecologists and are important in our understanding of evolution, the long term effects of interactions among plants themselves are far less studied, but could provide us with a greater insight into processes that organize communities (Thorpe et al. 2011). These interactions among plants can either be direct or indirect and could act via different mechanisms. These positive and negative interactions are important drivers of population and community dynamics and could lead to evolutionary responses among the interacting plants as well as in other community members (Schöb et al. 2013). However, evolutionary responses of plant-plant interactions have received little attention. In this essay I will therefore discuss these interactions and their evolutionary consequences.

Of these plant-plant interactions, direct interactions such as resource competition, allelopathy (an organism influencing the growth, survival, and reproduction of other organisms by producing bio-chemicals) and facilitation (an interaction in which the presence of one species alters the environment in a way that enhances growth, survival or reproduction of a second, neighbouring species (Bronstein 2009)) are the simplest to understand. It is clear to see that all of these interactions (resource competition, allelopathy and facilitation) could have a great impact on the survival chances of an organism and could thus lead to evolutionary adaptations. These interactions between plants however have been much less considered as a mechanism for evolutionary adaptations and thus our understanding of them is minimal (Soliveres et al. 2014). Castellanos & Verdú (2012) showed that biotic factors, including interactions with neighbours, are stronger evolutionary selection forces than abiotic factors in plants. Yet to date our understanding of the evolutionary consequences of plant-plant interactions is minimal and more research is needed to assess the effects of plant-plant interactions on evolution, which might lead to a rethinking of fundamental community theory (Thorpe et al. 2011). Especially in light of the predicted global environmental change, there is a clear need to improve our understanding on how plant-plant interactions could lead to evolutionary adaptations, in particular in response to the presence of neighbours (Soliveres et al. 2014).

In this essay I will look into the interactions among terrestrial plants and discuss their potential as a mechanism for evolutionary adaptations. I will briefly discuss competition and allelopathy among plants as a mechanism for evolutionary adaptations, but will focus mainly on facilitation and its role in evolution, as facilitation is a relatively new topic and may play an important role in diminishing the impact of global environmental change on plant communities (Soliveres et al. 2014)

### **Competition as a mechanism for evolutionary adaptations.**

Resource competition has a strong effect on community composition and could thus be an important part of the selective environment experienced by plants. Because different plant species may require different resources, the selective forces experienced by plants and the evolutionary consequences of them could vary with different neighbouring species (Thorpe et al. 2011).

Nonspatial models predict that no more consumer species can coexist at equilibrium than there are limiting resources. Tilman (1994) however, showed, with a similar model in which he included neighbourhood competition and random dispersal among sites, that there can be a stable coexistence of a potential unlimited number of species on a single resource. The idea behind this model is that neighbourhood interactions and local dispersal increase intraspecific competition relative to interspecific, and thus encourage stable coexistence. If there are the necessary interspecific trade-offs among dispersal, longevity and competitive ability, Tilman's spatial competition model demonstrates that these could allow stable persistence of numerous species competing for a single resource. So as long as there is limiting similarity between species, coexistence could occur. He also performed simulations with a similar model, but in which the rate of competitive displacement within each site was slower when competitive abilities were more similar. This modification often led to a several fold increase in the species richness of a finite habitat. Tilman's models have been tested over the years and proven to be very valuable to show the importance of competition among neighbours and its impact on community structure and composition.

Parrish and Bazzaz (1976) measured weekly root extensions of six successional annuals and calculated Niche breadth and overlap. The six species showed marked differences in their total composition of N, K, Ca and Mg. They also found that the mean overlap in the use of underground space was considerably lower in stable prairie communities with a long community history than in early successional old-field communities composed of species without a common history. This suggests that resource competition may have an effect on a plants root network, minimizing the overlap of root systems with neighbouring plants. A similar result was found by Aarsen & Turkington (1985). They conducted an experiment in which they analysed vegetation patterns and species associations over a three year period in three different-aged pasture communities with similar diversity or composition but associations between species were less stable in younger than in older communities. They suggested that in communities where resources were limited, plants with a history of coexistence may develop balanced competitive abilities for limiting resources, niche differentiation not related to horizontal space, or some combination of the two. They transits from an essential unorganized assemblage of neighbourhoods in which significant deviations from random associations are in a constant state of flux, into a more stable community where neighbours of different species maintain a more or less permanent association.

Stöcklin (1997) did an experiment in which he studied the effects of competition and soil fertilization on variation of seed yield components of the outcrossing perennial *Epilobium dodonaei* Vill. using a randomized complete block design. He found no main significant effect of fertilization, but did find that competition reduced the number of flower buds per shoot (-29%), the number of ovules per fruit (-12%) and the number of ripe fruits per shoot (-51%). Competition also caused an increase in abortion of flower buds and a reduction in the proportion of late-aborted seeds. So *Epilobium dodonaei* grown with competitors initially invested less in reproductive structures and had a higher abortion rate early in the reproductive development, but a lower abortion rate later on during development when lots of resources had already been invested. *Epilobium dodonaei* grown with no competitors, however, showed

the opposite. They invested more in reproductive structures and had a low abortion rate in the early reproduction stages, but had a higher abortion rate in the later stages of reproduction. Competition, thus had a clear effect on the pattern of fruit and seed regulation and thus a considerable effect on the plants reproductive success.

More recently Leger (2008) found evidence for selection in the North American native perennial grass *Elymus multisetus* M.E. Jones caused by competitive interactions with the invasive annual grass, *Bromus tectorum* L. She collected *Elymus multisetus* individuals from sites invaded by *Bromus tectorum* (Experienced individuals) and from sites not invade by *Bromus tectorum* (naïve individuals). Fig. 1 shows the effect of *Bromus tectorum* (cheatgrass) presence on community composition and size of *Elymus multisetus*. When grown in competition with *Bromus tectorum*, the experienced individuals experienced a smaller decrease in growth than naïve individuals. She also found that experienced *Elymus multisetus* individuals responded more quickly to watering and grew faster than naïve individuals. *Bromus tectorum* has the ability to pre-empt resources by germinating early in the season, and thus having a competitive advantages over neighbours of different species. Leger suggested that this competitive advantage selected for earlier growth in *Elymus multisetus*, allowing it to better compete against *Bromus tectorum*. Which is possible, because she found that there is variation in natural populations of *Elymus multisetus* for competitive ability with *Bromus tectorum*. She found that besides non-competitive individuals, there were also a few competitive individuals in uninvaded sites, showing there is variation for natural selection to act on.

### **Allelopathy as a mechanism for evolutionary adaptations.**

Allelopathy could also drive evolution in neighbouring species (Thorpe et al. 2011). Biochemicals produced by plants may differ between species and thus the selective forces experienced by plants and their evolutionary consequences may differ with different neighbouring species. There are many plant species that produce secondary compounds that can affect the neighbouring community (allelopathy). The effects of these allelochemicals on other plants performance may vary from inhibitory to facilitative and may also depend on the other plants life-stage (Grøndahl & Ehlers 2008). Via leaching of allelochemicals, some of these plants have the ability to modify their local environment in such a way, that it puts neighbouring species under selective pressure to adapt to the effects of these allelochemicals (Jensen & Ehlers 2010).

One plant genus that is well known for its production of secondary compounds is the aromatic *Thymus*. Ehlers & Thompson (2004) examined the effects that *Thymus vulgaris* L. has on *Bromus erectus* Huds., an associated grass species. They collected *B. erectus* seeds from plants growing near *T. vulgaris* from three phenolic (varvacrol and thymol) and three non-phenolic (geraniol, alpha-terpinol, thuyanol and linalool) populations. A reciprocal transplant experiment showed that *B. erectus* collected for non-phenolic sites performed significantly better on soil collected from non-phenolic sites (home soil), than on soil collect from phenolic sites (away soil). But these difference in performance on home and away soil were only detected on soil collected from within *T. vulgaris* patches (soil influenced by the allelochemicals from *T. vulgaris*) and not on soil from patches where *T. vulgaris* is absent. Table 1 clearly shows the difference in top soil composition in soil collected from within *T. vulgaris* patches and soil collected from patches without *T. vulgaris*. The difference in topsoil is likely due to leaching of allelochemical into the soil by *T. vulgaris*, and thus clearly shows the impact of allelochemicals on a plants local environment. This difference in performance on home and away soil suggest that the possible adaptive response of *B. erectus* is associated with the local thyme chemotype. Seeds collected from *B. erectus* from phenolic locations, however, showed no pattern in response to soil type. Ehlers & Thompson attributed this difference among others to the fact that thyme-brome combinations are more frequent in non-phenolic sites than in phenolic sites, which may strengthen patterns of local adaptation. These differences in selective pressure have the potential to created different genetic strains in *Bromus erectus*, one that is adapted to phenolic populations and one that is adapted to non-phenolic populations of *T. vulgaris*.

A similar result was found by Grøndahl & Ehlers (2008), who found that some of the neighbours (*Agrostis capillaris* L., *Achillea millefolium* L., *Plantago lanceolata* L. and *Galium verum* L.) of *Thymus pulegioides* L. and *Thymus serpyllum* auct, non L. seemed to be adapting to the specific terpenes produced by the *Thymus* species. Plants from sites where they co-occurred naturally with one of the *Thymus* species, performed better on soil treated with the specific terpene produced by that *Thymus* species (home soil). They also showed that the two plant species (*A. capillaris* and *A. millefolium*), who showed the strongest evidence of local adaptation, also had the lowest coefficient of variation (CV) in plant traits on home soil. This means that there is less variation in plant traits on home soil than on away soil, which suggests that there is selection for these traits in their original environment. These results demonstrate that plants can adapt to their allelochemicals producing neighbours and that these chemical neighbours may serve as strong local selective agents capable of shaping the their local plant community.

Jensen & Ehlers (2010) looked for the presence of genetic variation for the sensitivity to the thyme monoterpene carvacrol, produced by *Thymus pulegioides*. They used seed families from three different species (*Plantago lanceolata* L., *Campanula rotundifolia* L. and *Agrostis capillaris* L.) from sites where they either co-occurred with *T. pulegioides* (experienced populations) or from sites where they did not co-occur (naïve populations). They found genetic variation for responses to carvacrol in both naïve and experienced populations, but more importantly, the response varied not only among individuals between species but also within a species (Table 2). This shows that the effect of the interaction (positive or negative) between *T. pulegioides* and its neighbours, not only depends on the specific species interacting with it but also on the specific genotype of a species. This strong contrast of positive and negative effects of *T. pulegioides* interactions with different individuals of the same species could lead to two different evolutionary pathways within the same species which could ultimately lead to speciation.

Iason et al. (2005) found similar results of the effect of allelochemicals produced by *Pinus sylvestris* L. (Scots pine tree) on the neighbouring plant community. They found a positive correlation between the chemical diversity of monoterpenes of individual scots pine trees and the species richness of the ground vegetation beneath each tree. Suggesting an adaptation to specific monoterpenes. Another study that shows the potential of allelopathy as a mechanism for evolutionary adaptation is a study by Callaway et al (2005). They showed that native plants species may evolve to tolerate the allelopathic effects of an exotic invader, although the results may be confounded by maternal effects. It has been hypothesized that the success of exotic invaders is because their allelochemicals are new to the communities they invade (Callaway et al 2005). The previous mentioned studies have shown that plants are able to adapt to allelochemicals produced by neighbouring plants, if native plants are also able to adapt to allelochemicals produced by invading exotic plants, as suggested by Callaway et al (2005), plant communities may be more resilient than once thought and may ultimately even be able to coexist with the new invading species (Callaway et al 2005).

### **Facilitation as a mechanism for evolutionary adaptations.**

Most of the ecological literature about plant-plant interactions is dominated by competition and allelopathy (Brooke et al. 2008). Facilitation is far less studied. Especially the role of facilitation as a mechanism for evolutionary adaptation has been mostly neglected (Soliveres et al. 2014). Besides, most of the studies looking into facilitative interactions have been dominated by a unidirectional approach, focusing on the effects of the facilitating species on the facilitated species (Schöb et al. 2013). The effects of the facilitated species on the facilitator, in other words the cost of facilitation, have received far less attention (Bronstein 2009). It is not hard to imagine that by facilitating growth of neighbouring species, the facilitator increase the competition for water and nutrients. This means that the facilitator and the facilitated may undergo different selective forces. If there are any cost of the facilitative interactions, selection may favour facilitators to escape from this relationship or reduce the effects facilitation has on the facilitator (reduce the costs of facilitation) (Bronstein 2009). The selective forces on the facilitated however may select for a strengthening of the facilitative relationship. How

facilitation will evolve should depend on the cost and benefits of both partners in the relationship and not only on the costs and benefits of the facilitated species (Bronstein 2009). Given that facilitative interactions between plants are widespread and that they can regulate the success of neighbouring individuals and therefore the community composition, there is a clear need to explore how facilitation could fit into mainstream ecological theory (Brooker et al 2008).

There are different views to what degree facilitative interactions change with increased environmental stress. One recent idea is that, instead of facilitative interactions being more common in harsh environments, facilitative interactions should be more common in medium harsh environments (Smit et al 2007; Brooker et al 2008; Holmgren & Scheffer 2010). The idea is that when environmental conditions become more severe the positive effects of facilitation cannot outweigh the detrimental effects in extremely harsh environments, leading to a humped-back curve favouring facilitation in medium harsh environments. Holmgren & Scheffer (2010) also suggested two other reasons why facilitation may be more important in medium harsh environments. First, they found evidence that in some communities the net effect of amelioration of a deficiency of a limiting resource may be beneficial under medium harsh conditions whereas in extreme harsh conditions it can be overruled by increased competition for the same limiting resource. Secondly, they stated that, given that in any ecosystem the suite of organisms is adapted to local conditions, even under conditions that appear less stressful, facilitation may play an unexpectedly large part as organisms in less stressful environments are more sensitive than those found under more stressful environments. This means that unlike previously thought (see Bertness & Callaway 1994), facilitation is not mostly found in extreme environments but may play an important role in communities with medium to high environmental severity (Brooker 2008). Since facilitative interactions could therefore be more common than previously thought, also the role of facilitation in community structure and composition, and the effect of facilitative interactions on species evolution could be more important than once thought.

Seeing that facilitative interactions are more common and widespread than once thought, there is a growing need to determine and understand the long-term consequences of facilitation for the interacting plants and their community and its role in the evolution of these plants and their community. There are two major roles that facilitation can play in evolution (Soliveres et al 2014). Facilitative interactions may help to preserve lineages less adapted to changing environmental conditions (both biotic and abiotic), working as an ecological time machine for less adapted lineages and pull, as it were, the less adapted lineages through time over millions of years (Soliveres et al 2014; Lortie 2007). The second role facilitation may play is that it may work as a process driving speciation. This means that if facilitation can evolve new species, it does not only need to enhance performance of maladapted ecotypes but also generate reproductive isolation (Soliveres et al 2014). And as mentioned before the facilitator and the facilitated may undergo different selective forces to either escape or strengthen the facilitative relationship, depending on the effect the facilitative interaction has on the facilitator (positive, negative or neutral)

### **Facilitation as an ecological time machine**

That facilitative interactions can work as an ecological time machine and pull less adapted lineages over millions of years, was shown by Valiente-Banuet & Verdú (2006). They found, by integrating paleobotanical, ecological and phylogenetic analyses, that a large number of ancient Tertiary plant species in Mediterranean-climate ecosystems seem to have been preserved by facilitative effects of modern Quaternary plant species and that these interdependent relationships among plants have played an important role in creating today's plant community composition and diversity. They found that these facilitative interactions were especially important during climatic changes between the Tertiary and Quaternary period, during which the climate shifted from moderately moist to unusually dry. Despite the wave of extinctions that occurred with this shift in climatic conditions, the fossil record shows that large taxonomic components of these ancient Tertiary plant species are still present in today's Mediterranean-climate communities around the world. Facilitation from other (more adapted)

plants was necessary for the regeneration of species that evolved during the moderately moist Tertiary period, because the fleshy fruits of Tertiary species depended on the facilitative effects of other species to establish. Of the 113 taxa, evolved during the Tertiary period, across the six regions they had examined, 86 were identified as species that recruited more beneath other species canopies than in open spaces. In contrast, of the 100 species evolved during the Quaternary period, 97 recruited more in the open than under canopies of other species (Fig. 2). Valiente-Banuet & Verdú (2006) also found that Quaternary species are earlier colonizers than Tertiary species, who could only establish themselves after the more drought-tolerant Quaternary species had created moderately moist conditions, resembling the ancestral conditions of the maladapted Tertiary species. Tertiary species seem to only colonize Mediterranean-climate communities that are dominated by Quaternary species, clearly demonstrating the Tertiary species need for the facilitating effects of Quaternary species. Besides surviving the climatic shift between the Tertiary and Quaternary period, present Tertiary species also have ecological traits that have remained similar for millions of years, suggesting that the facilitating effects of Quaternary species not only conserved Tertiary species but also their ecological traits. To test whether or not these traits actually have been maintained by stabilizing selection through facilitation, Valiente-Banuet & Verdú (2006) mapped an index of the regeneration niche (the percentage of seedlings recruited under shrubs) for each Mexican species in a phylogenetic tree and compared the fit of several models of evolution, each depicting a different selective regime (Fig. 3). A simple evolutionary model accounting for stabilizing selection explained the observed regeneration niche significantly better than the neutral Brownian motion model. This suggests that facilitation has indeed promoted stabilizing selection through evolutionary time.

In another study Valiente-Banuet & Verdú (2007) tested whether, if facilitation among distant species has preserved the regeneration niche of plant lineages, this has increased the phylogenetic diversity of plant communities. Given that there is often conservatism of traits in evolutionary lineages, and positive relationships between species phylogenetic relatedness, overall life history and ecological similarity, they proposed that the phylogenetic structure of a community can provide insight into how facilitation affects evolutionary relationships between species and community structure and composition. If the regeneration niche is indeed conserved over evolutionary time and facilitative interactions mainly occur between phylogenetic distant species, then facilitation should lead to phylogenetic overdispersion of the community (Fig. 4). Fig. 5 shows that closely related species have similar niches, thus suggesting a strong conservation of the regeneration niche over evolutionary time. There were 51 evolutionary transitions between facilitated and non-facilitated regeneration niches, which was significantly lower than the null model (120 transitions). They also found that the mean phylogenetic distance (240 million years) between nurse species and the associated facilitated species, of three communities driven by facilitation, was significantly greater than expected by the null model (226 million years). Thus suggesting that facilitated tend to occur between phylogenetic distant species. This facilitation of distant related species leads to a phylogenetic overdispersion and this combined with the spatial characteristics of facilitation (affecting neighbours) leads to a checkerboard pattern (Fig. 4). This shows that facilitation has a big influence in shaping community structure and composition and also in maintaining regeneration niche heterogeneity and thus species richness.

### **Facilitation as a driver of speciation**

The studies by Valiente-Banuet & Verdú showed that facilitation can bridge the divide between disciplines by generation a mechanism of stabilizing selection for the regeneration niche. This means that facilitation can increase biodiversity and, if consistent, the association of one species with another can provide a set of stabilizing selection processes that can lead to coevolution (Lortie 2007). And if there is reproductive isolation between the facilitated individuals and the non-facilitated individuals of a species it could ultimately lead to speciation (Soliveres et al 2014). However, coevolution can only occur if the facilitative interactions between the species are constant. How constant these interaction are depends on the effect these facilitative interactions has on the facilitator. If the increased success of the beneficiary

species increase the competition for resources by the facilitator, these facilitative interactions could be far from constant, as the facilitator seeks to escape this relationship. A study by Schöb et al (2013) shows that facilitation can indeed come with a cost to the facilitator. Using data collected from 35 arctic-alpine sites on four continents and a sub-Antarctic island, they found negative feedback effects of cushion-associated species on cushion facilitators across 14 cushion plant species. Fig. 6 shows that the reproductive output (number of flowers, fruits and seeds) of these cushion plants are higher when grown without the facilitated cushion-associated species than when grown with them. Clearly showing the cost of facilitation for the facilitator. Also facilitative interactions may be dependent on a species life history (Valiente-Banuet & Verdú 2007). Seedlings and young individuals may experience facilitative effects from a certain species, but in mature individuals of the same species this facilitative relationship may no longer exist. In this case facilitation only influences the species juvenile stages and not its mature reproductive stages. So while facilitation during germination can select for certain genotypes, the lack of this facilitative effect in later reproductive stages means that over a species lifespan the net effect of facilitation maybe non-existent and therefore the selective pressure induced by the initial facilitation may not be sufficient to induce speciation.

One of the key things necessary for facilitation induced speciation is reproductive isolation (Soliveres et al 2014). However whether or not facilitation leads to reproductive isolation is not yet clear. One way that reproductive isolation can occur is when facilitative interactions change flowering phenology of the facilitated species and thus promoting reproductive isolation from the non-facilitated individuals. Another way that reproductive isolation may occur is when a nurse plant protects facilitated plants against grazing, which reduces the production of flowers and seeds of these facilitated plants outside the canopy of the nurse (Soliveres et al 2014). This way the facilitator acts as a kind of barrier between the facilitated and non-facilitated individuals, leading to reproductive isolation. However some suggest that facilitation does not lead to reproductive isolation, but instead maintains gene flow between adapted and maladapted ecotypes. Liancourt et al (2012) argued that facilitation is likely to maintain gene flow among incipient species by enabling adapted and maladapted ecotypes to occur in the same habitat (Fig. 7). Fig. 7 shows that facilitation may result in a stable coexistence between the two genotypes and thus leading to an increase in overall genetic diversity, a decrease in inbreeding and a decreased potential to adapt to the marginal conditions. Facilitation may thus be able to maintain gene flow between populations and thus counteracting diversifying selection. Although they found it most likely that facilitation is a cohesive force, they also considered possible conditions under which facilitation may contribute to ecological speciation, rather than impeding it. One such condition is the patchy distribution of biological engineered favourable microhabitats, induced by facilitative interactions, which can lead to disruptive selection between nearby subpopulations. Local adaptation in the understory could lead to ecological speciation, especially when these local adaptations lead to differences in reproductive systems (also argued by Soliveres et al 2014). While this is possible, they found it unlikely due to the small spatial scale of environmental heterogeneity created by the facilitators and thus likely to still be within dispersal and pollination distance from each other. Furthermore, nurses may also function as a sink for seeds. Thus making it unlikely, but not impossible, that gene flow will be severely restricted between populations of the understory habitats and those outside and thus will not lead to ecological speciation.

## **Discussion**

In this essay I looked at the long term effects of plant-plant interactions and tried to answer whether or not these interactions could act as mechanism for evolutionary adaptations. Research has shown that competition can indeed lead to evolutionary adaptations. Some studies (Parrish & Bazzaz 1976; Aarsen & Turkington 1985; Leger 2008) showed that communities/individuals with a history of competition are more adapted to each other than communities/individuals without a history of competition. The same can be said of allelopathy as a mechanism for evolutionary adaptations. Current research (Ehlers & Thompson 2004; Grøndahl & Ehlers 2008; Jensen & Ehlers 2010; Iason et al 2005) shows that species grown

near allelopathic neighbours, adapt to the specific allelochemicals produced by that neighbour. Thus, this clearly shows the potential of allelopathy as a mechanism for evolutionary adaptations.

Facilitation as a mechanism for evolutionary adaptation on the other hand is another story. Unlike competition and allelopathy, the long term effects of facilitation have received far less attention and thus our understanding of them is minimal. Current research shows that facilitation can act as an ecological time machine, where better adapted Quaternary lineages pulled less adapted Tertiary lineages over millions of years (Valiente-Banuet & Verdú 2006 and 2007). This suggests that facilitation can be a stabilizing force throughout evolutionary time. But whether or not facilitation can lead to adaptations and perhaps even speciation is yet unclear. One of the key questions is whether or not facilitation will lead to the reproductive isolation needed for speciation to occur, and to the present day our knowledge and available research is insufficient to be able to answer that question. Another problem is that for speciation to occur there needs to be a long term association between the facilitating and facilitated species, and this may not always be the case as facilitating species may want to escape that relationship due to possible detrimental effects of the facilitated species. So an interaction between two species can be perceived differently by the species involved: while one experiences facilitation, the other might experience competition. There is a clear need for experiments testing the evolutionary consequences of facilitation. Especially in light of the predicted global environmental changes, which will increase the stress level for many species, there is a clear need to better understand the long term effects of facilitative interactions, as facilitation can alleviate the increased stress induced by environment changes. A better understanding of facilitative interactions and their long term effect will help us to better deal with restoration and conservation challenges imposed by global environment change.

Facilitation is a relatively new topic and despite the fact that over the years its importance in community structuring and composition has been acknowledged more and more, a lot is still unclear. Perhaps one of biggest questions involving facilitation, is the one how common facilitative interactions are. Currently there are different views about the commonness of these facilitative interactions. One view is that they are more common in harsh environments, where they alleviate the stress experienced by less adapted species. Another view is that they should be more common in medium-harsh environments, suggesting that in harsh environments the facilitative interaction cannot outweigh the detrimental effects of these harsh conditions. If we want to know how or if facilitation could lead to evolutionary adaptations it is important that we find out how common facilitative interactions are. If facilitation is not limited to harsh environments but is in fact more common and widespread, the role of facilitation in shaping communities can perhaps be as important as that of competition. If this is the case than competition is no longer the dominant factor in shaping communities, but instead the interplay of competitive and facilitative interactions will be the dominant factor shaping communities. Which means that when we look at the long term effects of competition and facilitation, we cannot look at each of them separately, but in fact have to look at them as two halves of the same coin. Where not one of the two, but the delicate interplay between them will be the main driving force in community evolution.

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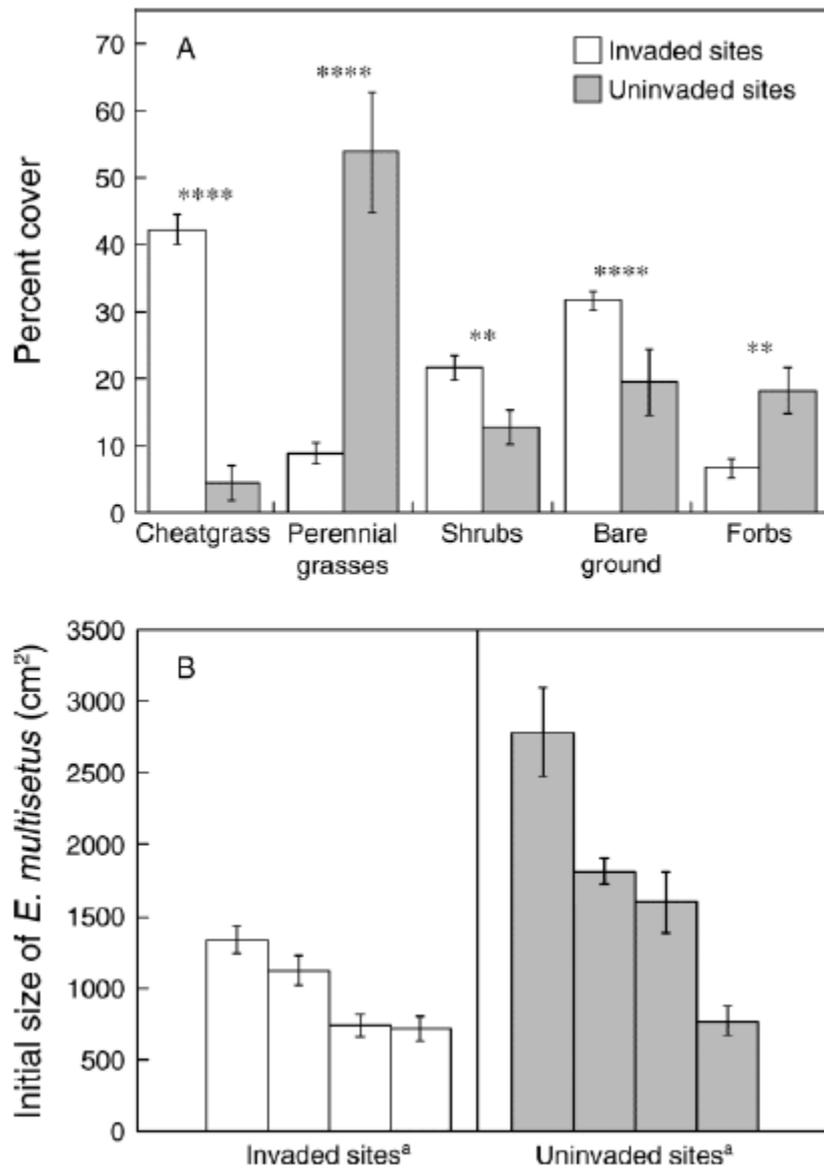
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## Appendix



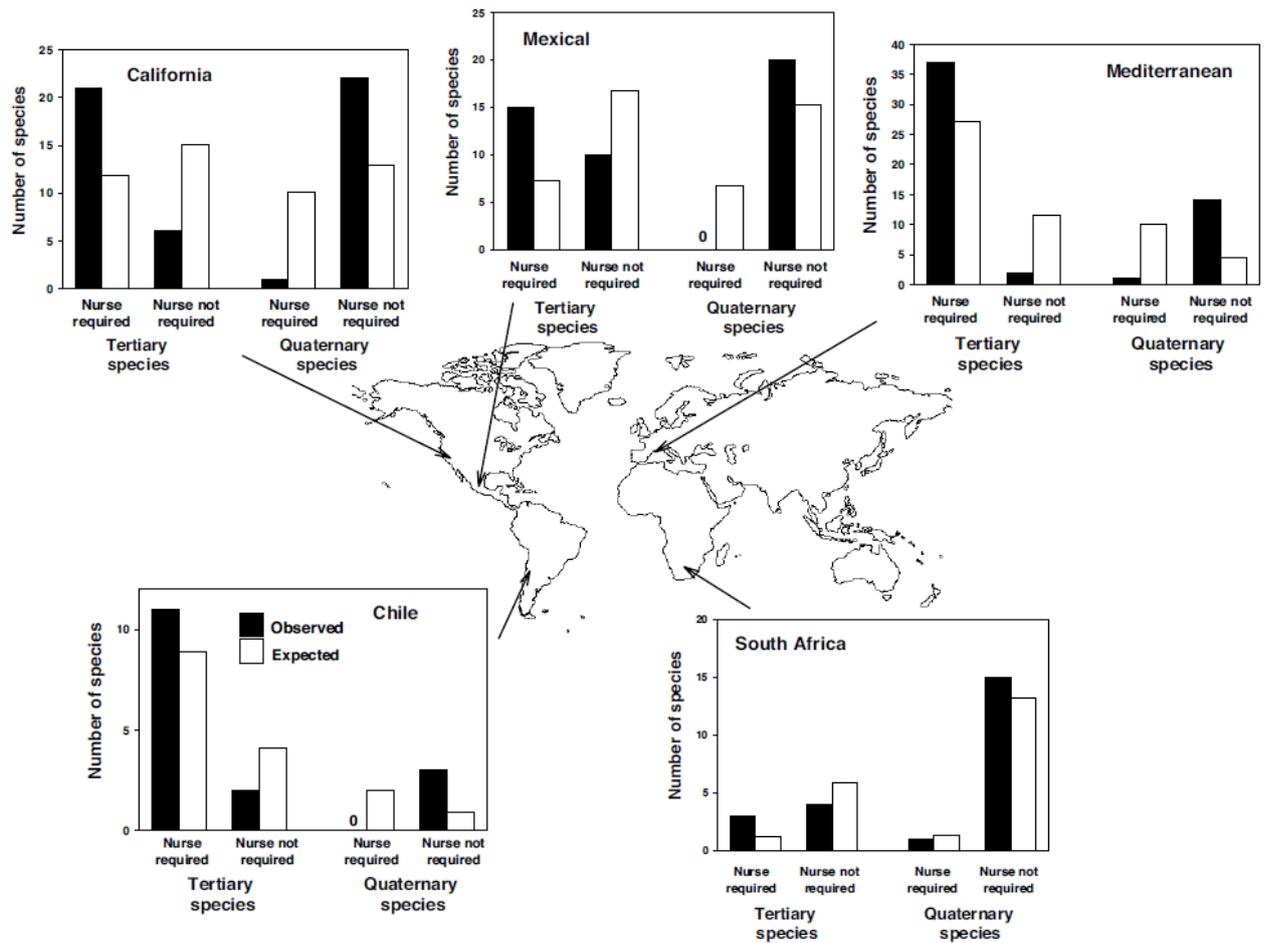
**Fig. 1** (A) Community composition, by cover (mean  $\pm$  SE), of invaded and uninvaded sites. (B) Size of *Elymus multisetus* transplants collected from four invaded and four uninvaded sites. There is no significant overall difference between invaded and uninvaded areas (as indicated by same superscript lowercase letters for each group of sites pooled). However, there are significant differences at the site level between the populations sampled ( $P < 0.0001$ ). \*\*  $P < 0.01$ ; \*\*\*\*  $P < 0.0001$ . (Copied from Leger 2008)

Site	Non-phenolic						Phenolic					
	NP1		NP2		NP3		P1		P2		P3	
Soil type	Thyme	Grass	Thyme	Grass	Thyme	Grass	Thyme	Grass	Thyme	Grass	Thyme	Grass
Organic matter	72.7	50.0	38.4	21.9	58.3	39.9	39.4	45.9	56.2	28.6	80.5	42.3
C (%)	42.3	29.1	22.4	12.7	33.9	23.2	22.9	26.7	32.7	16.8	46.8	24.6
N (%)	4.3	1.9	2.0	1.2	2.9	2.0	2.4	2.7	3.5	1.5	3.9	1.8
PH	8.1	8.3	8.3	8.5	8.2	8.4	8.2	8.3	8.2	8.4	8.1	8.4

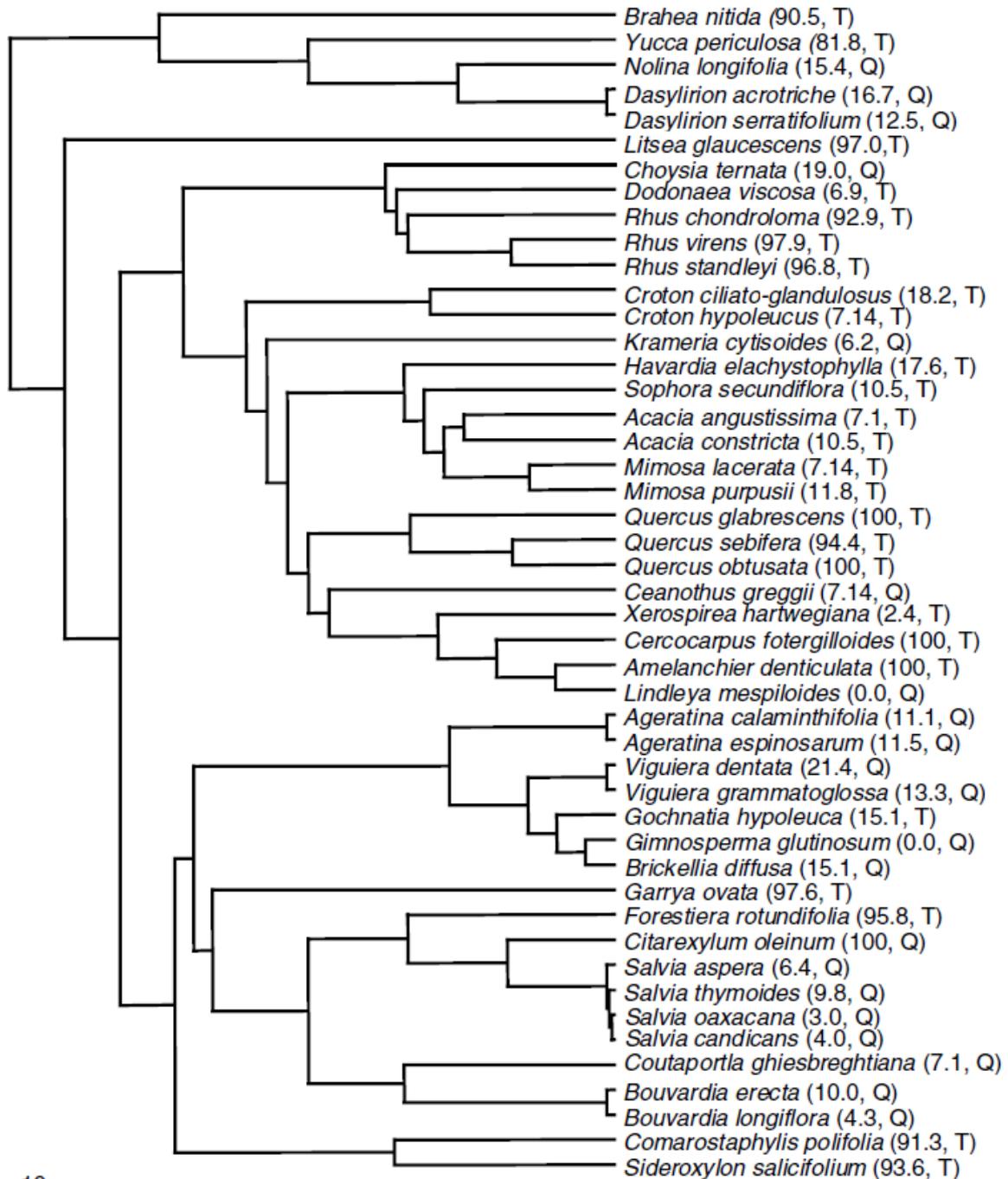
**Table 1** Analysis of top soil collected from six sites, three non-phenolic and three phenolic (NP1-3 and P1-3 respectively). At each site, soil was collected from thyme patches (thyme-soil) and grass patches (grass-soil). Samples of grass- and thyme-soil in each site were always less than 5 m apart. (Copied from Ehlers & Thompson 2004)

Species	Naive (N)/ Experienced (E)	<i>n</i>	Positive reaction norm	Negative reaction norm	LRT <sup>a</sup> ( <i>P</i> -value)
<b>Total biomass</b>					
<i>Plantago</i>	N	24	1	23	4.57
<i>Plantago</i>	E	24	6	18	( <i>P</i> = 0.032)
<i>Campanula</i>	N	17	5	12	1.63
<i>Campanula</i>	E	20	10	10	( <i>P</i> = 0.2)
<i>Agrostis</i>	N	20	3	17	3.41
<i>Agrostis</i>	E	18	9	9	( <i>P</i> = 0.0009)
Pooled	N	61	8	53	8.6
Pooled	E	62	22	40	( <i>P</i> = 0.003)
<b>Aboveground biomass</b>					
<i>Plantago</i>	N	24	1	23	4.57
<i>Plantago</i>	E	24	6	18	( <i>P</i> = 0.032)
<i>Campanula</i>	N	17	4	13	3.88
<i>Campanula</i>	E	20	11	9	( <i>P</i> = 0.048)
<i>Agrostis</i>	N	20	2	18	3.19
<i>Agrostis</i>	E	18	6	12	( <i>P</i> = 0.07)
Pooled	N	61	7	54	11.41
Pooled	E	62	23	39	( <i>P</i> = 0.0007)
<b>Root biomass</b>					
<i>Plantago</i>	N	24	1	23	0
<i>Plantago</i>	E	24	1	23	( <i>P</i> = 1)
<i>Campanula</i>	N	17	6	11	0.1
<i>Campanula</i>	E	20	8	12	( <i>P</i> = 0.77)
<i>Agrostis</i>	N	20	9	11	7.82
<i>Agrostis</i>	E	18	15	3	( <i>P</i> = 0.005)
Pooled	N	61	16	45	2.19
Pooled	E	62	24	38	( <i>P</i> = 0.14)

**Table 2** Summary of likelihood ratio test (LRT) for differences between experienced and naive populations in proportion of seed families showing a positive growth response on carvacrol soil. (Copied from Jensen & Ehlers 2010)

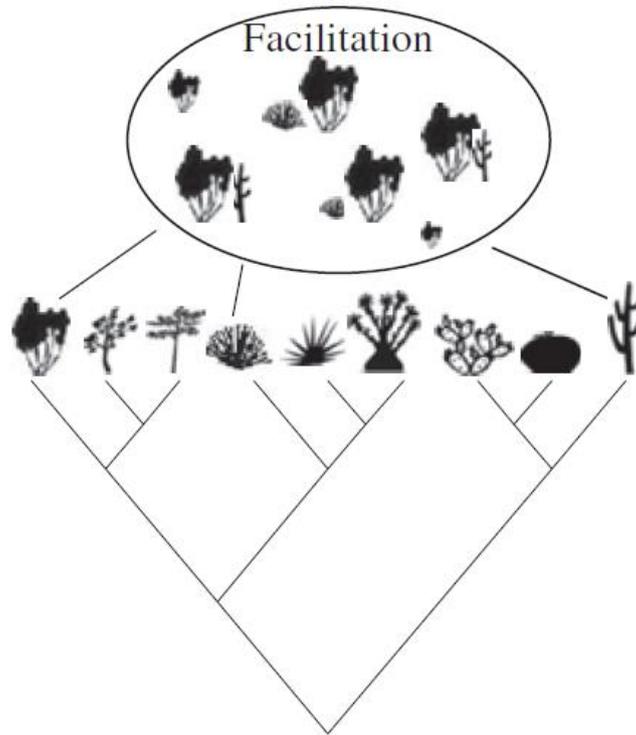


**Fig 2.** Regeneration niche requirements of Tertiary and Quaternary lineages, based on fossil record, in the five Mediterranean areas (Australia not present, because the data did not allow to run the  $X^2$  test) of the world and in the Mexical shrub land of central Mexico. Filled bars show the observed numbers of species from each lineage reported in the literature that occupy particular regeneration niches, and open bars show the expected numbers of species of each lineage. (Copied from Valiente-Banuet & Verdú 2006)

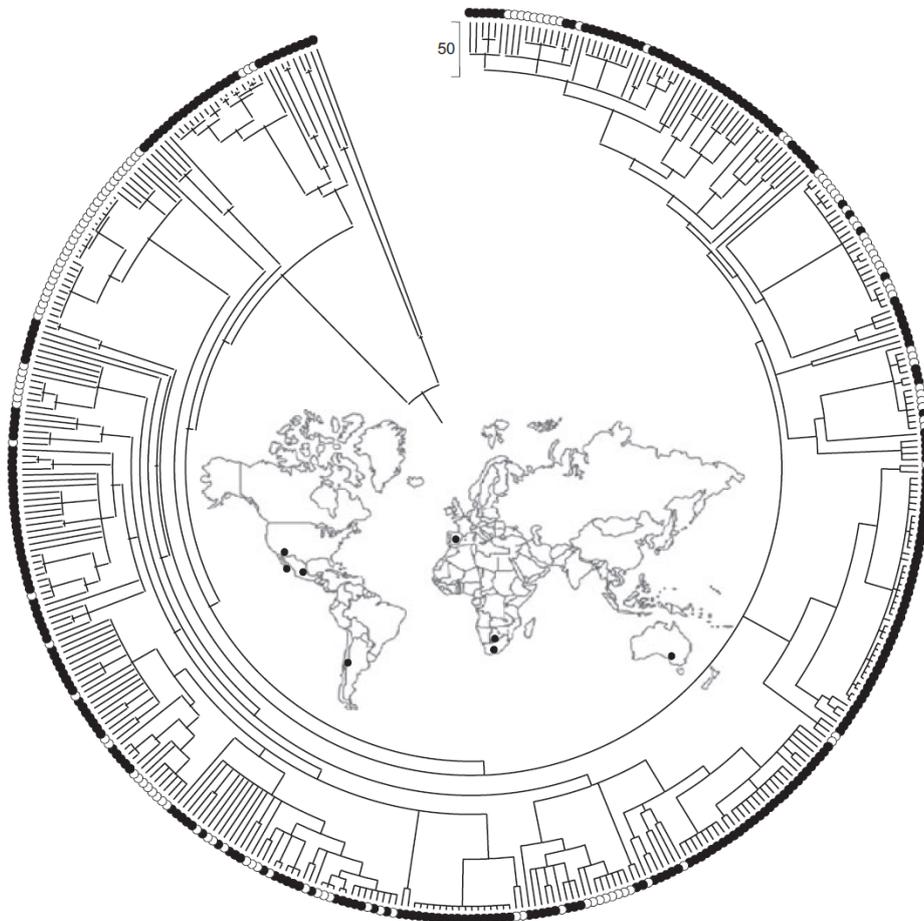


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**Fig. 3** Phylogenetic tree for species in the Mexical shrub land. The scale for the branches is presented in millions of years. Values associated with each species show the percentage of young individuals recruiting beneath the canopy of perennial nurse plants. T, Tertiary lineage; Q, Quaternary lineage. (Copied from Valiente-Banuet & Verdú 2006)

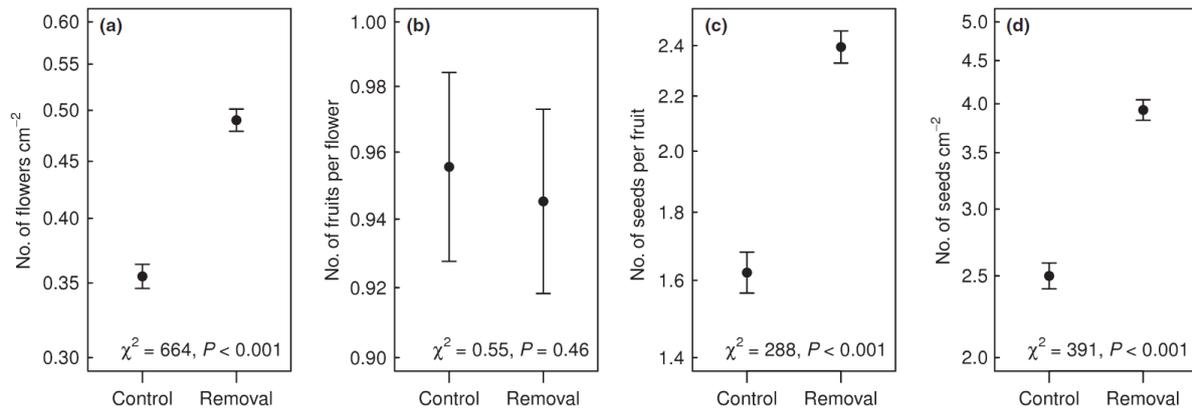


**Fig. 4** Phylogenetic overdispersion due to facilitation, producing a checkerboard spatial pattern. (Copied from Valiente-Banuet & Verdú 2007)

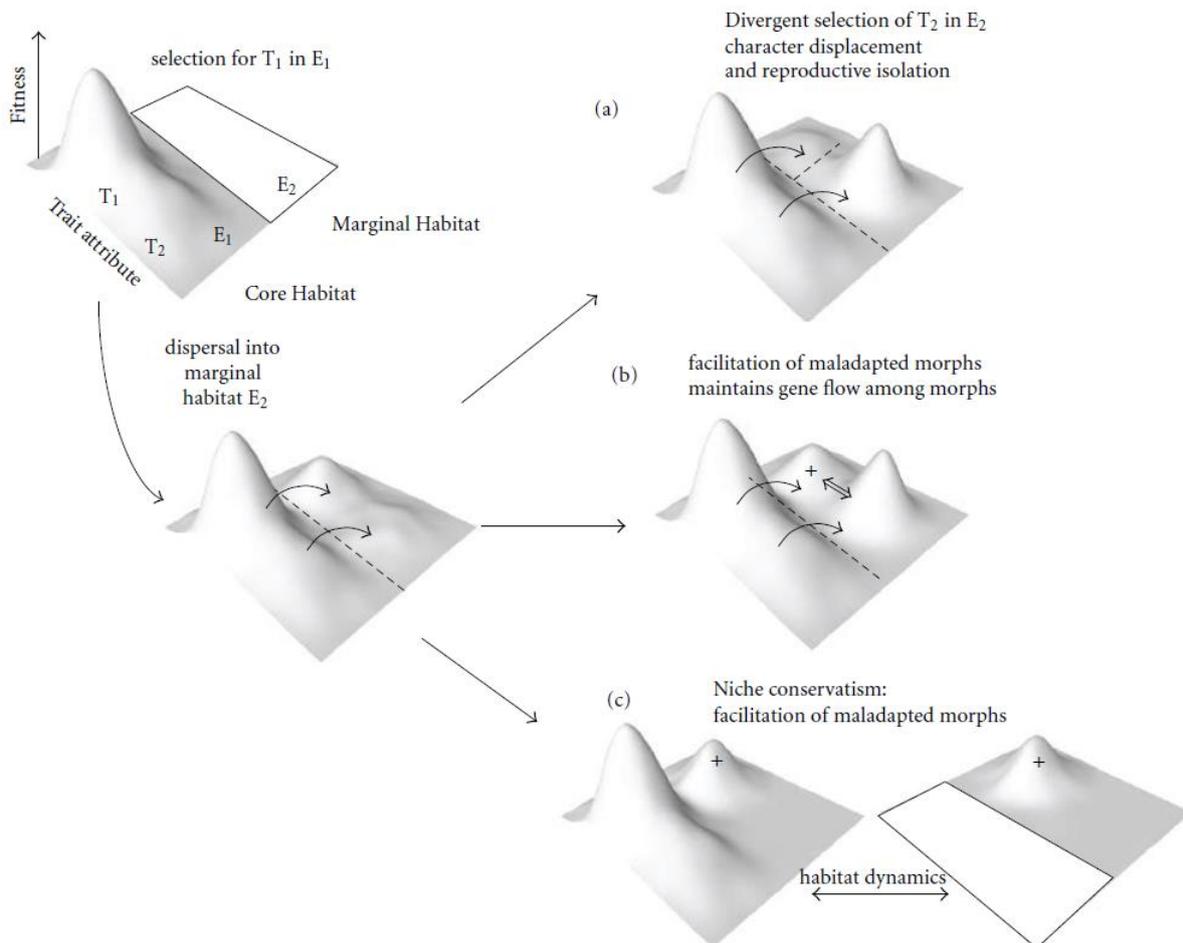


**Fig 5.** Phylogenetic tree showing the evolutionary relationships between the study species and the regeneration niche mapped onto the tips. Filled dots represent facilitated niches while unfilled dots represent non-facilitated

niches. The world map shows the sites where the data was obtained. (Copied from Valiente-Banuet & Verdú 2007)



**Fig 6.** Response of flower density (a), fruit set (b), seed set (c) and seed density (d) of cushions to experimental removal of plants growing inside cushions. Shown are model predicted values of the effect of the removal treatment  $\pm$  95% CI's and Wald  $\chi^2$ -tests for treatment as a main effect of generalized linear mixed models. Note the  $\log_e$  scale of the y-axis. (Copied from Schöb et al 2013)



**Fig. 7** How facilitation may interfere with ecological speciation and niche conservatism. These 3D plots sketch ongoing disruptive selection and trait divergence of incipient species. The vertical axis represents the relative fitness of genotypes in a trait-ecological space. The assumption is that ecologically marginal conditions (E2) also correspond to peripheral areas. Solid arrows are for gene flow including dispersal of propagules, individuals, and sexual reproduction. Dotted lines denote reproductive isolation. A common starting point is immigration of genotypes from the favourable part of the gradient to marginal/peripheral habitats. (a) Diversifying selection without facilitation, and reproductive isolation that eventually arises as a by-product of trait divergence. (b) Maladapted forms persist in marginal habitats because of facilitation and a maintained gene flow among genotypes prevents ecological

speciation.(c) Facilitation allows maladapted forms to persist in a changing environment, that is, niche conservatism.  
(Copied from Liencourt et al 2012)