



Review

Direct plant–plant facilitation in coastal wetlands: A review

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ABSTRACT

Coastal wetlands provide important ecosystem services to humanity, but human activity and climate change are rapidly degrading these ecosystems. Thus the conservation and restoration of coastal wetlands becomes an urgent issue. Species facilitation among plants has regained attention of ecologists recently. Many studies in coastal wetlands have revealed direct plant–plant facilitation influencing community structure and ecosystem function, thus improving our understanding of community organization and giving new directions for the restoration of degraded coastal wetlands. Our paper examines studies of direct plant–plant facilitation in coastal wetlands with an emphasis on tests of the stress gradient hypothesis and influences of species facilitation on species zonation, species diversity patterns, phylogenetic diversity and ecosystem function. Investigating how plant–plant facilitation affects ecosystem function is an important future direction, which can provide basic knowledge applicable to the preservation and recovery of coastal wetlands in these times of rapid global change.

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Coastal areas make up only 4% of the earth's surface, but more than 1/3 of the world's population resides in these areas. Coastal wetlands provide important ecosystem services to humanity, such as food, storm protection, shoreline protection and fishing nurseries (Gedan et al., 2009). However, human activity (e.g., agriculture and urban development) and climate change (e.g., rising sea level) diminish these areas and strongly disrupt coastal ecosystem functions (e.g., Comeaux et al., 2012). Restoration of disrupted coastal wetlands has been an urgent issue (Spencer and Harvey, 2012). Understanding when and how interactions among plants influence ecosystem functions (e.g., productivity, ecosystem stability) of coastal wetlands will provide basic knowledge for us to protect and recover these important ecosystems (Halpern et al., 2007). On the other hand, it is widely known that coastal wetlands provide an ideal ecosystem to investigate the basic hypotheses of community ecology because of their simple plant community composition and long-length distinct and strong abiotic stress gradients from sea to inland. The influences of plant–plant interactions and their interactions with environmental stress on coastal wetland community organization have been well studied. Here, we review recent developments in the field of direct plant–plant interactions including: (1) the prevalence of direct plant–plant interactions in coastal wetland plant communities (e.g., salt marshes, cobble

beaches, mangroves, and coastal forests); (2) mechanisms of direct plant–plant interactions in coastal wetlands and how to determine if plant–plant interactions are positive or negative; (3) how the strength of interspecies interactions vary across stress gradients and how these interactions influence species zonation and species diversity patterns along stress gradients; (4) the relationships between species interactions and species invasions. Then we propose a hypothesis of how species facilitation affects ecosystem function of coastal wetland.

1. Direct plant–plant facilitation in coastal wetlands

Direct plant–plant interactions include positive and negative interactions (i.e., species facilitation and competition). Plant–plant facilitation occurs when the presence of neighboring plants enhances survival, recruitment or growth of the target plant through modifying environmental conditions or providing associational defenses against herbivores. Almost a century ago, ecologists discovered that both species competition and facilitation were ubiquitous in natural plant communities. Subsequently, the influence of species competition on community organization has been thoroughly investigated; however, the importance of species facilitation has been largely neglected.

Recently, accumulating evidence suggests that species facilitation is essential in structuring plant communities, particularly in high stress environments (Bertness and Yeh, 1994; Bruno et al., 2003; Brooker et al., 2008). Both competition and facilitation among plants have been observed in coastal wetlands. For example,

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species showed a hierarchical structure in terms of competitive ability in a New England salt marsh. Species investigated, in order of competitiveness, were *Iva frutescens*, *Jucus gerardi*, *Spartina patens* and *Spartina alterniflora* (Pennings and Bertness, 2001). Competition among these species and species tolerance of environmental stress formed distinct plant zonation in the salt marsh. However, in the *Spartina*–*Juncus* zone of high salinity the salt tolerant but less competitive species, *S. Patens* ameliorated the abiotic stress of high salinity and facilitated colonization by the salt intolerant *J. Gerardi* (Bertness and Shumway, 1993).

Though most plant–plant facilitation experiments have focused on salt marshes, some have investigated cobble beaches or estuarine marshes and very few have investigated coastal forests or mangrove forests in particular (Huxham et al., 2010, Table 1). Moreover, most studies have assessed interspecific facilitation and largely disregarded intraspecific facilitation (i.e., positive density dependence). Negative density dependence, which can be caused by strong competition for resources, habitat overlap for individuals, increasing susceptibility to infection by pathogens or detection by consumers, is regarded as a key organization rule in traditional population dynamics. However, when the benefits of conspecific group living outweigh the effects of resource competition or other negative density dependence mechanisms, positive density dependence may occur, particularly in high stress environments (Goldenheim et al., 2008; Fajardo and McIntire, 2011). This type of positive density dependence is very useful in restoration management of coastal wetlands (Halpern et al., 2007). We recommend researchers consider both interspecific and intraspecific facilitation and compare the relative role of inter- and intraspecific facilitation in shaping coastal wetland populations and communities to avoid underestimating the role of plant–plant facilitation.

2. Mechanisms of plant–plant facilitation in coastal wetlands

The major mechanism for species facilitation among plants in coastal wetlands is the reduction of abiotic or biotic stress (Fig. 1). Biotic stresses, such as herbivory, could be reduced by neighboring plants decreasing the probability of encounters between target plants and animal consumers, thus defending target plants from animal consumption (Alberti et al., 2008; Daleo and Iribarne, 2009). Abiotic stresses often reduced through plant–plant facilitation include high salinity, flooding, and nutrient limitation stress.

Salinity stress may be reduced through the presence of neighboring plants shading their surrounding soil, thus decreasing water evaporation rate and preventing salt accumulation in the soil. Alternatively, neighboring plants could absorb salt from the soil and store it in their tissues or excrete it from their salt glands, thus reducing the salinity of their ambient environment (Bertness et al., 1992). An additional mechanism could be increased proline production in target plant cells enabled by nitrogen supplementation from neighboring plants (Levine et al., 1998). Flooding stress may

also be reduced by neighboring plants. Flood-tolerant plants could ameliorate anoxic substrate conditions by enhancing soil oxygen levels through rhizosphere oxidation. Alternatively neighboring plants could lift the soil to decrease waterlogging (Fogel et al., 2004). Limiting nutrient stress could be decreased through plant–plant facilitation when neighboring plants enrich the soil with nutrients (Levine et al., 1998). Facilitating tolerance of other biotic and abiotic stresses such as sea waves, pollination or dispersal stress has also been proposed as mechanisms of species interaction (Table 1). However, the cumulative effects of co-occurring environmental stresses, particularly abiotic and biotic stresses on species interactions, which may play an important role in community assembly are still poorly understood (Bulleri et al., 2011).

3. Experimental approaches to studying plant–plant facilitation

In contrast to studies on other ecosystems (e.g., semiarid grasslands or alpine plant communities) which have employed removal experiments to investigate plant–plant facilitation (e.g., Choler et al., 2001), studies in coastal wetland employed transplant experiments. Removal experiments involve the elimination of all neighboring plants around the target individual. Target plant performance is then compared between removal and control treatments. In transplant experiments, patches of conspecific individuals are transplanted into another plant zone (with or without neighboring plants). Then plant performance is compared between transplant and control treatments. Both experimental approaches are popular methods for detecting of plant–plant facilitation, and both have their own advantages and disadvantages.

Removal experiments are suitable for species with a scattered distribution, but can only be operated on widely spread species. Moreover, it is impossible to detect species-specific interactions in removal experiments. On the other hand, transplant experiments can only be conducted on densely populated species and are inappropriate for species with a scattered population distribution (except when cultivating seedlings). Approaches such as spatial point process, Hierarchical Bayesian analysis which was designed to investigate community-level (larger than only one or a few pairs of species in the community) consequences of species interactions (Raventos et al., 2010; Wang et al., 2011) are rarely used in coastal wetland studies. Additionally, many studies on species facilitation are too short term to achieve equilibrium in species interactions, thus longer observations are necessary.

4. Tests of the stress gradient hypothesis in coastal wetlands

The stress gradient hypothesis (SGH) was put forward by Bertness and Callaway (1994) at a time when ecologists did not appreciate the role of facilitation in communities. The SGH was

Table 1
Direct plant–plant facilitation in different coastal wetlands.

Ecosystem	Benefactor	Beneficiary	Mechanism	Study sites	Literature
Salt marsh	<i>Spartina patens</i> ; <i>Distichlis spicata</i>	<i>Juncus gerardi</i>	Lowering salinity	Southern New England salt marsh, USA	Bertness and Shumway (1993)
Salt marsh	<i>Triglochin maritima</i>	<i>Plantago maritima</i> ; <i>Limonium nashii</i>	Decreasing waterlogging and salinity	Northern New England salt marsh	Fogel et al. (2004)
Estuarine marsh	<i>Sarcocornia perennis</i> .	<i>Spartina densiflora</i>	Reducing herbivory by crabs	Mar Chiquita coastal lagoon and the Bahia Blanca estuary, Argentina	Alberti et al. (2008)
Cobble beach	<i>Spartina alterniflora</i>	<i>Suaeda linearis</i>	Buffering sea waves	Rhode Island, USA	Irving and Bertness (2009)
Cobble beach	<i>Suaeda linearis</i>	<i>Suaeda linearis</i>	Reducing evaporative stress	New England shore, USA	Goldenheim et al. (2008)
Coastal forest	<i>Cladium jamaicense</i>	<i>Pinus taeda</i> ; <i>Pinus serotina</i>	Lowering salinity	Swanquarter National Wildlife Refuge, USA	Poulter et al. (2009)
Mangroves	<i>Avicennia marina</i>	<i>Ceriops tagal</i>	Reducing salinity	Gazi bay, Kenya	Huxham et al. (2010)

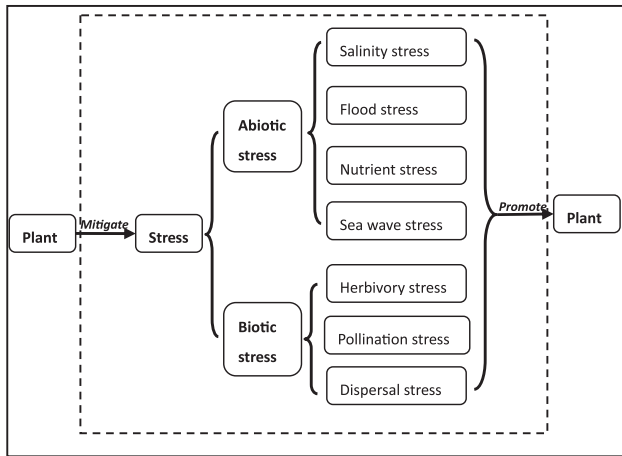


Fig. 1. Key mechanisms of direct plant–plant facilitation in coastal wetlands. Species facilitation is due to neighboring plants mitigating environmental stress including abiotic stresses such as salinity, flood, nutrient, sea wave stress and biotic stresses such as herbivory, pollination and dispersal stress in order to promote fitness of target plant.

based on the species competition model of Grime (1979), which proposes that the importance of species competition decreases along the stress gradient as productivity decreases or abiotic stress increases. Bertness & Callaway's (1994) SGH expands Grime's model to incorporate species facilitation. The SGH predicts that the frequency of facilitative and competitive interactions between species will vary inversely to each other across abiotic or biotic stress gradients and that species facilitation is more likely to occur in high stress environments. Nevertheless, many of the experiments testing the SGH have examined the strength, but not the frequency of species competition and facilitation along abiotic stress gradients (Maestre et al., 2009). Maestre et al. (2005) employed a meta-analysis to investigate tests of the SGH in plant communities of arid environments and found that the SGH was not a general rule in arid plant communities, although Lortie and Callaway (2006) disapproved this argument and re-analyzed the data and supported the SGH. Thus, for some specific studies, the interactions may depend on the types of abiotic stress gradients and measurements of plant performance. Hence, the predictions of the SGH were refined according to life history traits (i.e., competitive species or stress-tolerant species; He et al., 2012) and stages (i.e., sapling, seedling, juvenile or adult) of interacting species, types of abiotic stress gradients (i.e., resource or non-resource) and biotic stresses (Maestre et al., 2009; Smit et al., 2009). Their updates improved the SGH, and may provide a way to explain variations in results across various ecosystems.

For coastal wetlands, support or not for the SGH depends on spatial scale. Studies on a local or landscape scale commonly support the SGH, but studies across a geographic scale do not support the SGH. Alberti et al. (2008) found that crab herbivory stress regulated species interactions between plants in Argentinean marshes. Competitive interactions dominated when crab herbivory stress was low in the spring and summer, but facilitative interactions dominated when crab herbivory stress was high in the fall. On a landscape-scale, Crain's (2008) work on species interactions in the presence of consumers in oligohaline, brackish and salt marshes also provided evidence supporting the SGH. On a geographic scale, 3 studies that investigated the same species, but in high latitude, low salinity Maine marshlands (Ewanchuk and Bertness, 2004a,b), intermediate latitude and salinity Rhode Island marshlands (Bertness and Ewanchuk, 2002) or low latitude, high salinity Georgia and Alabama marshlands (Pennings et al.,

2003) found conflicting results. Species facilitation by neighboring plants was rare in the Maine, Georgia and Alabama salt marshes, but common in the Rhode Island marshlands. However, many of the experiments testing the SGH in coastal wetlands only take a few dominant species into account; few experiments in any ecosystem have investigated the SGH with whole community-level dynamic data (Goldberg et al., 1999; Rajaniemi et al., 2009). Thus, testing the SGH at the community-level in coastal wetlands while taking types of environmental stresses (or crossed stresses) and species with different life-history traits and stages into account will fill the gap in studies of direct species facilitations.

5. Species facilitation and plant zonation in coastal wetlands

The arrangement of plant communities in coastal wetlands exhibits zonation gradients from the seaside inland or toward estuarine marshes. Species competition, abiotic stress and herbivory are regarded as the regulators of communities across these gradients (Pennings and Bertness, 2001; Crain et al., 2004). Species facilitation is anticipated to extend the ecological realized niche of species, and thus expand species distribution or provided refuge for rare species of the community (Bruno et al., 2003). Bertness and Hacker (1994) revealed that *Jucus gerardi* facilitated the extension of *Iva frutescens* distribution into a more stressful environment in New England salt marshes. Hence, interspecific facilitation clearly extends the habitable zones of some species; meanwhile the intraspecific facilitation extends and regulates species zonation.

6. Species facilitation and diversity patterns in coastal wetlands

The intermediate disturbance hypothesis proposes that the relationship between species richness and the stress gradient is a humped-back shape (Sousa, 1979) and the stress tolerance ability of species and degree of competition faced by species are the most important underlining processes of species richness patterns in plant communities (Shea et al., 2004). On the other hand, Hacker and Gaines (1997) put forward a conceptual model including species facilitation to explain species richness patterns. This model proposed that species facilitation increases species numbers in intermediate, high stress environments and that stress tolerant species are released from intensive species competition in intermediate stress environments which increases species richness.

Recently, Michalet et al. (2006) proposed a new concept model to explain species richness patterns along stress gradients. The common point of the Hacker and Gaines (1997) and Michalet et al. (2006) models is that species facilitation could increase species diversity when facing harsh environmental stress (i.e., biotic and abiotic stress). This point is supported by many experiments. In northern New England salt marshes, *Triglochin maritime* surrounded themselves with elevated rings that ameliorated water-logging stress and harbored more species than neighboring bare spaces (Fogel et al., 2004). However, Michalet et al. (2006) pointed out that species facilitation cannot extend species distribution into very high stress environments, because above a threshold level of stress, the effect of species facilitation would gradually reduce with increasing stress levels and vanish at very high stress levels. They also proposed that the role of species facilitation on species richness patterns along stress gradients depends on the life-history strategy of both the benefactor and beneficiary. The Michalet et al. (2006) conceptual model, predicted that the impact of species facilitation protecting beneficiaries from competition is highest in the intermediate stress zones, while the impact of species facilitation increasing the stress tolerance of beneficiaries is highest at high stress levels. These impacts would increase the species

richness in intermediate and high stress zones. Xiao et al. (2009) employed simulation techniques to assess the impact of species facilitation on species richness patterns across stress gradients. They found that species facilitation indeed increased species richness in medium and high stress zones but not in very high stress zones, thus supporting the Michalet et al. (2006) model. On the other hand, from low to medium stress zones, species facilitation decreased species richness.

However, to reveal the relationship of species facilitation and species richness, more research on how species facilitation influences the humped-back shape of the stress gradient-species richness curve is needed, especially through experiments on natural plant communities along strong stress gradients and for longer periods of time. Coastal wetlands provide a perfect ecosystem to test these models because species composition is relatively simple and the stress gradient is strong.

7. Species facilitation and invasion in coastal wetlands

Invasion of exotic species into native plant communities presents a challenge to preserve local and regional species diversity. Invasions due to anthropogenic impacts are also an ecological problem for coastal wetland ecosystem (Gedan et al., 2009). For example, the invasive species *Spartina alterniflora* occupies large areas of southeast coast of China (Yuan et al., 2011) and *Phragmites australis* has invaded the east coast of North America. Both invasive species were introduced through human activity. To date, many hypotheses have been proposed to explain the invasion success of exotic species. Some of the species invasion hypotheses include: the natural enemy hypothesis, the evolution of increased competitive ability hypothesis and the novel weapon hypothesis. These hypotheses emphasize the effect of the absence of natural enemies; increased competitive ability in the absence of natural predators due to the ability to allocate more resources to growth and/or fecundity and biochemical interactions between native and invasive species, respectively (Callaway and Ridenour, 2004). Species facilitation has also been reported as an explanation for successful invasion of exotic species. Maron and Connors (1996) demonstrated facilitation of invasion of exotic weedy plants into disturbed Californian coastal prairies through soil enrichment by the nitrogen-fixing shrub *Lupinus arboreus*. Cavieres et al. (2008) found nurse cushion species (*Azorella monantha*), which is native to the high Andes of central Chile, also exhibited a facilitative effect specific to the invasive species, *Taraxacum officinale*. Tecco et al. (2006) revealed that the invasive species, *Pyracantha angustifolia* facilitated recruitment of both the native species, *Condalia montana* and the exotic species, *Ligustrum lucidum*.

In coastal wetlands, species invasions have been linked with human disturbances and eutrophication. Few studies have linked species facilitation with invasion. Battaglia et al. (2009) reported that the native, *Morella cerifera* facilitated seed spread and seedling establishment of the invasive, *Triadica sebifera* in a floating marsh, but impeded its further growth. Cushman et al. (2011) found native plant species protected the exotic plant, *Ehrharta calycina* from herbivory by black-tailed jackrabbits in a coastal foredune system of northern California. Thus, it is important to further our understanding of the positive and negative interactions between invasive species and native species in coastal wetland plant communities to improve the management of coastal wetlands.

8. Species facilitation and ecosystem function in coastal wetland

Productivity of plant communities is an important ecosystem function of coastal wetland which indicates ecosystem health. Here

we have focused on predictions of how species facilitation may influence productivity in coastal wetland plant communities. However, to the best of our knowledge, no studies linking species facilitation with productivity in coastal wetland plant communities exist. Thus, we propose a conceptual model to explain the relationship between species facilitation and coastal wetland community productivity based on studies of other ecosystems (Fig. 2). Our model proposes that direct interspecies facilitation can increase productivity of the plant community through diversity functions (e.g., species diversity or phylogenetic diversity; Valiente-Banuet et al., 2006; Maestre et al., 2010). These functions include niche complementarity (maximizing resource usage among species with different functional traits), sampling effects (increasing the probability of including dominant species with greater productivity in more diverse communities) or species facilitation (increasing survival of species and thus increasing numbers of individual plants) under a particular environmental stress.

Direct interspecies facilitation can increase species diversity (as discussed above) or even phylogenetic diversity (Valiente-Banuet and Verdu, 2007; Verdu and Valiente-Banuet, 2008), which would increase productivity of plant communities through the process of niche complementarity (Verdu et al., 2009). If the functional traits of the benefactor and the distantly related beneficiary are niche conservative, that is each species has distinct demands on the niche, the benefactor facilitates the distantly related beneficiary, thus species facilitation increase phylogenetic diversity of the plant community. Phylogenetically diverse communities can maximize resource use among species, and thus enhance functional complementarities to increase overall productivity of the community (Webb et al., 2002; Maherali and Kironomos, 2007; Cavender-Bares et al., 2009). Cadotte et al. (2008) found the phylogenetically diversity can even explain more of the variation in productivity of plant communities than species diversity and diversity of functional groups. This is likely because species and functional group diversity do not necessarily bring about functional trait diversity. However, if functional traits are not evolutionary niche conservative, benefactors may facilitate closely related species with different functional traits and enhance species diversity but not phylogenetic diversity in that community. In such cases, niche complementarity is still an important process of species diversity functions. On the other hand, sampling effects and species

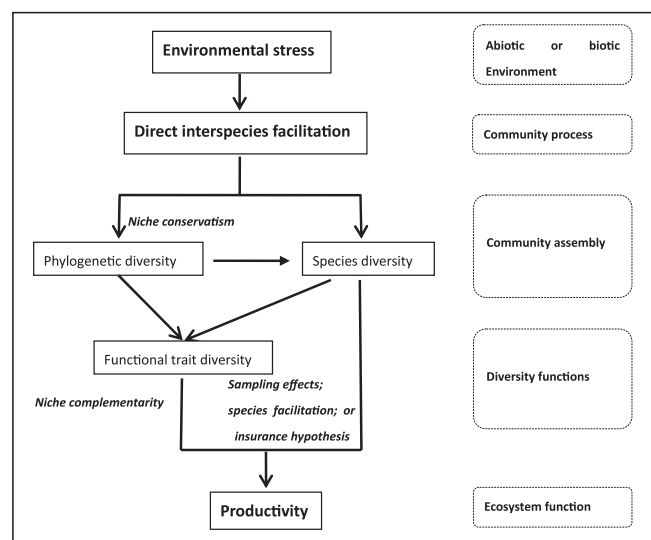


Fig. 2. Framework of interspecies facilitation and productivity of coastal wetland plant communities.

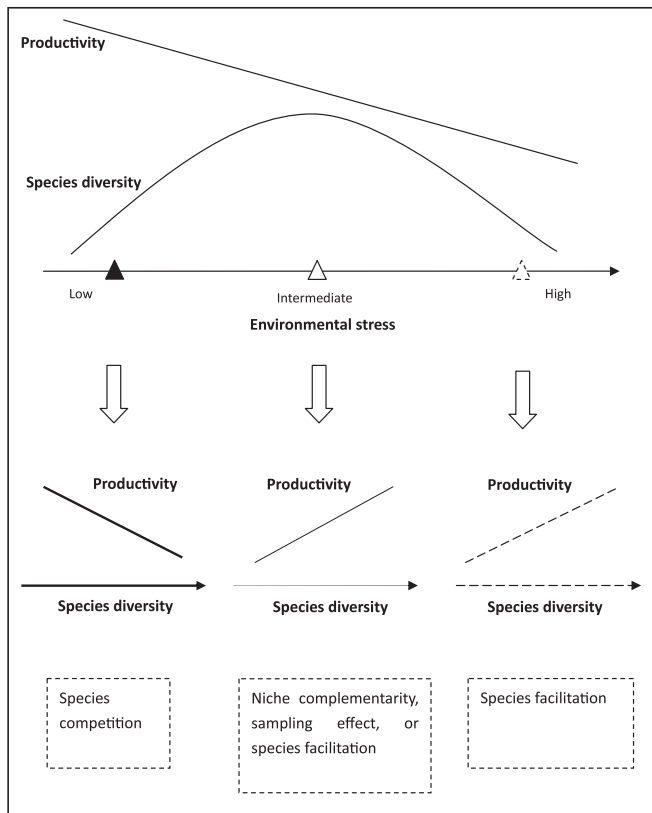


Fig. 3. Predictions of relationships between species diversity and community productivity along environmental stress gradients in coastal wetlands.

facilitation can also be central processes of species diversity functions through increasing productivity. Loreau and Hector (2001) and Mulder et al. (2001) have suggested methods to separate the effects of these processes leading to a positive relationship between species diversity and productivity.

When considering the interrelationships among environmental stress, productivity and diversity, we predict that environmental stress is the most important factor regulating productivity in coastal wetland plant communities and that productivity decreases as environmental stress increases along the environmental stress gradient of the coastal wetland. On the other hand, environmental stress and species diversity have a humped shape with positive or negative relationships depending on the level of environmental stress (Fig. 3). At low stress levels, species diversity has a negative relationship with productivity due to intense species competition. At intermediate stress levels, species diversity has a positive relationship with productivity due to niche complementarity, sampling effect and/or species facilitation. At this level of stress, phylogenetic diversity may be a better factor than species diversity to explain changes in productivity. At high stress levels, species diversity has a positive relationship with productivity due to processes of species facilitation. These predictions about the relationships between diversity and productivity are suggested to test in future studies.

9. Conclusions

Plant–plant competition and facilitation have been observed and reported in coastal wetland ecosystems and the balance between species competition and facilitation depends on environmental stress. Plant–plant facilitation is important for the establishments of species and thus affects community structure including species zonation, species diversity, phylogenetic diversity

and ecosystem functions (Fig. 3). The influence of species competition on plant communities is well-known, whereas, the influence of species facilitation on species diversity patterns and ecosystem functions in coastal wetland plant communities are poorly understood. Furthermore, plant–plant facilitation may increase spread of invasive species in coastal wetlands but also promote restoration of disturbed wetlands. Hence, the significance of facilitation for conservation and restoration is context dependent.

Authors contribution

Liwen Zhang formulated the idea and wrote the manuscript, and Hongbo Shao assisted with revising the manuscript.

Conflict of interest

None.

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