

Ecological and Evolutionary Misadventures of *Spartina*

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Abstract

Spartina species of the mid–low intertidal areas are powerful ecological engineers that are highly valued where they are native. Elsewhere, they overgrow native salt marsh and open intertidal mudflats, diminish biota, increase costs of managing wildlife, and interfere with human uses of estuaries. Huge efforts have been mounted to kill some populations of invading *Spartina*. All large *Spartina* invasions are by *S. densiflora* ($2n = 7x = 70$) or *S. alterniflora* ($2n = 6x = 62$) or hybrids between the hexaploid species ($2n = 6x$). Hybridization is a recurrent theme in *Spartina*; the allododecaploid *S. anglica* ($2n = 12x = 120$) and the hybrid swarm in San Francisco Bay arose through the introductions of *S. alterniflora* into the range of native *Spartina* species. The ancient hybrid *S. densiflora* also hybridized with native *Spartina* species. Hybridization promotes the evolution of highly invasive populations and hampers control efforts. Whether *Spartina*, native and not, would protect the shore as sea levels rise depends upon unimpeded areas for upward marsh growth and sufficient sediment, conditions that are often not satisfied.

1. INTRODUCTION

Maritime cordgrasses in the genus *Spartina* define the shorelines of estuaries and coastlines where they are native and where they have invaded. Natives of mid-latitude marshes, few if any species penetrate far into equatorial latitudes dominated by mangroves (Comeaux et al. 2012, Zhang et al. 2012). On the Atlantic temperate coasts of North and South America, vast intertidal areas are covered with monocultures of the tall dense stems of *S. alterniflora*. Higher on the intertidal plane, *S. densiflora* joins *S. alterniflora* in temperate South America. They are native to these coasts (Figure 1).

Two small-statured species are geographical outliers: *S. foliosa*, native to California, USA, and *S. maritima*, native to northern Europe and South Africa (Adams et al. 2012). *Spartina alterniflora* and *S. densiflora* have hybridized with both species every time they have been brought together (Section 3.2). The ecology and evolution of these species and hybrids are the central topics of our review.

Low intertidal *Spartinas* are powerful ecological engineers that shape the physical and biological environment (Strong & Ayres 2009). Their erect, stiff stems create drag, dissipate hydrodynamic force, reduce current velocity, and dampen wave height in estuaries and on low-energy shores where they grow (Bouma et al. 2010). Roots and rhizomes grow up into the mineral sediment that precipitates from tidal waters. Together, the mineral and organic materials elevate the salt marsh, and tidal flood and ebb carve channels through it, increasing relief and complexity of the habitat. These plants are foundation species, with substantial influence on productivity, communities, and food webs (Pennings & Bertness 2001).

Wherever these grasses are native, the high productivity and physical structure of intertidal *Spartinas* interact to support many heterotrophic species. A classic example is the trophic cascade with herbivorous snails, which, in high density, can defoliate *S. alterniflora* (Silliman et al. 2005). Carnivorous blue crabs suppress the numbers of snails, protecting the plants and the sediments, which can erode without cover by *S. alterniflora*. Drought increases salinity of marsh soils and renders *S. alterniflora* more vulnerable to the snails. The blue crabs range widely in the sea beyond the salt marshes, and heavy fishing of them could release the snails from top-down control. Another example of the strength of trophic forces concerns burrowing crabs that have become unusually



Figure 1

(Left) *Spartina alterniflora* at the southern limit of its North American range, Tamaulipas, Mexico. Mangrove is in background. Photo by Arturo Moro. (Right) *Spartina densiflora* in its native range, Mar Chiquita Biosphere Reserve, Argentina. Photo by Gary Williams.

abundant in areas where recreational fishing has depleted their predators (Altieri et al. 2012). Species interactions and food webs in areas where *Spartina* has invaded are treated throughout this review.

Spartina introductions began as early as the sixteenth century (Section 2), when *S. densiflora* from South America appeared on the Iberian Peninsula. Most purposeful introductions had the aim of terrestrializing salt marshes or protecting the shore from erosion and sea-level rise (Section 4). By and large, opinions changed from favorable to unfavorable as these powerful ecological engineers transformed open intertidal mud to tall, dense vegetation in the introduced areas. In France, the invasions of *S. anglica* and its hybrid predecessor *S. × townsendii* during the early twentieth century were known as the Green Peril as they covered the open mud at Mont Saint-Michel (Kahn 1973). Nonnative *Spartina* has negatively affected native species of plants, benthic invertebrates, fish, and birds. It has threatened native species, increased the difficulty and expense of managing wildlife, and interfered with human use of estuaries (Section 3). Multiple expensive control programs have followed large-scale invasions of nonnative *Spartina*. The world's largest invasion is in China, where *S. alterniflora*, brought from North America, is spreading rapidly and now occurs over 19 degrees of latitude (Sections 3.4.4 and 4.5). The invasive traits of this population are reminiscent of those of the hybrid swarm of *S. alterniflora* × *foliosa* in San Francisco Bay (SF Bay) (Section 3.4.2), as is the evolution of sentiment in China about the benefits versus costs (Section 4.5).

Although *Spartinas* and other salt marsh vegetation have contributed to the maintenance of shoreline equilibrium with sea level for thousands of years (Redfield 1972), they no longer do so in some regions of the world where humans dominate shorelines. Decreased sediment delivery rates and increased channelization (Morris et al. 2005), eutrophication that increases vegetation biomass leading to collapse of channel edges (Deegan et al. 2012), and excessive herbivory by burrowing crabs of cordgrass roots (Coverdale et al. 2012) can combine to degrade *Spartina*-dominated salt marshes. Sea-level rise has caused *S. alterniflora* to advance up the intertidal plane to overgrow other species, such as *S. patens*, *Distichlis spicata*, and *Juncus gerardii*, which were characteristic of the higher marsh (Donnelly & Bertness 2001).

The attenuation of wave force by intertidal *Spartinas* can protect the shore from erosion during storms and high tides (Strong & Ayres 2009). Moreover, roots growing upward into organic and inorganic sediments harvested from the tide can lead to positive feedback in marsh elevation (Morris et al. 2005, Bouma et al. 2010, Marani et al. 2013). This process has elevated the surface of salt marshes over large areas (Wang & Temmerman 2013) and leads some to expect protection of the shore as sea level rises (Zuo et al. 2012). However, such protection depends upon sediment availability sufficient to foster marsh elevation at a rate that matches sea-level rise as well as territory to support upward transgression of the marsh (Voss et al. 2013, Kirwan et al. 2012). Even the prodigious *S. alterniflora* cannot elevate marshes without abundant inorganic and/or organic sediment as well as space to grow upward. Dikes, berms, roads, and other structures above marshes impede upward growth and thwart protections that the *Spartina* and other marsh plants could provide. The plants drown in marshes that grow upward more slowly than sea level rises.

2. TWISTED SISTERS: *SPARTINA* ORIGINS

2.1. Thirteen Original Species

Spartina is a small genus within the grass subfamily Chloridoideae, characterized by a base chromosome number of $x = 10$, a preference for saline habitats, and C4-type photosynthesis. All species are polyploid (Ainouche et al. 2012). The genus is split mostly into two clades (**Figure 2**).

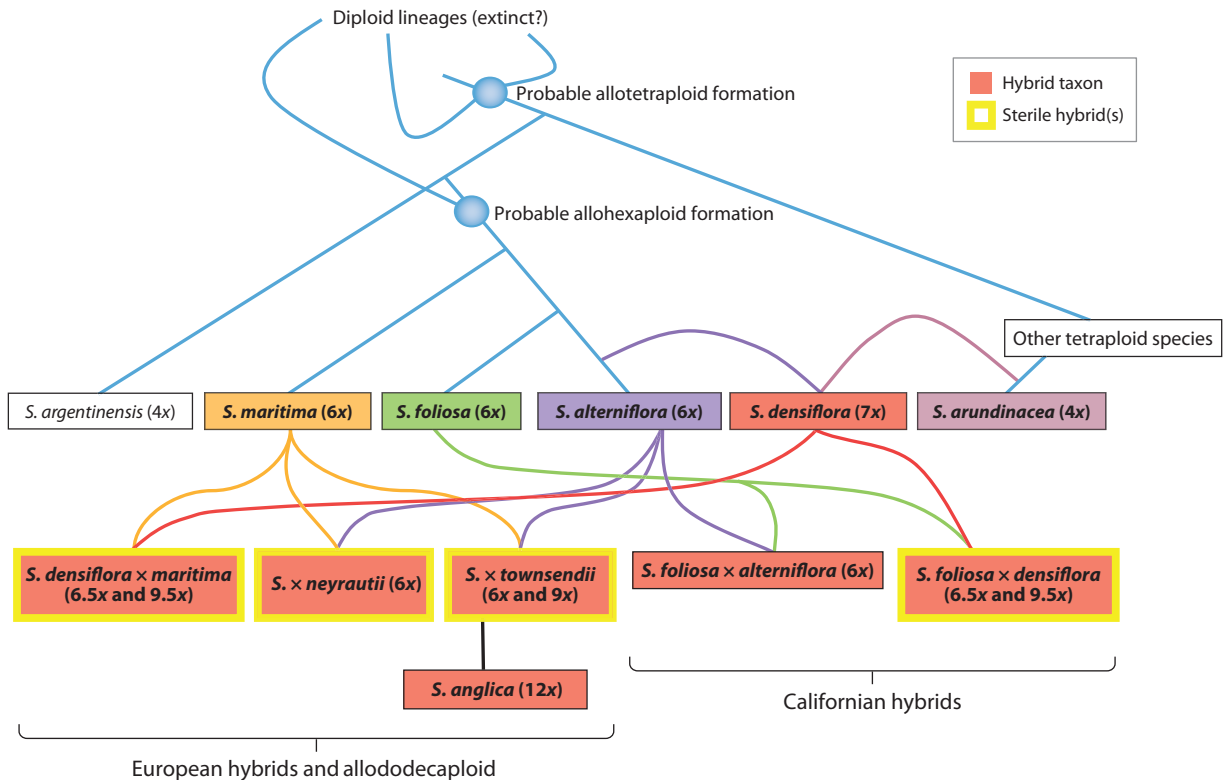


Figure 2

Twisted, reticulate phylogeny of *Spartina* with ploidy in parentheses; taxa in bold are hybridizing or hybrid taxa. Each species has color-coded lines leading to its hybrid taxa. Redrawn from Ainouche et al. (2009).

A hexaploid clade ($2n = 6x = 60, 62$) contains *S. maritima* and the closely related sister species *S. alterniflora* and *S. foliosa*, and a tetraploid clade ($2n = 4x = 40$) contains *S. argentinensis*, *S. arundinacea*, *S. bakeri*, *S. ciliata*, *S. cynosuroides*, *S. gracilis*, *S. patens*, *S. pectinata*, and *S. spartinae*.

The tetraploid *S. argentinensis*, at the base of the hexaploid clade, shares a common ancestor with the hexaploid clade. *Spartina densiflora* is heptaploid ($2n = 7x = 70$) and the product of an ancient hybridization between tetraploid seed parent *S. arundinacea* and hexaploid *S. alterniflora* or their ancestors (Fortune et al. 2008). Reticulate evolution by interspecific hybridizations formed the heptaploid and likely the hexaploid *Spartina* species (Ainouche et al. 2012).

2.2. *Spartina* Polyploidy

As many as 70% of angiosperms are polyploids (Masterson 1994), and paleopolyploids date back to the origin of Angiosperms (Jiao et al. 2011). Autopolyploids are species that have duplicated genomes. Allopolyploids are interspecific hybrids with duplicated genomes. When the disadvantages of polyploidy—disrupted nuclear and cellular volumes, aberrant mitoses and meioses, and gene regulation instabilities (epigenetics)—are overcome (Comai 2005), fertility in early-generation polyploids increases rapidly owing to natural selection against aneuploid gametes (Ramsey & Schemske 2002). This allows the new species to join “the evolutionary fray as efficient competitors. . .” (Comai 2005, p. 836). The advantages of polyploidy include gene redundancy



Figure 3

A raft of seed-bearing inflorescences of *Spartina alterniflora* floating on Willapa Bay, WA. The raft contains thousands of viable seeds. Three inflorescences from the raft are held in hand.

that buffers genetic load, heterozygosity that confers vigor, and the opportunity for duplicated genes to evolve in novel ways. Polyploids differ from their progenitors in a broad spectrum of traits (Ramsey & Schemske 2002).

3. INVASIONS AND HYBRIDIZATIONS

3.1. Propagules and Failed Introductions

Spartina spreads by seed that floats on the tide (Strong & Ayres 2009, Sloop et al. 2011; **Figure 3**). The roots of most fragments are laden with mud, sink, and die. *Spartina anglica* probably invaded France from its site of hybrid origin in England as seed that floated across the English Channel to La Baie des Veys. It spread southward through Brittany by floating seed after its detection in 1906. In contrast, the vigorous but sterile F_1 hybrid from which *S. anglica* arose has not spread widely from its origin site. Hence, seed production, rather than clonal spread or fragmentation, is the key to *Spartina* spread.

Most introductions of all kinds of organisms fail, some survive without spreading, a small fraction thrives to spread and invade, and some species invade sporadically (Zenni & Nuñez 2013). Although much evidence has undoubtedly disappeared, a few failed and failing *Spartina* introductions are known. Species in the tetraploid clade rarely become invasive. One of the most serious cordgrass invaders worldwide, *Spartina anglica*, collapsed after widespread planting in China (An et al. 2007, Zuo et al. 2012), failed in 22 out of 44 introduction sites around the world (Ranwell 1967), and became extinct after surviving twentieth century introductions to the Falkland Islands and Tierra del Fuego (Orensanz et al. 2002). It also did not spread from its introduction site in SF Bay (Hogle 2011b). No introductions of any *Spartina* species are known to have succeeded on the Atlantic coasts of North and South America, where the natives of this genus thrive. Remarkably, the most notorious cordgrass invader of all, *S. alterniflora*, failed to spread in either England or France after its introductions in the early nineteenth century

(Marchant & Goodman 1969). It sets seed neither in England (Marchant 1968) nor in the recently discovered population in South Africa (Adams et al. 2012).

3.2. Hybridization in *Spartina*

Interspecific hybridization has occurred every time *S. densiflora* or *S. alterniflora* has been introduced into the range of *S. foliosa* and *S. maritima*. The results include sterile F₁s involving *S. densiflora*, a new allopolyploid species, *S. anglica*, and introgressing hybrids between sister species *S. alterniflora* and *S. foliosa*. All *Spartina* invasions are due to the species *S. densiflora* or *S. alterniflora* or to hybrids between *S. alterniflora* and congeners in the hexaploid clade (Section 2). Given the allopolyploid origin of *S. densiflora*, the most invasive *Spartina* taxa contain some or all the genome of *S. alterniflora* or its ancestor.

3.3. *Spartina densiflora*: Introductions and Hybrids

Hybrids between introduced *S. densiflora* and native species in the hexaploid clade have occurred in Europe and California. Hybrids might have occurred without human help in Argentina, where *S. densiflora* grows naturally with other native *Spartina* species (Section 3.3.4).

3.3.1. Gulf of Cádiz: hybrids. *Spartina densiflora* was introduced in the sixteenth century from South America to the Gulf of Cádiz on the Iberian Peninsula, where *S. maritima* is native (Castillo et al. 2010). It spread to form vast monocultures along the Atlantic coast and into the Mediterranean Sea. It repeatedly hybridized with the European native *S. maritima*, and the hybrids have thrived. F₁ hybrids with a 1*n* contribution by each species (~65 chromosomes) as well as hybrid triploids (~94 chromosomes) containing 2*n* from *S. maritima* (2*n* = 60) and 1*n* from *S. densiflora* (1*n* = 35) are in these populations. The triploids grew in the low marsh close to *S. maritima* and had *S. maritima* as a seed parent, whereas diploid plants had the chloroplast DNA (cpDNA)—denoting maternal origin—of *S. densiflora* and grew in the middle marsh near *S. densiflora*. The hybrids did not set seed. *Spartina maritima* does not frequently set seed in Europe, whereas *S. densiflora* sets profuse seed everywhere it is known to occur (Castillo et al. 2010).

The Iberian *S. densiflora* hybrids spanned the intertidal gradient from low marsh, where *S. maritima* grows, to middle-high marsh, where *S. densiflora* reaches its highest cover (as in its native range). Transplanted hybrid plants grew as well as or better than the parental species at most elevations. Hybrid plants were found in five marshes in three estuaries. Although four of the five marshes contained only a few hybrid individuals, over 100 hybrid plants grew at Guadiana estuary, suggesting that the hybrids need not be fertile to pose conservation and invasion threats. Origin of a new fertile allopolyploid species would lead to rapid hybrid spread (Castillo et al. 2010). Little prospect is held for control of the vast *S. densiflora* invasion in Iberia, and hybrids probably will continue to arise there (Jesus Castillo, personal communication).

3.3.2. Humboldt Bay, CA: no hybrids. The next known introduction of *S. densiflora* was to Humboldt Bay, CA in the mid-nineteenth century. This was inferred to be an incidental consequence of lumber trade with Chile, where *S. densiflora* is native. By 1999, *S. densiflora* had spread to ~320 ha and 94% of the salt marshes in Humboldt Bay and was threatening the federally endangered Menzies' wallflower, *Erysimum menziesii*, and the beach Layia, *Layia carnosa*. An expensive campaign of mowing, eradication, and herbicide applications succeeded in removing only 14 ha out of 688 ha (2%) in one area of Humboldt Bay (Pickart 2005), suggesting how difficult complete elimination would be. *Spartina densiflora* sets on average 2,000 viable seeds per plant annually, and

its high fecundity contributes to the pessimism about eradicating this invasion (Kittelson & Boyd 1997). No native or other species of *Spartina* occur in Humboldt Bay and no hybridization has occurred there.

3.3.3. San Francisco Bay: hybrids. In 1972, *S. densiflora* and *S. anglica* were deliberately introduced to Creekside Park, Marin County in northern SF Bay, CA during restoration (Faber 2000). *Spartina alterniflora* was introduced to SF Bay at about the same time (Section 3.4.2). In the mid-1990s, unusual *Spartina* plants, intermediate between the native *S. foliosa* and the alien *S. densiflora*, were found there spreading by rhizomes among low-elevation *S. foliosa* and *S. anglica* and growing in tufts in the high marsh near dense tufts of *S. densiflora*.

The unusual plants were F₁ hybrids of *S. foliosa* ($2n = 6x = 62$) and *S. densiflora* ($2n = 7x = 70$); they were sterile, and most had 66–67 chromosomes [$1n$ (32) + $1n$ (35)]. Three hybrids had a few alleles and/or the cpDNA of *S. alterniflora* denoting three-species hybrids that likely originated from *S. alterniflora* × *foliosa* hybrids, as both seed and pollen donors, crossing with *S. densiflora*. Two plants were triploids containing $2n$ *S. foliosa* and $1n$ *S. densiflora*; one triploid plant had the cpDNA haplotype of *S. alterniflora*, whereas the other triploid had the cpDNA haplotype of *S. foliosa* (Ayres et al. 2008a).

Salinity tolerance of some of these hybrids exceeded that of the parental species. None of these hybrids produced seed in the field, and they produced only shriveled anthers in a greenhouse experiment (Ayres & Lee 2010). However, by 2009 *S. densiflora* × *foliosa* hybrids were found in 23 out of 32 marshes where *S. densiflora* and *S. foliosa* grew together (Hogle 2011a). None but the Creekside Park plants were evaluated for chromosome number or seed fertility, leaving open the question of whether a new hybrid species had evolved via allopolyploidization in California. Intense herbicide and eradication (digging up roots) and mowing campaigns have reduced *S. densiflora*, its hybrids, and *S. anglica* close to elimination from SF Bay (Hogle 2011b). The total coverage of *S. densiflora* in SF Bay was much less than that in Humboldt Bay.

In both California and Spain, repeated creation of hybrid seed in the flowers of the parental species and its potential export could contribute to a serious conservation threat even without a speciation event that would confer fertility to the hybrid taxa. In addition, fertile triploids are known from the genus; *S. densiflora* is $2x$ (*S. arundinacea*) + $1x$ (*S. alterniflora*), or their ancestors.

3.3.4. *Spartina longispica*: a natural hybrid? *Spartina longispica* is a curiosity known only from 19 herbarium specimens mostly from the Rio de la Plata marshes of Uruguay and Argentina. It was inferred to be a hybrid of *S. alterniflora* and *S. densiflora*, both natives of Argentina estuaries (Bortolus 2006).

3.4. *Spartina alterniflora*: Introductions and Hybrids

3.4.1. European F₁ hybrids: *S.* × *townsendii* and *S.* × *neyrautii*. The sole native species in Europe is *S. maritima*. *Spartina alterniflora* was introduced in the early 1800s to Southampton Water, England (Ayres & Strong 2001) and to southwest France, near Hendaye (Baumel et al. 2003). In England, by 1870, a sterile F₁ hybrid had arisen at Hythe that was called *S.* × *townsendii*. In France, in 1892 a new sterile hybrid was discovered near Hendaye that was called *S.* × *neyrautii*. *Spartina* × *townsendii* grows in a vigorous population at Hythe in Southampton Water (Renny-Byfield et al. 2010) and was spread widely around the world in the nineteenth century (Ranwell 1967). *Spartina* × *neyrautii* is quite rare, has not spread, and is not known to have given rise to any other taxon (Baumel et al. 2003). Both hybrids have 62 chromosomes. Morphologically *S.* × *townsendii* is intermediate between *S. alterniflora* and *S. maritima*, whereas *S.* × *neyrautii* is

similar to *S. alterniflora* (Marchant 1967, Baumel et al. 2003). *Spartina* × *townsendii* gave rise to the important invader *S. anglica*.

Genetic differences between *S.* × *townsendii* and *S.* × *neyrautii* indicated separate hybridization events in England and France. The *S. alterniflora* portion of *S.* × *townsendii* nuclear DNA is identical to that observed in one plant, perhaps the only surviving original *S. alterniflora* plant in England, in Southampton Water (Marchant 1968, Ayres & Strong 2001). The *S. alterniflora* portion of *S.* × *neyrautii* is identical to *S. alterniflora* co-occurring locally with that hybrid (Baumel et al. 2003). The genetic uniformity of *S. maritima* and the introduced *S. alterniflora* has thwarted determination of the frequency with which F₁ hybrids formed, perhaps only once in France and once in England (Ayres & Strong 2001, Baumel et al. 2003, Yannic et al. 2004).

The maternal parent of both of these hybrids was *S. alterniflora*. They have the same cpDNA haplotype (Baumel et al. 2003), probably B2. This is the most commonly recovered *S. alterniflora* cpDNA haplotype in a large part of the source area of *S. alterniflora* between Delaware and Maine, USA and the only haplotype known for Europe (Blum et al. 2007).

3.4.1.1. *Spartina anglica*: allododecaploid. *Spartina anglica* is a fertile allododecaploid ($2n = 12x = 120, 122, 124$) species that arose from *S.* × *townsendii* at Hythe in Southampton Water in England in the 1880s. *Spartina anglica* is about as tall as *S.* × *townsendii*, but has thicker, longer rhizomes, with only half the tiller density of *S.* × *townsendii* (Marchant 1967). It sets abundant seed by both selfing and outcrossing (Dethier & Hacker 2005). The nuclear genotype and cpDNA haplotype of *S. anglica* were identical to those of *S.* × *townsendii* (Ayres & Strong 2001, Baumel et al. 2001, Salmon et al. 2005, Ferris et al. 1997).

Salmon et al. (2005) examined the parental species, F₁ hybrids, and *S. anglica* for genetic and epigenetic changes. They found *S. anglica* exhibited over 99% of the diagnostic amplified fragment length polymorphisms (AFLPs) fragments present in *S.* × *townsendii*. However, 30% of the parental methylation patterns (epigenetic) were altered in the F₁ hybrids, and the altered pattern was maintained after genome doubling in *S. anglica*, suggesting that the hybridization was the driving force behind the reorganization. This level of epigenetic change, accompanied by the evolution of gene expression evaluated at the transcriptomic level (Chelaifa et al. 2010), could account for the pronounced morphological differences between the French and English F₁ hybrids. These results, although limited to this single case, suggest that the particular individuals participating in an interspecific hybridization can have a large influence on morphological and evolutionary outcomes. Further investigations of *S. densiflora* hybrids using these methods could test the generality of this hypothesis for the genus.

It is likely that *S. anglica* arose from the union of unreduced gametes from *S.* × *townsendii*, perhaps only once. However, the triploid bridge may have played a part in the speciation. Marchant (1968) reported finding a nonaploid plant of $2n = 9x = 90$ at Hythe in 1967 composed of $2n$ *S. alterniflora* and $1n$ *S. maritima*. This nonaploid could have arisen via mechanisms of triploid formation described in **Figure 4** (orange box). He also found two possible progeny from a nonaploid that had 75 and 76 chromosomes [$1n$ (45) + $1n$ (30)], suggesting the nonaploid was fertile. Two nonaploid plants of the same composition were found more than 40 years later at Eling, Marchwood, six shoreline miles upstream from Hythe (Renny-Byfield et al. 2010). Clones live long lives, and aging these plants is not possible. Were they present in the mid-1800s, the triploid bridge could have provided an additional route to the formation of *S. anglica* and explained the chromosome races of *S. anglica* described by Marchant (1968). In addition, the question arises as to the origins of triploids in *S. densiflora* hybrids, as backcrossing to a new allopolyploid species (**Figure 3, VI**) could not occur in Spain or in California. In England, Spain, and California, the triploids contained $2n$ of the hexaploid seed parent, suggesting unreduced eggs (**Figure 3,**

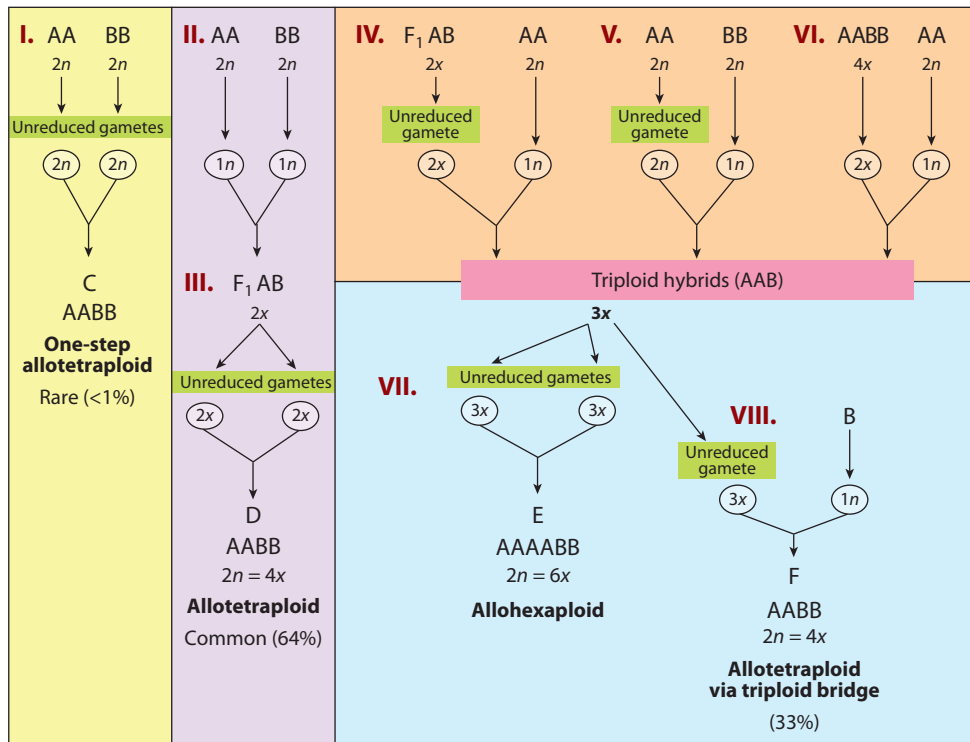


Figure 4

Mechanisms of allopolyploid formation between diploid species A and B (genotypes AA and BB); gametes are encircled, unreduced gametes are indicated by green boxes, and ploidy is listed directly under the genotypes.

V) as the route to triploid formation. *Spartina* hybrids present the opportunity to investigate the relative importance of triploids and homoploid hybrids on allopolyploid formation (see the sidebar, Mechanisms of Allopolyploid Formation) within a phylogenetically constrained system.

3.4.1.2. *Spartina anglica* introductions. This species was deliberately introduced widely around the world in the early twentieth century (Strong & Ayres 2009), most recently to China (An et al. 2007) and inadvertently to Fraser River, BC, Canada (Williams et al. 2010).

3.4.2. San Francisco Bay: hybrid swarm. The US Army Corps of Engineers introduced *Spartina alterniflora* into SF Bay during the early 1970s (Faber 2000, Strong & Ayres 2009). It grew intermixed with native *S. foliosa*, which is short, with sparse tillers and shallow root mats, and does not grow far down the intertidal gradient. *Spartina alterniflora* is much taller than the native and has dense tillers and a deep root mat, and it grows far down the intertidal gradient (**Figure 5**).

Hybridization of *S. alterniflora* and *S. foliosa* created a backcrossing hybrid swarm that probably began soon after the introductions to Alameda Island (Sloop et al. 2011) and Hayward (Faber 2000). Both species were seed parents of hybrids (Anttila et al. 2000). F₁ hybrids were fewer than 4% of over 1,700 genetically tested hybrids, leading to the conclusion that the initial interspecific hybridization was rare and backcrossing among hybrids and with the parents, rather than frequent F₁ formation, drove the invasion (Ayres et al. 2008b) (see **Supplemental Figure 1**; follow the **Supplemental Material link** from the Annual Reviews

Supplemental Material

MECHANISMS OF ALLOPOLYPLOID FORMATION

The simplest route to a new allopolyploid species is by way of unreduced parental gametes uniting in the zygote (**Figure 4, I**). This is rare, as unreduced gametes are produced at a rate of less than 1% (Ramsey & Schemske 1998). More commonly, the first step is the formation of F_1 hybrids; then unreduced F_1 gametes, produced at a frequency of 27.5%, unite to form an allopolyploid (**Figure 4, II to III**). These two routes account for ~65% of new allopolyploids. An important additional route, which could account for 33% of allopolyploid formation in outcrossing species, is the triploid bridge pathway (**Figure 4, VIII**). In this pathway, an unreduced gamete from a triploid unites with a reduced gamete of the “missing” parental species to form a balanced allotetraploid. The union of two unreduced triploid gametes would produce an allohexaploid (**Figure 4, VII**). Triploids are formed (**Figure 4, IV to VI**) by an unreduced gamete from the F_1 hybrid backcrossing with a reduced parental gamete (**Figure 4, IV**), or an unreduced parental gamete, likely ova, uniting with a reduced gamete from the other parent (**Figure 4, V**), or a reduced gamete from an allotetraploid uniting with a reduced gamete from a parental species (**Figure 4, VI**).

home page at <http://www.annualreviews.org>). In an intensely studied marsh, hybrids produced 400 times the pollen of native *S. foliosa*, and over 90% of seed produced was hybrid. Between 1998 and 2004, over 80% of seedlings recruiting into restoration sites, native marshes, and open mudflats were hybrid; 18% were native *S. foliosa*; and only a single seedling of *S. alterniflora* was found, leading to the conclusion that hybrids, not *S. alterniflora*, were driving the invasions of these diverse habitats (Ayres et al. 2008b).

Hybrids were highly variable in height, culm width (Ayres et al. 2004a), lateral expansion rates (Ayres & Strong 2010a), flower production, seed production, pollen viability and pollen production (Ayres et al. 2008b), and salinity tolerance (Pakenham-Walsh et al. 2010) (**Figure 6**).

Some hybrids were transgressive and exceeded both parental species in these traits (Ayres et al. 2004a). Flowering phenology was also highly variable, and the hybrid population spanned the temporal valley in flowering between the early flowering native and later flowering invader,



Figure 5

Spartina alterniflora introduced from the Atlantic growing among native *S. foliosa*, California cordgrass. Blackie's Pasture, Tiburon, Marin Co., CA. The city of San Francisco is behind the fog bank in the background.



Figure 6

Variable morphology of hybrid *Spartina alterniflora* × *Spartina foliosa*. San Bruno Marsh, San Mateo Co., CA.


promoting introgressive hybridization (Zaremba 2001). High pollen production by hybrids generated positive feedback in hybridization rate, and just a few hybrids could sire a substantial fraction of hybrid seed in native *S. foliosa*. This created the unusual situation of a genetic threat by a rare invader to a common native (Anttila et al. 1998, Ayres et al. 2004b). Modeling of the hybridization process and backcrossing predicted the extinction of both parental species as distinct genetic entities (Hall et al. 2006). Clonal longevity of the parents draws the extinction probabilities out from several decades to centuries (**Figure 7**).

Although the parental species and early generation hybrids lacked self-fertility, some later-generation hybrids set large numbers of self-pollinated seeds that germinated in profusion over



Figure 7

Hybrid *Spartina alterniflora* × *Spartina foliosa* at San Bruno Marsh about one year after the photo in **Figure 6**.

 Supplemental Material

hundreds of meters around the parents. A few of these self-pollinating plants showed outbreeding depression when outcrossed (Sloop et al. 2009). Local recruitment by selfed progeny created fine-scale temporal and spatial genetic structure. We found evidence of at least two introductions of *S. alterniflora* from different source populations at Hayward and Alameda Island; hybrid plants and seedlings found at each site contained the genetic signature of each *S. alterniflora* source population, creating regional structure (Sloop et al. 2011) (**Supplemental Figure 2**).

Early research had lower resolution for *S. alterniflora* × *S. foliosa* hybrids than later work (Ayres et al. 1999, Blum et al. 2004, Sloop et al. 2011). We suggest that the traits of early invasive *Spartina* in SF Bay—attributed in these publications to *S. alterniflora* alone—were traits that had evolved in hybrids: high variability in pollen production and seed set (Anttila et al. 1998), self-fertility (Daehler 1998), and loss of inbreeding depression (Daehler 1999). It is our view that this variability was due to unrecognized hybrids, as more than 50% of plants collected in the early 1990s from the introduction sites were hybrids (Ayres et al. 1999). This perspective is consistent with the fact that the invasive but unhybridized *S. alterniflora* in Willapa Bay, WA retained high degrees of self-sterility for over 100 years while facing the same selection pressures for rapid spread as the invasive *Spartina* in SF Bay (Davis et al. 2004b, Section 3.4.3).

Considering that self-fertility was part and parcel of hybridization (Sloop et al. 2009), we suggest that the high selfing rates and low inbreeding depression seen as early as 1992 indicated that selfing hybrids were abundant by that time.

The rate of increase in area covered by hybrid cordgrass increased during its spread around SF Bay (Ayres et al. 2004a). We posit this was due to natural selection for vigorous, tall plants with high rates of lateral expansion and superior seed set, high pollen production, and selfing ability. However, selection is a two-way street. Beginning in 2004, herbicide treatment greatly reduced numbers of tall *S. alterniflora* and hybrids. The result was that short-statured hybrids, which resembled native *S. foliosa*, rose in relative frequency to all suspicious plants tested (see figure 1.7 of Hogle 2011a) (**Supplemental Figure 1**). Cryptic hybrids are revealed by molecular genetic techniques.

3.4.3. Willapa Bay, WA: no hybrids. *Spartina alterniflora* arrived at Willapa Bay, WA from the Atlantic on the transcontinental railroad during the last years of the nineteenth century. Seed and/or root fragments were incidentally mixed with iced, live oysters. The earliest populations of *S. alterniflora* were found in the seven areas of Willapa Bay where oyster growers cultivated the oysters from the trains (Civille et al. 2005). Large clones photographed in the 1940s would have been seedlings shortly after the trains began delivering oysters to Willapa Bay in 1894 (Dennis et al. 2011). At the peak in 2003, ~3,500 ha of *S. alterniflora* grew in the mudflats of Willapa Bay (Wash. State Dep. Agric. 2011).

Isolated clones received much less pollen and set much less seed than clones growing in dense meadows (Davis et al. 2004a) (**Figure 8**). Experimental pollen addition increased seed set of isolated but not meadow plants, consistent with self-infertility and suggesting an Allee effect of *S. alterniflora* (Davis et al. 2004b, Taylor et al. 2004). By contrast, a spatial analysis of *S. alterniflora* spread showed an influence of climate but no large-scale Allee effect (Buhle et al. 2012). Only isolated clones had survived control by 2008, and only 3 out of 61 set viable seed, consistent with the findings of self-sterility (Patten & Milne 2008, their table 3). The small colony of *S. alterniflora* in South Africa also sets no viable seed and is spreading by clonal expansion alone (Adams et al. 2012).

3.4.4. China: introduction and intraspecific hybrids? The world's largest invasion is in China (Zuo et al. 2012), where *S. alterniflora* from Florida, Georgia, and North Carolina were planted



Figure 8

Spartina alterniflora clones in Willapa Bay, WA. Each clone arose from a single seed. The most widely separated clones set little seed.

in a garden in 1979 (Xu & Zhuo 1985). Seeds from this garden were dispersed widely for the anticipated benefits of production of biomass, habitat for native species, shore protection, sediment capture and desalination, and agriculture on intertidal lands, *inter alia*. By 2007, *S. alterniflora* had established in 10 provinces and Hong Kong, covering more than 34,000 ha, ~10 times the extent of 3,500 ha at its peak in Willapa Bay, WA. In China, *S. alterniflora* extends over more than 19 degrees of latitude and about the same number of degrees of longitude from North Korea to Vietnam.

We can find no reference to a breeding program for *S. alterniflora* either at the introduction site in Lo Yuan Bay, Fujian Province or elsewhere. However, it is reasonable to infer that people disseminated the seed from the most vigorous plants. The tallest, densest *Spartina* that senior author D.R.S. and *Spartina* expert Steven Pennings (personal communication) have experienced in a combined 50 years of research with this genus the world over is in China. At places in China, height, density, and morphology of invading *S. alterniflora* are as highly variable from clone to clone as they were in the hybrid swarm that swept across SF Bay.

3.4.5. Rates of spread. Unhybridized *S. alterniflora* grew from ~3 to ~1,607 solid ha from 1945 to 2000 at a fairly constant rate in Willapa Bay, WA (Civille et al. 2005), giving a doubling time of ~5.3 years. In SF Bay, coverage of hybrid *S. alterniflora* × *foliosa* grew from ~5 ha in 1990 to ~814 ha in 2003, with a doubling time of about 1.6 years. As discussed in Section 3.4.2, self-fertile hybrids arose in SF Bay by the early 1990s. Their seed spread widely (Sloop et al. 2011), suggesting a contribution of self-fertility to the more rapid spread of SF Bay hybrids than of the unhybridized Willapa Bay *S. alterniflora*. In the Yangtze River of Jiangsu Province, China, coverage of *S. alterniflora* grew from 0.08 km² in 1985 to 137 km² in 2001 (Zhang et al. 2004), with a doubling time of about 1.5 years. We are intrigued by the possibility of the evolution of

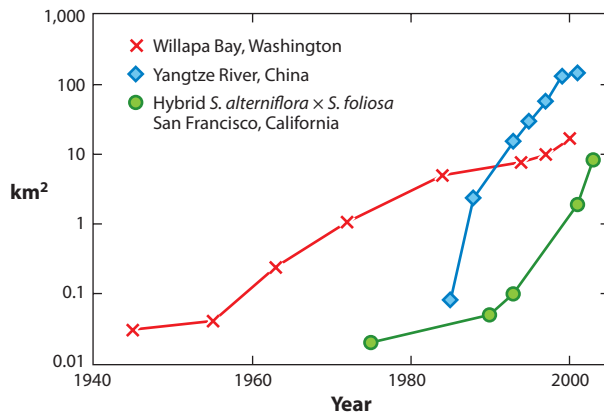


Figure 9

Coverage of three invasive *Spartina* populations through time. All of these invasions were aided by human dispersal. Willapa Bay, Civille et al. (2005); San Francisco Bay, Sloop et al. (2011); Yangtze River, China, Zhang et al. (2004).

self-fertility in China facilitated by crossing among the three provenances from the native range. In this case, intraspecific hybridization would have produced genotypes in China with particularly rapid spread (**Figure 9**).

4. CONSEQUENCES

The intention of most *Spartina* introductions was to terrestrialize salt marshes for human use or to protect the shore from erosion. In several places, opinions changed from favorable to unfavorable as these powerful ecological engineers transformed open intertidal mud to tall, dense vegetation that interfered with human uses of estuaries and increased the difficulty and expense of managing wildlife living in the invaded habitat. Concerted control programs have followed large invasions of nonnative *Spartina* in Australia (Weiss & Iaconis 2002), Tasmania (Kriwoken & Hedge 2000), New Zealand (Shaw 1999), Europe (Strong & Ayres 2009), and the west coast of North America.

4.1. Birds and Invasive *Spartina*

Invading *Spartina* overgrows intertidal mudflats, where migratory shorebirds feed upon the benthic infauna. The spread of *S. anglica* was correlated with reduced dunlin numbers in English estuaries (Goss-Custard & Moser 1988). Shorebird numbers were reduced by as much as 67% at the height of the *S. alterniflora* invasion of Willapa Bay, WA (Jaques 2002). Although meadows heavily invaded by *S. alterniflora* and untreated with herbicide were “rarely used,” birds increased greatly in areas from which *S. alterniflora* had been removed (Patten & O’Casey 2007). In contrast, dunlin numbers did not increase where *S. anglica* had naturally died, perhaps because the thick algal mats that followed discouraged the birds (Goss-Custard & Moser 1988).

Invasive *S. alterniflora* displaced *Scirpus*, *Phragmites*, and resident passerine birds that nest in these native plants in the Yangtze River estuary of China (Li et al. 2009, Gan et al. 2009). Estuarine specialist passerines were also reduced in numbers by this invasive cordgrass (Ma et al. 2011). At the same time, the migratory, threatened marsh grassbird *Locustella pryeri* has thrived by building nests upon invasive *S. alterniflora* in the Yangtze estuary near Shanghai, China (Ma et al. 2013). The complicated interaction of birds with invasive hybrid *Spartina* in SF Bay is described in Section 4.3.


4.2. Invertebrates and Invasive *Spartina*

The effects of invasive cordgrass on benthic invertebrate communities and food webs were well studied in SF Bay, CA in marshes invaded by hybrids (Grosholz et al. 2009). Plants in established meadows shaded the substrate and reduced light for microalgae. Belowground, *Spartina* biomass physically excluded burrowing invertebrates. These influences increased with the progress of the invasion. Greater complexity of the physical environment was found at the diffuse front of expanding clones, which enriched the biota; shade and root/rhizome biomass were low. As *Spartina* became denser, the base of infaunal food webs shifted from algae to detritus, favoring subsurface deposit-feeders and detritivores at the expense of grazers, suspension feeders, and surface deposit-feeders. Similar mechanisms reduced species richness and abundance of infauna in *S. anglica* marshes in Australia (Cutajar et al. 2012), but the effect of *S. anglica* upon invertebrates and fish in Tasmania was virtually zero (Hedge & Kriwoken 2000), perhaps because the study was conducted at the diffuse front of the invading *Spartina* (Cutajar et al. 2012). In northern Europe, dead *S. anglica* in the mud depressed infaunal abundance and lessened food availability for higher trophic levels, especially birds (Tang & Kristensen 2010). In the Yangtze estuary, invasive *S. alterniflora* alters the trophic structure of infaunal invertebrate communities and reduces food for a number of bird species (Li et al. 2009).

4.3. The Epic in San Francisco Bay

A farrago of invasion, control, and conservation continues to play out in the SF Bay estuary, where attempts to preserve native *S. foliosa* make control of the hybrids much more difficult than control of *S. alterniflora* in Willapa Bay, Australia, or New Zealand, where there were no native species of *Spartina*. Nests of rare Alameda song sparrows, *Melospiza melodia*, had fledging rates reduced by 30% in hybrid cordgrass compared with native vegetation (Nordby et al. 2009). The open intertidal mud of the estuary is by far the most important foraging habitat for migrating shorebirds on the Pacific coast of North America. Over 900,000 birds of 38 species rely upon the infauna of these mudflats for food in the spring (Stralberg et al. 2010). A loss of between 27% and 80% of foraging areas was estimated to be the result of unchecked spread of hybrid *Spartina*. An intensive herbicide campaign begun in 2004 greatly reduced the extent of hybrid *Spartina* and eased the threat to migratory shorebirds (McBroom 2012).

In a surprising twist, the success in rescuing shorebird habitat by killing hybrid *Spartina* has caused populations of the endangered, nonmigratory California clapper rail (CLRA), *Rallus longirostris obsoletus*, to fall. This bird, a salt marsh specialist restricted to SF Bay, probably was recovering numbers in hybrid *Spartina* that it had lost during destruction of salt marshes in the SF estuary during the first half of the twentieth century. (See **Supplemental Figure 3**.) Hybrid *Spartina* marshes have supported some of the highest densities of CLRAs (Hogle 2011a). Even with reservations that research was insufficient to establish causality, the correlation between removal of hybrid *Spartina* and CLRA decline was sufficiently compelling to cause a shift from only killing hybrid *Spartina* to replanting native *S. foliosa* and other species of native marsh plants while elements of the herbicide campaign continued (McBroom 2012). In her blog on January 24, 2013, Ingrid Taylar discusses the conservation efforts for the CLRA (<http://birdnote.org/blog/2013/01/california-clapper-rail-study-usgs>). Artificial floating islands for breeding were another tactic used to rebuild CLRA numbers. The Invasive *Spartina* Project cost \$21 million between 2000 and 2012 (M. Latta, personal communication). Hybrid *Spartina* remains adjacent to where it was removed and where revegetation is proceeding (see table 1 of Hogle 2011b). One possibility is that hybrids might reinvade via floating seed and proliferate in the remaining and replanted

 Supplemental Material

S. foliosa by the same processes that drove the invasion of the original hybrid swarm (Ayres & Strong 2010b). The South Bay Salt Pond Restoration Project (<http://www.southbayrestoration.org/>) also manages habitat that could face invasion from the hybrid *Spartina* that remains in SF Bay.

4.4. Willapa Bay, WA: Elimination, Almost

Oyster growers expressed concern as early as 1939 about *S. alterniflora* overgrowing the mud where these valuable animals are cultured in Willapa Bay (Sayce 1990). During the 1980s, groups opposed to herbicides were effective in delaying control of *S. alterniflora* despite worries about negative effects of the rapidly spreading cordgrass upon native species, wildlife management, hydrology, boating, shore access, and oyster culture (Hedge et al. 2003). In 1995, the Washington State Department of Agriculture assumed leadership of the control program. The combined efforts of the State of Washington, the Willapa Bay National Wildlife Refuge, tribal owners of intertidal lands, oyster growers, and other private parties led to repeated herbicide treatment, mowing, and mechanical crushing of *S. alterniflora* in Willapa Bay, WA. Coverage continued to grow until 2003 when ~3,600 ha of dense *S. alterniflora* grew distributed over ~23,000 ha of mudflats with another ~4,000 ha at elevations above open mud in Willapa Bay (Wash. State Dep. Agric. 2011). Intensified efforts and replacement of glyphosate with imazapyr herbicide (Patten 2002) led to rapid decrease and elimination of all but a few hectares of *S. alterniflora* by 2011 (Bennett 2011). (See **Supplemental Figure 4.**) Smaller infestations of *S. alterniflora*, *S. anglica*, *S. densiflora*, and *S. patens* at other areas in Washington State are being reduced in parallel with the Willapa Bay effort (Wash. State Dep. Agric. 2011). The total cost of the control effort in Willapa Bay through 2011 was ~\$30 million with additional resources expended against cordgrasses in other tidewaters of the state (M. Wecker, personal communication).

Supplemental Material



Figure 10

A woman practicing mariculture in an area under invasion by *S. alterniflora* at Zhangjiang Estuary, Fujian Province, China. Photo by C.S. Yang.

4.5. China

Invasive *Spartina* is in the process of transforming vast areas of mudflats into salt marshes along the entire coast of China, with enormous ecological, social, and economic implications. From an engineering point of view, multiple authors have touted the introduction as a success in poldering, creating fodder, sediment capture, desalination, and agriculture on intertidal lands in China (Zuo et al. 2012). Recent assessments from an ecological point of view show a change in perspective reminiscent of that in the other places where non-native *Spartina* spread widely. Invasive *S. alterniflora* threatens Chinese biodiversity, mudflats, mariculture, fishing, and mangroves, which are valued for protection from storms and for biological treatment of wastewater (An et al. 2007, Ding et al. 2008, Li et al. 2009, Wu et al. 2009, Zuo et al. 2012, Zhang et al. 2012). In Fujian Province, *S. alterniflora* overgrows open mud, which hampers mariculture (Zhang et al. 2012). Mangroves, which protect the shore from typhoons, are invaded by *S. alterniflora* and prevented from regenerating (Figure 10).

SUMMARY POINTS

1. Maritime *Spartinas* are potent ecosystem engineers that create costs to wildlife and human uses of shores where they invade. Protection they might afford against sea-level rise depends upon unimpeded high shoreline and abundant sediment supply, both of which are hindered by human occupation of the shore.
2. Invasion rates depend upon seed set. Self-fertile species and hybrids spread most rapidly. Self-fertility arose in hybrids of *S. alterniflora* and *S. foliosa* in San Francisco Bay. The traits promoting invasion can evolve in contemporary time.
3. Hybridization within the hexaploid clade, and between the hexaploid clade and *S. densiflora*, has always occurred when one of these species is introduced into the other's range.
4. All invasive and/or hybridizing *Spartina* descended from, and contain part of the genome of, *S. alterniflora* or its ancestor.
5. Natural experiments on the interplay of invasion, hybridization, and (potentially) speciation are currently running in places where *Spartina* is invading.
6. Mechanical removal and herbicides provide *Spartina* control in some circumstances. These are very expensive.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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