

Diversity and Distributions

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Front cover: The cryptic invasion, over 200 years, by the iconic cordgrass *Spartina alterniflora* challenges what scientists have long considered pristine native coastal environments along the Atlantic coast of South America, where it often dominates the sea-land margin (top and bottom), and where macro-regional key components of the salt marsh community such as the ecosystem engineer crab *Necohelice granulata* (right), feed, reproduce and interact. Bortolus et al. (pages 1267–1283, this issue) found that early records of this cordgrass remained hidden in mycological collections with reference to the presence of a fungus (*Siderostium*) growing on it (left). Photo credits: A. Bortolus.

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Reimagining South American coasts: unveiling the hidden invasion history of an iconic ecological engineer

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ABSTRACT

Aim The smooth cordgrass *Spartina alterniflora* is an iconic ecological engineer that has inspired some of the more insightful concepts and perspectives in modern theoretical ecology and environmental management, from population to community and ecosystem scales. Although it is currently considered native over more than 100 degrees of latitude along the Atlantic coast of the Americas, we challenge the default assumption that this cordgrass is native to South America, and propose an alternative hypothesis that it was introduced in the 18th or early 19th century by human activity.

Location World-wide.

Methods We applied nine criteria that have been proposed for the recognition of non-native species. These criteria consider the historical, biological, geographic, dispersal, ecological and evolutionary evidence that classically underpin the distinctions between native and non-native species.

Results Our results strongly support the hypothesis that *S. alterniflora* is not native to South America. Herbarium collections, historical floristic descriptions and extensive literature reports clearly indicate that *S. alterniflora* was absent prior to the early 1800s in South America. *S. alterniflora* shows a reduced morphological, ecological and physiological variability along the South American coast and demonstrably increased in both regional extent and abundance over the 20th century.

Main conclusions We conclude that what are now extensive *S. alterniflora* marshes in this region were probably bare mudflats and that there have been vast unrecorded and thus overlooked shifts in bird, fish and invertebrate biodiversity, and immense shifts in algal vs. detritus production, with the concomitant trophic cascades that these changes imply. Our results change the way we perceive “natural” coastal ecosystems on the Atlantic coast of South America as a whole. Indeed, most South American coastal marshes currently are what we term “ecological mirages” – illusions that have seriously hampered our ability to recognize the nature of pre-existing native ecosystems.

Keywords

ballast, biological invasions, coastal biogeography, historical ecology, introduced, *Spartina alterniflora*.

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INTRODUCTION

The smooth cordgrass, *Spartina alterniflora* Loiseleur-Deslongchamps, 1807 (Poaceae; Peterson *et al.*, 2014a,b), is an abundant salt marsh plant of temperate and subtropical coasts (Strong & Ayres, 2013) with occasional tropical

infringement (Chapman, 1977). This iconic species has inspired some of the more insightful concepts and perspectives in modern ecology, including the study of plant zonation processes, negative vs. positive interactions in community ecology, outwelling–pulsing events in holistic ecology and top-down vs. bottom-up processes in ecosystem

ecology (Weinstein & Kreeger, 2000; Silliman *et al.*, 2009; Strong & Ayres, 2013). Smooth cordgrass has further figured prominently in global studies in environmental engineering and conservation relative to coastal accretion and marsh creation, and it is one of the ten best studied invasive plants world-wide (see Table S1, Pyšek *et al.*, 2008). Widely regarded as an aggressive non-native species around the world (including Europe, the North American Pacific coast, China, New Zealand and South Africa), *S. alterniflora* rapidly reshapes marine ecosystems, altering coastal geomorphology, biodiversity and primary and secondary productivity, resulting in strong cascading socio-economic impacts in recipient regions (Weinstein & Kreeger, 2000; Strong & Ayres, 2013).

Spartina alterniflora is also one of the most widely distributed marsh halophytes in the western Atlantic Ocean, where it ranges over more than 100 degrees of latitude from Canada to Argentina (Saint-Yves, 1932; Chapman, 1960, 1977; Day *et al.*, 1989; Adam, 1993; Mitsch & Gosselink, 2000; Blum *et al.*, 2007; Ainouche *et al.*, 2009; Mora-Olivo & Valdés-Reyna, 2011; Saarela, 2012; further historical records are available at <http://www.theplantlist.org>), albeit with an important gap between 10° and 19° N from northern South America to southern Mexico, a geographic break encompassing all of Central America. While studies of salt marsh dynamics, and of *S. alterniflora* specifically, are deeply rooted in North America (Mitsch & Gosselink, 2000; Weinstein & Kreeger, 2000), salt marsh ecology is a relatively young discipline in South America (Bortolus & Schwindt, 2007). Along the Atlantic coast of South America, the smooth cordgrass, *S. alterniflora*, and the austral cordgrass, *S. densiflora* Brong., form a predominant seascape feature and have been the basis of numerous quantitative and experimental studies elucidating the structure, community dynamics and energy flow of coastal marsh ecosystems (e.g. Costa & Davy, 1992; Cagnoni, 1999; Costa *et al.*, 2003; Silliman & Bortolus, 2003; Botto *et al.*, 2005; Canepuccia *et al.*, 2007; González Trilla *et al.*, 2009; Pratolongo *et al.*, 2010; Idaszkin & Bortolus, 2011; Idaszkin *et al.*, 2011; Negrin *et al.*, 2012).

In these subtropical and temperate salt marshes of South America, *S. alterniflora* produces up to $1450 \pm 276 \text{ g m}^{-2}$ of aboveground biomass (Cunha *et al.*, 2005; González Trilla *et al.*, 2009) and may cover 70% or more of the surface, together with the co-dominant *S. densiflora* and the pickleweed *Sarcocornia* spp. (Seeliger, 1992; Bortolus, 2006; Isacch *et al.*, 2006; Bortolus *et al.*, 2009). In Argentina, for example, many square kilometres of *S. alterniflora* may completely dominate the sea-land margin, with only scattered populations of other intertidal halophytes (Vinci, 2004; Isacch *et al.*, 2006; Bortolus *et al.*, 2009).

Despite the ecological importance of *S. alterniflora* in Argentine coastal communities, it appears that the possibility of its historic absence from South America has never been questioned (Parodi, 1919; Chapman, 1977; Zuloaga & Morrone, 1999; Costa *et al.*, 2003; Strong & Ayres, 2009, 2013; Marangoni & Costa, 2012; Negrin *et al.*, 2013), despite the history, noted above, of its successful invasion around

the world throughout the 19th and 20th centuries. Carlton (1996, 2003, 2009) predicted that many species amenable to global transport by human activity for centuries have been mistakenly interpreted as native, leading to significant misinterpretations of the evolutionary history and ecology of many communities and ecosystems. In noting that the North American opossum shrimp (mysid) *Neomysis americana* (S.I. Smith, 1873) (introduced by ballast water to South America) had become the major food item for juvenile fish in the Río de la Plata on the Uruguay–Argentina border, but had passed without comment as a non-native species, Carlton (2011a) remarked, ‘It is difficult to begin to imagine how many other overlooked *Neomysis*-like case histories have occurred over the past 30 years, let alone the past 300 years’.

Given the striking propensity of *S. alterniflora* to be a successful invader of considerable plasticity, we challenge the default assumption that this cordgrass is native to the southwest Atlantic Ocean, and propose an alternative hypothesis that it was introduced by human activity. We further ask what the implications are of considering *S. alterniflora* to be non-native relative to fundamentally changing our understanding of the evolution and ecology of South American coastal ecosystems.

METHODS

To address the hypothesis that *S. alterniflora* may owe its presence in South America to relatively recent anthropogenic transport, we applied the criteria proposed by Chapman & Carlton (1991, 1994) for the recognition of non-native species. These criteria consider the historical, biological, geographic, dispersal, ecological and evolutionary evidence that classically underpin the distinctions between native and non-native species. To search for applicable and reliable data and records (see Bortolus, 2008a, 2012), we conducted extensive searches in personal, regional and specialized institutional libraries, as well as the multidisciplinary electronic databases Scopus and Web of Science. We also searched floras and herbarium collection databases, both virtual (Biodiversity Heritage Library, Internet Archive Books, Open Library, The Plant List, Tropicos, Global Plants, Harvard University Herbaria, Herbario Nacional of the Muséum National d’Histoire Naturelle of France, National Herbarium of The Netherlands, The New York Botanical Garden Virtual Herbarium) and actual (Instituto de Botánica Darwinion, Herbario Gaspar Suarez-UBA, Herbario Nacional de Plantas Vasculares-MACN, Herbario del Instituto de Recursos Biológicos-INTA Castelar). We used the search terms ‘*Spartina*’, ‘*alterniflora*’, ‘*brasiliensis*’ (a synonym of *alterniflora*; see Appendix S1 in Supporting Information), ‘cordgrass’, ‘espartina’, ‘espartillo’, ‘halophyte’, ‘marisma’, ‘marsh’ and appropriate combinations. The list of keywords was longer when searching in older diaries and reports of expeditions conducted along South American coastal environments, further including more general terms such as ‘coastal’, ‘shore’, ‘estuary’, ‘mud’, ‘flat’, ‘intertidal’, ‘swamp’ and ‘grass’, and we included

Spanish, Portuguese, French, German and English translations when appropriate. We also used ‘*alternifolia*’, a common misspelling of ‘*alterniflora*’. Nomenclature follows The Plant List (botanical) and WoRMS (zoological) online databases (accessed on March 2015).

RESULTS

Spartina alterniflora was described from the port city of Bayonne, in south-western France, based on a specimen collected in 1803 at the Adour river estuary (see Saarela, 2012, p. 30; for further type information). Subsequent work [beginning with the speculations of Bromfield (1837) and Hooker (1837) and summarized by Mobberley (1956)] established that *S. alterniflora* was native to the western Atlantic Ocean, where Clayton had collected it sometime prior to 1753 in Virginia (Linnaeus, 1753; as *Dactylis cynosuroides* var. β ; see also Mobberley, 1956, pp. 472, 491 and 533). The first description of species in locations where they are not native (in this case, the type locality of *S. alterniflora* being in France) is common (Bortolus, 2008a; Carlton, 2009) and in the 1800s was particularly linked to the phenomenon of species being accidentally transported to countries with a higher density of taxonomists than the ones from which the species originated (and for the latter, in many cases, where no taxonomists existed at all). As discussed below, *S. alterniflora* was introduced to Europe, probably in the late 1700s, accidentally in solid ballast, in dunnage or as a cargo contaminant. It was collected by William Borrer in southern England in 1829 at Southampton (in the River Itchen, Hampshire) (Stapf, 1908), although first formally reported by William Bromfield, who thought he was the first to discover it at that locality in 1836 (Bromfield, 1837; p. 1095; we follow Sprague, 1933; in dating the Bromfield papers). Bromfield (1837, 1850, p. 1096, footnote) cited local knowledge that *S. alterniflora*, long used for home roof thatching, may have been present as early as about 1816 (as also noted by Marchant, 1967, pp. 5–6).

For the history of *S. alterniflora* in South America, we summarize below the results of our studying the nine attributes that serve to potentially distinguish native from non-native species.

Attribute 1: appearance in regions where not previously found

Spartina alterniflora was collected in South America (Fig. 1) beginning in 1817 and later years, and starting an introduction process, we synthesize below and for which historical and naturalistic details are presented in chronological order in Appendix S1. The first Europeans travelling across southern South American coastal lands since the early 1500s were not academic or trained naturalists but missionaries and illiterate adventurers, military personnel, and merchants (Hicken, 1923; Vervoorst, 1967). These first travellers in the pampas and coastal marshes repeatedly mentioned the

‘espartillo’ (cordgrass) or ‘paja de techar’ (roofing grass; De Angelis, 1836), both of which appear to be (for the reasons discussed below) classical regional allusions to needle grasses (*Stipa* spp.), dropseeds (*Sporobolus* spp.) or the native cordgrass *Spartina densiflora* (Arechavaleta, 1894; Spegazzini, 1905; Bortolus, 2006).

Spartina densiflora was used as roof-building material by natives and Spaniards because of its compact, resistant and long-lasting structure and its wide distribution, noted in the regional maps, with a large number of Estancias and country sites called ‘espartillar’ or ‘espartillo’ (Vervoorst, 1967, p. 139 and plate XLIV #2). *Spartina alterniflora* is a notably taller, greener and softer plant, with wider and longer leaves than the native *S. densiflora*. We did not find any records suggesting that the *alterniflora*-type morphology was recorded or mentioned in historical plant descriptions anywhere on the South American coast. It seems highly unlikely that, for instance, the early travellers riding across the discoloured coastal landscapes of the Argentinean Pampas (Fig. 2), and explicitly concerned with locating usable pasture land (Falkner, 1774; De Angelis, 1836), would not have noticed and remarked on the presence of conspicuous *S. alterniflora* grasslands, if these had been present. Indeed, the strong contrast in colour and shape compared to indigenous plants permitted botanists to quickly notice the introduction of *S. alterniflora* in other regions of the world (see Kew Bulletin, 1907, p. 193). Moreover, considering that this species has been historically important for rural economies as a satisfactory forage ‘greedily eaten by horses and cattle...’ that ‘...affords good pasturage for out-door stock, and is becoming valuable and valued as a manure’ (Elliott, 1821, p. 96; describing South Carolina and Georgia usages; see also Bromfield, 1850; Kew Bulletin of Miscellaneous Information, 1907; Rousseau, 1945; Burkholder, 1956; Chapman, 1960; Settle *et al.*, 1998), the chances of it being overlooked or ignored are little.

In all sites, of course, *S. alterniflora* may have been present for some years prior to the first collections we note here; we are not arguing that this plant did not exist in a given country the year before the first collection. Rather, the evidence indicates that the earliest surveys – decades or centuries before these first records – did not discover *S. alterniflora*, in contrast to its collection sometime before the 1750s in North America. Rarely, in invasion biology, is a species first encountered during the year of its actual introduction, because of well-known lags in population growth (Crooks & Soulé, 1999; Carlton, 2003). Thus, a newly inoculated population may require some years to grow to levels at which a species will be first encountered in general survey work (as opposed to targeted searches for a specific species). We address in the Discussion, below, an alternative hypothesis that *S. alterniflora* may have been a rare native plant, the modern-day abundance and geographic expansion of which is due to habitat changes, climate change or other factors.

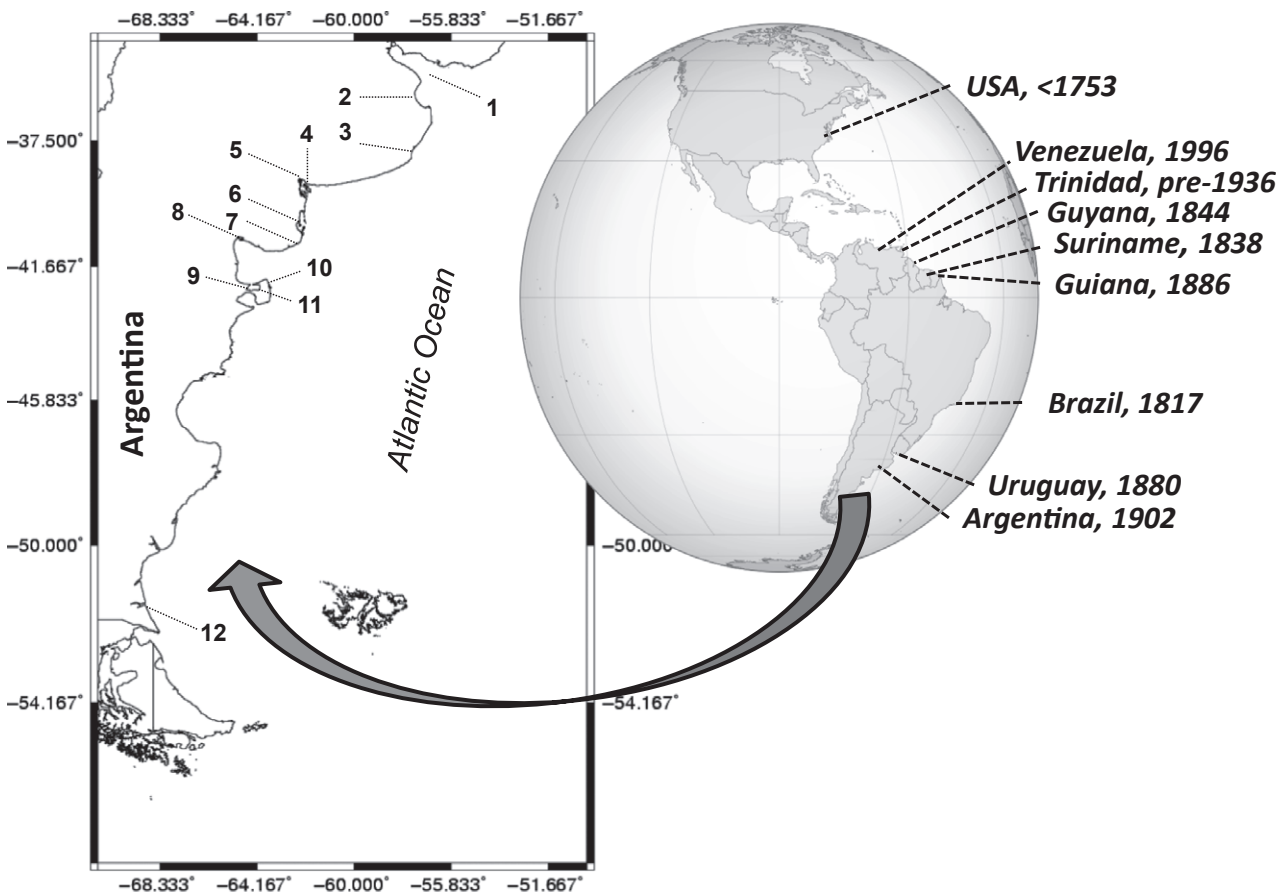


Figure 1 *Spartina alterniflora* key distribution sites and earliest collection dates (Appendix S1). Right: first collection dates recorded across the Americas. Left: major salt marsh areas associated with *S. alterniflora* along the Argentinean coast: 1, Río de La Plata estuary; 2, Samborombón Bay; 3, Mar Chiquita coastal lagoon; 4, Punta Alta; 5, Bahía Blanca estuary; 6, San Blas Bay; 7, Río Negro estuary; 8, San Antonio Bay; 9, Riacho; 10, Fracasso; 11, Valdes Peninsula; and 12, Río Gallegos estuary.

Attribute 2: initial expansion of geographic range subsequent to introduction

The dearth of South American naturalists in the early to mid-1800s did not permit detailed or regular monitoring of the geographic expansion of most non-native species. Nevertheless, early South American records (Appendix S1) may suggest a steady expansion of range from Rio de Janeiro, if this was the first port where *S. alterniflora* became established. Thus, *S. alterniflora* may have first spread to the north, arriving on the coasts of Suriname and Guyana by the 1830–1840s, or within 20–30 years of its introduction in Brazil. To the south, *S. alterniflora* was detected about 60 years later, in 1880, in Uruguay, and only about 20 years thereafter, it had reached Argentina (1902; Fig. 1, Appendix S1).

While lack of pre-1880s records (e.g. in French Guiana or Uruguay) may be an artefact of collecting history in those countries, long, multidecade delays in the coastal expansion of non-native species, regardless of the apparent availability of active or passive dispersal vectors, are not uncommon. Thus, while vectors may have been available (as discussed under attributes 3 and 8 below) for the coastal spread of

S. alterniflora after the early 1800s, a delay in establishment until the late 19th and early 20th centuries to the south of Brazil may reflect any of a number of common phenomena and processes in invasion ecology, including lack of a sufficiently large inoculum, a mismatch of habitat at the site of propagule release and failure to reproduce after initial establishment due to specific weather or climatic events. Even species with a much higher probability of post-invasion dispersal than *S. alterniflora* can remain restricted to a given site for decades. For example, the Australasian serpulid polychaete *Ficopomatus enigmaticus* (Fauvel, 1923), which has planktotrophic larvae of at least several weeks duration (Kupriyanova *et al.*, 2001), remained in San Francisco Bay, California (where it was abundant), from the 1920s to the 1990s before being detected elsewhere on the California coast (Heiman *et al.*, 2008). The Chinese clam *Potamocorbula amurensis* (Schrenck, 1861), which also has long-lived planktotrophic larvae, remains established and very abundant in San Francisco Bay, where it has been for over 25 years, but has not spread elsewhere yet (JTC, pers. obs.). Many processes impact the spread of introduced species, often delaying their progress (or increase in abundance) for decades (e.g.



Figure 2 South American *Spartina* landscapes and cattle grazing effect. Upper left: the contrasting colours of the *Spartina densiflora* (light brown higher band) and *Spartina alterniflora* (dark green lower band) zones in South American salt marshes are intense throughout the year, as a consequence of their highly contrasting phenotype and physiology (photograph from Riacho marsh, Valdes Peninsula). Upper right: close ups of dense patches of *S. densiflora* (above) and *S. alterniflora* (below) from Riacho marsh. Bottom: cattle grazing on *S. alterniflora* at Loros salt marsh (Patagonia, Argentina) can reshape the landscape by notably depleting the aboveground plant structures (circled close up). Horses and native guanacos also feed on *S. alterniflora*. Photograph credits: A. Bortolus.

Bortolus, 2008a, p. 116). *Spartina alterniflora* has continued to expand its range along the southern South American coast, from the Negro River estuary, where it was first detected in 1912 (Hauman, 1913), to the Valdes Peninsula, where it was first detected in 2001, across the San Matías Gulf (Fig. 1; Bortolus *et al.*, 2009; Idaszkin *et al.*, 2011).

Attribute 3: association with human-mediated mechanisms of dispersal

Spartina species have long been associated with a number of human-mediated dispersal mechanisms (e.g. Bryce, 1936). We consider five such mechanisms here: dry ballast, dunnage, hay or similar media, commercial oyster importations, and intentional importation of *Spartina* species for coastal erosion and shore stabilization management.

As early as the first half of the 19th century, Bromfield (1837) and Hooker (1837) speculated that solid (dry) ballast (see Carlton, 2007, 2011b) or dunnage ('packing material in stowing the hold'; Bromfield, 1850, p. 262) could have transported *S. alterniflora* from North America to Europe. Hooker (1837) particularly noted the association, in this regard, of *S. alterniflora* with, at the time, solely seaport locations in England and France. Similarly, although on the Atlantic coast of North America *S. alterniflora* shows a continuous distribution through both rural and urban sites (Mobberley, 1956; Adam, 1993; Mendelssohn & McKee, 2000; also note Hooker's (1837, p. 1096) very early comment along the same lines), in South America this species is particularly concentrated in

areas historically used as major harbours and ports including the Orinoco and Amazon estuaries, Rio de Janeiro, La Plata River estuary and Samborombón Bay, Bahía Blanca estuary, San Blas Bay, Negro River estuary and San Antonio Bay (Fig. 1, Martyn, 1934; Mobberley, 1956; Isacch *et al.*, 2006; Schwindt *et al.*, 2014). Overall, these patterns for *S. alterniflora* in Europe and South America, as well as for the introduced populations of the austral cordgrass *S. densiflora* in California (Spicher & Josselyn, 1985) and Chile (Bortolus, 2006; Fortune *et al.*, 2008), agree well with the hypothesis that seeds and vegetative fragments were long transported by ships.

That plants from overseas were regularly invading South American coastal systems via ocean commerce has long been recognized. Schomburgk (1848, p. 792) wrote, '... da nicht nur unsere Cerealien, sondern auch grosse Quantitäten Heu aus Europa nach Britisch-Guiana gebracht werden, wodurch eine bedeutende Menge europäischer Unkräuter und Grasarten heimisch geworden sind' ['... not only our cereal, but also large quantities of hay are brought from Europe to British Guiana, whereby a significant amount of European weeds and grass species have settled']. In an 1874 expedition that was one of the earliest contributions to the recognition of alien plant invasions in the south-west Atlantic Ocean, Berg (1877) enumerated 64 species of 'plantas europeas que se hallan como silvestres' ['European plants found growing wild'] in the Buenos Aires Province and Patagonia, which equalled the number (65) of native species; most of the former were found 'near the Rio Negro estuary', a major commercial port area.

Whether importations of hay (harvested from near-shore communities), or possibly even importations of *Spartina* hay, may have played a role in the introduction of *S. alterniflora* from Europe to South America is not known. We have found no records of *Spartina* associated with the history of the hay industry that mention South American locations. While *S. alterniflora* has a long history of intentional transplantations (for managing shore stabilization to prevent coastal erosion) around the world (Bryce, 1936), we also find no records of this for South America (but see Orensanz *et al.*, 2002, p. 134; for an account concerning *Spartina anglica*). Once present, however, various workers have discussed how *S. alterniflora* was deliberately moved and planted within a country, for example, British Guiana (Bartlett, 1908; Martyn, 1934). Finally, long-distance interoceanic or transcontinental transport of *Spartina* species, including *S. alterniflora*, as dunnage with commercial oysters has also been invoked (Stapf, 1908; Scheffer, 1945; Frenkel & Boss, 1988), but we know of no such introductions to South America, including from regions where *S. alterniflora* might have been used for such packing material.

Attribute 4: association with other introduced species

This attribute reflects the common observation that introduced species are often (but by no means always) clustered in similar habitats. Thus, species of uncertain origin (questionable endemicity) that are largely restricted or most abundant in habitats where many other introduced species are found may themselves prove to be non-native, with proper investigation. Not surprisingly (given the native status that we question for *S. alterniflora*), the extent of plant invasions in South American Atlantic salt marshes is not well known, making it a challenge to fully assess this attribute. Thus, the native status of certain South American salt marsh species of, for example, *Sarcocornia*, *Salicornia* and *Suaeda* (Amaranthaceae), which are often associated with *S. alterniflora*, remains unknown, and these may have been introduced from Europe or elsewhere (Gibert, 1873; Berg, 1877; Zuloaga & Morrone, 1999; Alonso & Crespo, 2008). Of no small related interest would be data on the historical biogeography of the abundant arthropod (insect and crustacean) fauna of South American marshes, by which also to judge the scale of invasions in those guilds.

This noted, non-native invertebrates are known from *S. alterniflora* marshes in Argentina, and we suspect the same is true all along the South American coast. In Argentina, the Asian orange-striped anemone *Diadumene lineata* (Verrill, 1869), the North American barnacle *Balanus glandula* Darwin, 1854 and non-indigenous species of oysters in the genus *Crassostrea* are all found on *S. alterniflora*, or in *S. alterniflora* marshes (Orensanz *et al.*, 2002; Excoffon *et al.*, 2004; Borges, 2005; Civile *et al.*, 2005; Molina *et al.*, 2009; Schwindt *et al.*, 2009; Mendez, 2013). All of these species,

however, invaded *Spartina* marshes long after this plant was established in Argentina; these invertebrate records do not indicate or imply a common introduction event or process, except for further indicating the high vulnerability of these southern salt marshes to marine invasions.

Attribute 5: prevalence in or restriction to new or artificial environments

As noted above, *S. alterniflora* is often found along the South American coast in locations that were or are now highly disturbed, especially major harbours and ports. Such sites converted what were aboriginal estuaries, lagoons and river mouths to new, highly urbanized, artificial environments, highly conducive to invasion by weed-like species such as *S. alterniflora*. These altered environments near dense human population centres may further be characterized by increased nutrient loads if not eutrophication, a phenomenon that may favour non-native over native salt marsh species (Bertness *et al.*, 2002; Tyler *et al.*, 2007), 'such that species invasions are more likely in marshes impacted by nutrient pollution' (Gedan *et al.*, 2009).

In turn, recent studies have shown that *S. alterniflora* rapidly colonizes new and artificially modified environments in Bahía Blanca estuary where human activities have reshaped the coastal landscape with an estimated increase of almost 50000% (from 1.3 to ~630 ha in 38 years) in land filling and dredging activities across the estuary (Mazzon *et al.*, 2012; Pratalongo *et al.*, 2014). Through analysis of satellite images and aerial photographs from 1967 and 2005, it has been estimated that ~66% of the *Sarcocornia perennis* marshes and ~65% of the halophytic steppes were lost. Within this same period and estuary, *S. alterniflora* showed an increase of 360% (from 215 to 774 ha) on lands that formerly were bare mudflats (Mazzon *et al.*, 2012; Pratalongo *et al.*, 2014).

Other locations with increasing abundance of *S. alterniflora* are Riacho and Fracasso marshes (Valdes Peninsula, Argentina, Fig. 1), where unplanned land filling, coastal roads and urbanization of the coast have altered the local geomorphology and often reshaped entire coastal landscapes and tidal creeks (Fig. 3).

Attribute 6: relatively isolated populations with restricted distribution (compared to distribution of native species) followed by local spreading and increase in abundance

Here we consider whether *S. alterniflora* (1) originally existed as isolated populations with a restricted distribution and abundance within a given country, but has since been documented to clearly increase in abundance, and (2) remains in other regions as scattered and patchy populations, as also compared to native species. Early records indicate that *S. alterniflora* was originally far less abundant and more restricted in distribution in certain countries than it is now.

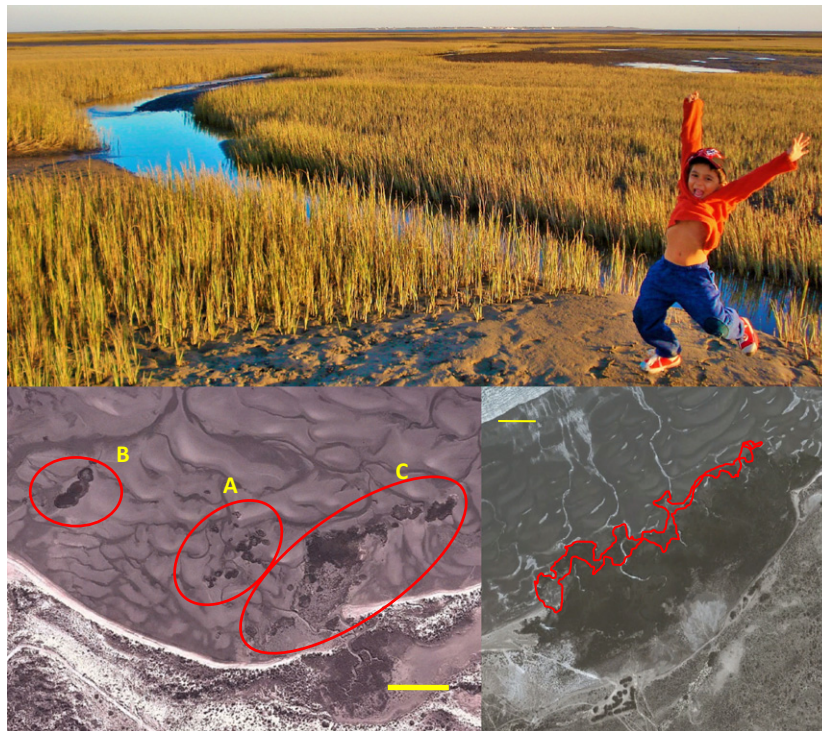


Figure 3 The cordgrass *Spartina alterniflora* colonizes the low marsh and mud flat areas previously devoid of vegetation in several sites along the Patagonian coast of Argentina. Above: a large monospecific *S. alterniflora* marsh is found in northern San Antonio Bay where, one century before, there may have been only bare mud flats. The complete absence of the tall *Spartina* phenotype makes it possible to see the distant bare mudflat patches and the San Antonio Oeste city in the background and encourages eco-touristic incursions (May 2009; photograph credits: A. Bortolus). Below: Enclosed areas mark *S. alterniflora* beds formed during the last 40 years in Riacho (left) and Fracasso (right) marshes (Google Earth accessed by March 2013). Letters mark different stages of the mud flat colonization by *S. alterniflora*: newly established patches (A), merging patches (B) and consolidated beds (C). Yellow scales: 100 m.

In Suriname, Pulle (1906) was unable to find *S. alterniflora* in 1902–1903 along the Saramacca River. Nearly one century later, Judziewicz (1990, pp. 602–603) reports *S. alterniflora* as a ‘widespread’ and ‘fairly common’ species for this general region.

In Guyana, Schomburgk (1847) found *S. alterniflora* to be ‘by no means abundant’ in Georgetown circa 1844, but by circa 1929–1933, Martyn (1934) found it (as *S. brasiliensis*) to ‘play a very considerable part in the primary colonization of the rising mud banks’, providing photographs of luxuriant meadows of *S. alterniflora* in Georgetown.

In Brazil in 1817, Raddi (1823) apparently did not find *S. alterniflora* to be notably common or abundant. Raddi made it clear when a species he described was abundant or not using expressions such as ‘Frequentissima in collibus herbosis proximis Rio-Janeiro’ [‘very frequent in the grassy hills near Rio Janeiro’] or ‘invenitur in Monte Corcovado, at non frequenter’ [‘found on Corcovado Mount, but not often’]. The absence of such comments accompanying Raddi’s description of *S. brasiliensis* suggests that the smooth cordgrass was not particularly abundant or sufficiently notable to Raddi to make it worthy of comment. Today, in the Rio de Janeiro region, *S. alterniflora* forms dense monospecific stands commonly reaching 25 m wide and 1000 m long,

and it is a first colonizer of bare mudflats in front of the mangrove forests along the Brazilian shore (Schaeffer-Novelli *et al.*, 1990; Lacerda *et al.*, 1997; da Silva Attolini *et al.*, 1997). Indeed, it is often the first species one sees when looking at the land from the sea.

In Argentina, there is a notable shift in the history of the descriptions of the abundance of this species. Many years after the early records by Spegazzini and Hauman, *S. alterniflora* was still considered by expert botanists as a ‘rare species for Argentina’ (Parodi, 1919, p. 30), while its relatives *S. densiflora* and *S. ciliata* were noted as abundant and widespread across the region. In contrast, by the late 20th century, *S. alterniflora* started to be consistently mentioned as one of the ‘principal marsh species’ that usually occupies most of the intertidal (Costa & Davy, 1992, pp. 183 and 191) with a solid cover dominating the wetter portion of the tidal zone (West, 1977, p. 195), forming a very dense ‘*Spartinetum alterniflorae*’ (Smith *et al.*, 1981, p. 403) and being the most abundant salt marsh species along the southwest Atlantic coast (Isacch *et al.*, 2006). It is noteworthy that these records and observations were made in coastal areas that are relatively densely populated and have been constantly traversed by Europeans since the beginning of colonial times. In fact, there is evidence clearly showing that

S. alterniflora is the only *Spartina* species that has expanded its range across this region, while the native austral cordgrass *S. densiflora*, a well-known aggressive invader in the Northern Hemisphere, seems to have maintained its presence or declined in the southernmost marshes of this region (Bortolus, 2006). Recent studies show that *S. alterniflora* is notably increasing its abundance in some of the largest and oldest salt marshes of South America in the Bahía Blanca estuary. There, *S. alterniflora* was observed during the last 38 years spreading very aggressively by vegetating the lower part of the channels and creeks, while the other dominant halophytic vegetation diminished in abundance (Mazzon *et al.*, 2012; Pratolongo *et al.*, 2014).

A topographic and botanical description of the San Antonio Bay (Rio Negro province) shoreline, made during the planning of the national railroad system between 1911 and 1914 (Willis, 1914), clearly described an intertidal area formed by bare mud flats devoid of *Spartina* below the terrestrial (supratidal) xerophyte communities. Since colonial times, this bay has always been one of the most important and active port areas of Argentina, and it is presently (one century after Willis' description) considered to be one of the largest salt marshes dominated by *S. alterniflora* in the country along with those in the Negro River estuary, San Blas Bay, Bahía Blanca estuary and Samborombón Bay (Isacch *et al.*, 2006; Bortolus *et al.*, 2009; Fig. 3). During the last 40 years, *S. alterniflora* has increased its abundance at the southernmost limit of its distribution, by vegetating marsh channels and colonizing mudflats with small patches that slowly merge into large beds within the Valdes Peninsula Reserve (42°24' S). Consistently similar expansion patterns have been reported repeatedly over the last two centuries in locations invaded by the smooth cordgrass world-wide (United Kingdom: Bromfield, 1837; north-west coast of North America: Civile *et al.*, 2005; China: Li *et al.*, 2009; Qiu, 2013; South Africa: Adams *et al.*, 2012).

In contrast, *S. alterniflora* remains restricted and patchy in many areas, again in striking contrast to its distribution and abundance in North America. As on the Brazilian coast (Seeliger, 1992), the distribution of *S. alterniflora* in the Bahía Blanca estuary, the largest salt marsh complex in Argentina (Isacch *et al.*, 2006), is commonly scattered and patchy and it is not as abundant as in the coastal marshes along the Atlantic coast of the USA (González Trilla *et al.*, 2009, 2013; Molina *et al.*, 2009). The Mar Chiquita coastal lagoon (Buenos Aires, Argentina) contains the largest known salt marsh system historically unaffected by important harbour and port development, and it is characterized by the absence of *S. alterniflora* (Fig. 1, Olivier *et al.*, 1972; Faggi *et al.*, 1997; Cagnoni, 1999; Iribarne, 2001; González Trilla *et al.*, 2009; González Trilla, 2010; González Trilla *et al.*, 2013; Pratolongo *et al.*, 2013). This coastal lagoon of 46 km² receives water from a 10,000 km² watershed that has existed for approximately 7000 years (Faggi *et al.*, 1997; Isla & Gaido, 2001; Stutz & Prieto, 2001). Its shorelines are dominated by vast monocultures of *S. densiflora* bordered by large

mud flats characteristically devoid of macrophytes except for the patchy occurrence of the subtidal seagrass (widgeon grass) *Ruppia maritima* L. (Bortolus *et al.*, 1998). The listing of *S. alterniflora* by Stutz (2001, p. 77; no specimens were collected) is a misidentification. Also, while all the dominant and subdominant salt marsh halophytes can be found in every salt marsh along the coast of southern South America, *S. alterniflora* is remarkably absent from many of them in Brazil (Giacobbo & Boechat, 1988), Uruguay (Clara & Maneyro, 1999) and Argentina (Isacch *et al.*, 2006; Bortolus *et al.*, 2009).

Spartina alterniflora remains absent along the Patagonian region south of 42°24' S. While this gap has been attributed to the poor physiological tolerance of current populations of *S. alterniflora* to regional environmental conditions (mostly temperature and humidity; Idaszkin *et al.*, 2011), there is no satisfactory explanation for its scattered distribution and relatively poor abundance along much of the Atlantic coast of South America, if we consider it a native species. If it is considered as an introduced species, a highly fragmented distribution and lack of robust adaptation to the full suite of regional climatic regions is to be expected.

Attribute 7: widespread globally disjunct distribution

This attribute addresses whether a species is reported to have 'isolated populations on different continents or in isolated oceans' (Chapman & Carlton, 1994). *Spartina alterniflora* fully satisfies this attribute: it now occurs with a globally disjunct distribution in countries throughout the Southern and Northern hemispheres, because of a mixture of accidental and intentional introductions, and continues to expand its range, having been detected in South Africa in 2004 (Adams *et al.*, 2012).

Attribute 8: insufficient dispersal mechanisms that could account for observed distribution

Spartina alterniflora lacks natural dispersal mechanisms for long-distance transport either (1) from the Gulf of Mexico (the natural southern limit of the species in North America) to Rio de Janeiro (where this species was first discovered in South America), a distance of over 7000 km, or (2) by drifting from Europe (the only other potential source in the Atlantic Ocean) to Brazil, a distance of over 9000 km.

Spartina seeds, seedlings and plant fragments may float in seawater and remain able to survive and proliferate through vegetative growth after travelling relatively short distances (Saint-Yves, 1932; Barrat-Segretain, 1996; Daehler & Strong, 1996; Bortolus, 2001). A study in the Netherlands concluded that the coastal dispersal of marsh plant fragments and seeds was determined by tidal currents rather than by wind direction and/or speed (Huiskes *et al.*, 1995). In contrast, wind direction and speed are reported as important in the dispersal of floating seeds, propagules and fragments of *S. alterniflora* along the north-west coast of North America (Pfauth

et al., 2003; Morgan & Sytsma, 2010). Indeed, although the successful water and wind dispersal of fruits and seeds is rare among macro-hydrophytes (Adam, 1993; Barrat-Segretain, 1996), the development of features such as air-filled spaces or hydrophobic coatings is frequent among these plants and might allow their seeds to float for weeks (Barrat-Segretain, 1996). *Spartina* species exhibit some of these features, but their seeds also often have hairy structures that trap air bubbles and increase their surface/weight ratio, which enhances buoyancy (Parodi, 1919; Saint-Yves, 1932; Mobblerley, 1956). However, an experimental study with *S. densiflora* seeds showed that buoyancy fails in turbulent waters that cause release of these bubbles (Bortolus, 2001). There is no evidence that *S. alterniflora* seeds, which have even fewer and shorter hair-like structures than *S. densiflora* (Mobblerley, 1956), could endure floating on surface waters from North America or Europe to South America.

Similarly, long-distance dispersal of *Spartina* seeds or plants for thousands of kilometres by migratory waterfowl from North America to South America is not supported. Migratory waterfowl pathways have been in place in the Americas for thousands of years, and if grebes, egrets, herons, whimbrels and other long-distance migratory birds had been ancient and continuous vectors for *Spartina*, we would expect that *Spartina* would have been in place in South America pre-historically, and not show highly disjunct distributions in South America, increased abundance in the 20th century and other biogeographic and ecological patterns noted above.

A study on the *S. alterniflora*-dominated marshes of the north-east USA found that salt marsh birds may carry (on their feathers and feet) an average of fewer than 3 seeds per bird but did not estimate the distance travelled by birds carrying the seeds (Figuerola *et al.*, 2005). Seagrass seeds may be successfully dispersed through endozoochory, depending on the season in which the seeds are eaten by waterfowl, but dispersal of viable seed was typically over relatively short distances (Vivian-Smith & Stiles, 1994). Waterfowl can successfully transport seeds of terrestrial and aquatic plants somewhat similar to *Spartina* (e.g. *Phragmites* sp., *Scirpus* spp., *Schoenoplectus* sp.) but always across relatively short distances compared to routes between the Americas or across oceans (e.g. North Europe: Clausen *et al.*, 2002; France: Brochet *et al.*, 2009, 2010a,b; Korea: Choi *et al.*, 2010; Romania: Takács *et al.*, 2013, p. 202). This said, local dispersal of *S. alterniflora* by aquatic waterfowl (as summarized in the above works) or by coastal currents (Sayce *et al.*, 1997) may explain some of the expansion observed for *Spartina* throughout the 19th and 20th centuries in South America.

Attribute 9: allochthonous evolutionary origin

Spartina alterniflora is considered to have evolved in the Northern Hemisphere as a member of a clade of three hexaploid species, including the western North American *Spartina*

foliosa Trin. and the European *Spartina maritime* (Curtis) Fernald (Baumel *et al.*, 2002; Fortune *et al.*, 2008; Peterson *et al.*, 2014a,b). Two additional sets of physiological and morphological traits suggest that South American *Spartina* originated in North America, as follows.

Intolerance to cold and lack of seasonal dieback

Recent experimental studies that focused on the absence of *S. alterniflora* in the southernmost salt marshes of Patagonia found that it was unable to overcome the local combinations of cold and humidity, which are considerably less harsh than in northern North America (Idaszkin & Bortolus, 2011). Moreover, while northern populations (New England) have a dormant period in winter during which all aboveground structures decay, the plants re-growing every spring (Bertness, 2006), in South America the plants appear to be perennial, as they stay mostly green all year round throughout their entire range (Idaszkin & Bortolus, 2011; Idaszkin *et al.*, 2011). Even in the southernmost marshes of Argentina dominated by *S. alterniflora*, there is a larger proportion of living than dead structures throughout the year, and a lower leaf turnover rate compared to the native *S. densiflora* (González Trilla *et al.*, 2009; Montemayor *et al.*, 2014). In North America, *S. alterniflora* extends north to approximately 50° N, where it tolerates the freezing conditions of snow, frost and the seasonal formation of ice sheets (Bertness, 2006). These patterns strongly suggest that South American *S. alterniflora* populations, at least in Argentina, originated from the warm temperate waters of the southernmost United States and that the cold-tolerant strains from high northern latitudes were not introduced to South America.

Reduction in Morphological Variation

In North America, *S. alterniflora* has three distinctive morphologies: short, medium and tall forms that may reach 3 m in height (Anderson & Treshow, 1980; Weinstein & Kreeger, 2000). In countries where it was intentionally planted, it rapidly displayed this phenotypic diversity (e.g. New Zealand: Bascand, 1970; China: Li *et al.*, 2009; USA: Callaway & Josselyn, 1992), reflecting importation of a broad genetic spectrum and perhaps high propagule pressure over time. In South America, these three forms and their classic zonation patterns have never been recorded, and plants rarely exceed 1 m in height (Schomburgk, 1847; Arechavaleta, 1894; Hauman, 1913; Parodi, 1919; Mobblerley, 1956; Correa, 1998; Isacch *et al.*, 2006; González Trilla *et al.*, 2013; see also comparative details in González Trilla *et al.*, 2009, pp. 131–132). South American literature on *S. alterniflora* consistently describes plants of a medium size, typically between 25 and 50 cm high. This is consistent with the notably lower net primary productivity recorded for *S. alterniflora* in South American marshes, commonly between 3% and 50% of that in North America (Negrin *et al.*, 2013). These patterns seem

to reflect the potential genetic constraint classically associated with introductions, as discussed below.

DISCUSSION

The combination of evidence from attributes 1–9, based on historical, environmental, biological, ecological, geographic, vector, physiological and morphological criteria, indicates that *S. alterniflora* – a species with a demonstrated remarkable propensity for successful colonization in regions where it did not evolve – was accidentally introduced to the Atlantic coast of South America, from either North America or Europe, sometime prior to 1817, by ocean commerce, perhaps with ballast or in cargo dunnage. After its introduction to Brazil, it may have spread both to the north and to the south, unless multiple separate introductions (see genetics discussion, below) from overseas were involved. The history of both local collections and floristic descriptions clearly indicates that *S. alterniflora* increased in both regional extent and abundance over the 20th century. *S. alterniflora* arose as a member of a hexaploid clade in North America, and we further suggest that the physiological repertoire of South American populations indicates an origin from the southern United States.

The great rise of intercontinental ocean commerce in the 1700s and 1800s leads to a constantly increasing number of invasions, many of which have not yet been recognized hundreds of years later (Carlton, 2009). As early as 1828, French scientists were speculating that the damp holds of cargo vessels could transport living marine organisms across the Atlantic Ocean (Carlton, 2011b). It is thus not surprising that *S. alterniflora* was one of the many species transported from the Atlantic coast of North America as French, British, Spanish and other nations' colonies flourished, grew and changed around the world.

It is natural to ask whether *S. alterniflora* may have been a rare 'background' native species that has expanded (in range and abundance) because of changes in climate, habitat, loss of predators, nutrient or other trophic shifts, or other phenomena. Four conditions motivate us to suggest that this was not the case. Under a model of rare indigenous species bloom, (1) *S. alterniflora* would have had to be uniformly rare along the entire coast of South America, from the Guianas to Argentina. Given the vast diversity of environmental regimes and habitat conditions along this 5000 km gradient, we do not find this tenable. In turn, (2) any theoretical environmental changes from the 19th to the 20th century – which would have caused a native marsh plant to expand its geographic range and increase in abundance – would similarly have had to be remarkably uniform along the entire South American Atlantic coast. We know of no such conditions (including climate change and sea level rise). Were widespread environmental changes inducing native coastal plant population expansion, we would further expect that (3) demonstrably native species (specifically those found nowhere else in the world) that were previously considered

rare would show responses similar to that of *S. alterniflora*. We know of no such reports in the nearly 200 years of South American botanical literature – or any other salt marsh literature, world-wide. Finally, (4) the global fate from the 18th to the 21st centuries of salt marshes and their constituent biota has, with rare exception, been the opposite of native species flourishing – rather, salt marshes have been characterized by widespread extirpation and the concomitant demise of many native plants and animals (Kennish, 2001; Gedan *et al.*, 2009; Silliman *et al.*, 2009).

The next steps: corroborating genetic and marsh core data

Two lines of additional evidence will be of value to corroborate our conclusions. At this writing, we lack data on South American *S. alterniflora* that would indicate the breadth of genetic variation, evidence of a founder effect or of strong genetic structure along this region. We predict, in concert with our suggestions above that the Southern Hemisphere populations were introduced from the southern United States, that *S. alterniflora* will be found to genetically match the southern North American stocks of this species, as elucidated by Blum *et al.* (2007). We further predict that when those data are in hand, South American populations will show reduced genetic diversity (the more so if introductions also occurred *via* European populations) compared to native North American populations. This prediction is underscored by the observation of reduced morphological diversity in *S. alterniflora* in South America. Xia *et al.* (2014) found that, as expected, introduced *S. alterniflora* in China (originally from North Carolina, Georgia and Florida) have low genetic diversity compared to North American Atlantic populations. They noted that ecotype hybrids and ecotype mixtures in China may be contributing to the species' robust success there.

This said, multiple inoculations over decades or centuries (a commonly observed phenomenon in invasion biology; Lonsdale, 1999; Verling *et al.*, 2005) could have expanded the genetic signature of *S. alterniflora* in the south-western Atlantic Ocean. Historical reconstructions showed that the massive invasion of *S. alterniflora* along the North American Pacific Coast was possible only after the combined result of repeated inoculations in multiple sites and by different means, including seed plantings, frequent seed and fragment dispersal, and multiple translocations (Civille *et al.*, 2005; Blum *et al.*, 2007), and it may be that similar scenarios of repeated inoculations have occurred in South America, leading to a reticulate evolutionary history (Ainouche *et al.*, 2004).

Second, we lack deeper historical floristic information for South American salt marshes based upon sediment core evidence. We predict that coastal sediments > 300 years old will lack any indication of pollen, phytoliths, seeds, rhizomes or other structures of *S. alterniflora* (see Davies, 1910, p. 631; Redfield, 1972).

Implications for the interpretation and understanding of the evolution of South American coastal salt marshes

Spartina alterniflora is a significant ecological engineer in coastal ecosystems. Vast areas of what conceivably would otherwise be open, bare mud flats have long been (Atlantic North America) or are newly (South America, Europe, China, Africa and elsewhere) high-density monospecific marine grasslands (Silliman *et al.*, 2009; Strong & Ayres, 2013). Where it has been introduced in China and California, *S. alterniflora* has caused habitat loss; reduced fish, bird and invertebrate diversity; out-competed native marsh plants; caused shifts from an algal-based to a detritus-based system; and transformed physical–chemical and hydrodynamic regimes, all resulting in vastly altered trophodynamic regimes (see summaries in Gedan *et al.*, 2009; Wan *et al.*, 2009; Adams *et al.*, 2012; Qiu, 2013; Wan *et al.*, 2014 and references therein). In China, where *S. alterniflora* displaced *Phragmites australis* (Cav.) Trin. ex Steud., the abundance of methanogens and sulphate-reducing bacteria has increased (Zeleeke *et al.*, 2013).

The revelation that *S. alterniflora*, one of the ten most intensively studied invasive plants world-wide (Pyšek *et al.*, 2008), is introduced to South America, standing as the world's largest invasion currently known involving this species, has profound implications for interpretation of the structure and function of marsh communities and those adjacent coastal systems that are linked to these marshes via detritus production and other subsidies (Bortolus, 2008b). In a period perhaps as short as 200 years, the invasion of South America by *S. alterniflora* has had catastrophic consequences, with this plant entirely reshaping coastal systems. Applying knowledge of the consequences of *Spartina* invasions elsewhere, we conclude that the vast *S. alterniflora* marshes along the Atlantic coast of South America were probably bare mudflats (below the zone of *S. densiflora*; Fig. 2), originally largely devoid of the dense meadows of intertidal halophytes that now characterize them. In turn, we conclude that there have been vast shifts in bird, fish and invertebrate biodiversity, and in algal vs. detritus production, with the concomitant trophic cascades that these changes imply. In south-west Atlantic salt marshes, *S. alterniflora* has higher decomposition rates than other salt marsh plants (Montemayor *et al.*, 2011), conceivably leading to greater detrital inputs into nearshore waters than was historically the case. Many questions cascade from these conclusions. For example, how did the addition of *S. alterniflora* influence the abundance, distribution and ecological roles of the native bioengineers such as the burrowing crab *Neohelice granulata* (Dana, 1851) (Bortolus & Iribarne, 1999; Botto *et al.*, 2005; Spivak, 2010; Alberti *et al.*, 2015) and the razor clam *Tagelus plebeius* (Lightfoot, 1786) (Addino *et al.*, 2015)? Has the invasion of *S. alterniflora* similarly altered the abundance and distribution of the *Spartina* stem-boring moth *Haimbachia* spp.,

which drives detritus production in Argentine marshes (Canepuccia *et al.*, 2011)? What was the impact of *S. alterniflora* on the distribution and abundance of native mangroves along the tropical north coast of South America through facilitation (Schaeffer-Novelli *et al.*, 1990)? What role has *S. alterniflora* played in the distribution and dynamics of the native mud snail *Heleobia australis* (d'Orbigny, 1835), which is (now) mainly associated with this introduced plant (Canepuccia *et al.*, 2007)? Has *S. alterniflora* been regulating the greenhouse gas effect in the region by altering emission/absorption rates of CH₄ and N₂O since its introduction (Yin *et al.*, 2015)?

In a similar case, the austral cordgrass *S. densiflora* was historically considered native in Chile (where the species was actually first described; Brongniart, 1829). Considerable efforts have been directed to understand its patterns of distribution and the ecological interactions that shape native plant communities along the Chilean coast, with the ultimate goal of improving regional environmental conservation strategies (e.g. San Martín *et al.*, 1992; Fariña *et al.*, 2009). It was not until 181 years after its first record that its introduction to Chile from the Atlantic coast of South America was first suggested (Bortolus, 2006) and later confirmed through molecular studies (Fortune *et al.*, 2008). It is thus difficult if not impossible to begin to conceive the scale of this wholesale conversion of seascape and landscape by an iconic, emblematic species, leading to the creation of extensive communities that have, until now, been studied – and interpreted – as the *natural* results of long-term evolution.

Our results change the way we perceive *natural* coastal ecosystems on the Atlantic coast of South America as a whole. In one sense, then, the current manifestation of most South American coastal marshes is what may be termed 'ecological mirages' – illusions that have seriously hampered and impeded our ability to perceive or recognize the nature of pre-existing native ecosystems, and thus leading us to believe in a supposedly pristine state of nature when, in fact, quite the opposite appears to be the case (Bortolus & Schwindt, 2007).

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REFERENCES

- Adam, P. (1993) *Saltmarsh ecology*, 1st edn. Cambridge Studies in Ecology. Cambridge University Press, Cambridge.
- Adams, J.B., Grobler, A., Rowe, C., Riddin, T., Bornman, T.G. & Ayres, D.R. (2012) Plant traits and spread of the invasive salt marsh grass, *Spartina alterniflora* Loisel., in the Great Brak Estuary, South Africa. *African Journal of Marine Science*, **34**, 313–322.
- Addino, M.S., Montemayor, D.I., Escapa, M., Alvarez, M.F., Valiñas, M.S., Lomovasky, B.J. & Iribarne, O. (2015) Effect of *Spartina alterniflora* Loisel, 1807 on growth of the stout razor clam *Tagelus plebeius* (Lightfoot, 1786) in a SW Atlantic estuary. *Journal of Experimental Marine Biology and Ecology*, **463**, 135–142.
- Ainouche, M.L., Baumel, A., Salmon, A. & Yannic, G. (2004) Hybridization, polyploidy and speciation in *Spartina* (Poaceae). *New Phytologist*, **161**, 165–172.
- Ainouche, M.L., Fortune, P.M., Salmon, A., Parisod, C., Grandbastien, M.A., Fukunaga, K., Ricou, M. & Misset, M.T. (2009) Hybridization, polyploidy and invasion: lessons from *Spartina* (Poaceae). *Biological Invasions*, **11**, 1159–1173.
- Alberti, J., Daleo, P., Fanjul, E., Escapa, M., Botto, F. & Iribarne, O. (2015) Can a single species challenge paradigms of salt marsh functioning? *Estuaries and Coasts*, **38**, 1178–1188.
- Alonso, M.A. & Crespo, M.B. (2008) Taxonomic and nomenclatural notes on South American taxa of *Sarcocornia* (Chenopodiaceae). *Annales Botanici Fennici*, **45**, 241–254.
- Anderson, C.M. & Treshow, M. (1980) A review of environmental and genetic factors that affect height in *Spartina alterniflora* Loisel (Salt Marsh Cord Grass). *Estuaries*, **3**, 168–176.
- Arechavaleta, J. (1894) *Las Gramíneas Uruguayas*. Establecimiento Tipo-Litográfico “Oriental”, Montevideo.
- Barrat-Segretain, M.H. (1996) Strategies of reproduction, dispersion, and competition in River Plants: a review. *Vegetatio*, **123**, 13–37.
- Bartlett, A.W. (1908) The use of “wild rice” grass in preventing coast erosion. *Journal of the Board of Agriculture of British Guiana*, **1**, 5–10.
- Bascand, L.D. (1970) The roles of *Spartina* species in New Zealand. *Proceedings of the New Zealand Ecological Society*, **17**, 33–40.
- Baumel, A., Ainouche, M.L., Bayer, R.J., Ainouche, A.K. & Misset, M.T. (2002) Molecular phylogeny of hybridizing species from the genus *Spartina* Schreb. (Poaceae). *Molecular Phylogenetics and Evolution*, **22**, 303–314.
- Berg, C. (1877) Enumeración de las plantas europeas que se hallan como silvestres en la provincia de Buenos Aires y en la Patagonia. *Anales de la Sociedad Científica Argentina*, **3**, 183–204.
- Bertness, M.D. (2006) *Atlantic shorelines: natural history and ecology*, 1st edn. Princeton University Press, Woodstock.
- Bertness, M.D., Ewanchuk, P.J. & Silliman, B.R. (2002) Anthropogenic modification of New England salt marsh landscapes. *Proceedings of the National Academy of Sciences of the United States of America*, **99**, 1395–1398.
- Blum, M.J., Bando, K.J., Katz, M. & Strong, D.R. (2007) Geographic structure, genetic diversity and source tracking of *Spartina alterniflora*. *Journal of Biogeography*, **34**, 2055–2069.
- Borges, M.E. (2005) La ostra del Pacífico *Crassostrea gigas* (Thunberg, 1793) en la Bahía Anegada (Provincia de Buenos Aires). *Invasores. Invertebrados exóticos en el Río de la Plata y región marina aledaña* (ed. by P.E. Penchaszadeh), pp. 311–367. Eudeba, Buenos Aires, Argentina.
- Bortolus, A. (2001) *Interacciones ecológicas entre el cangrejo cavadador Chasmagnathus granulata y los espartillares de Spartina densiflora, mesofauna asociada y características del sustrato en la laguna costera Mar Chiquita (Buenos Aires, Argentina)*. Doctoral Thesis, Universidad Nacional de Mar del Plata, Buenos Aires, Argentina.
- Bortolus, A. (2006) The austral cordgrass *Spartina densiflora* Brong: its taxonomy, biogeography and natural history. *Journal of Biogeography*, **33**, 158–168.
- Bortolus, A. (2008a) Error cascades in the biological sciences: the unwanted consequences of using bad taxonomy in ecology. *Ambio*, **37**, 114–118.
- Bortolus, A. (2008b) *Influencia de los ambientes costeros patagónicos sobre los ecosistemas marino-oceánicos: las marismas como caso de estudio*. El Mar Patagónico: Conservación y uso del ecosistema oceánico en América del Sur Meridional. Available at: www.marpatagonico.org (accessed 23 January 2015)
- Bortolus, A. (2012) Guiding authors to reliably use taxonomic names. *Trends in Ecology and Evolution*, **27**, 418.
- Bortolus, A. & Iribarne, O.O. (1999) The effect of the southwestern Atlantic burrowing crab *Chasmagnathus granulata* on a *Spartina* salt-marsh. *Marine Ecology Progress Series*, **178**, 79–88.
- Bortolus, A. & Schwindt, E. (2007) What would have Darwin written now? *Biodiversity and Conservation*, **16**, 337–345.

- Bortolus, A., Iribarne, O. & Martinez, M.M. (1998) Relationship between waterfowl and the seagrass *Ruppia maritima* in a Southwestern Atlantic coastal lagoon. *Estuaries*, **21**, 710–717.
- Bortolus, A., Schwindt, E., Bouza, P.J. & Idaszkin, Y.L. (2009) A characterization of Patagonian salt marshes. *Wetlands*, **29**, 772–780.
- Botto, F., Valiela, I., Iribarne, O., Martinetto, P. & Alberti, J. (2005) Impact of burrowing crabs on C and N sources, control, and transformations in sediments and food webs of SW Atlantic estuaries. *Marine Ecology Progress Series*, **293**, 155–164.
- Brochet, A.L., Guillemain, M., Fritz, H., Gauthier-Clerc, M. & Green, A.J. (2009) The role of migratory ducks in the long-distance dispersal of native. *Ecography*, **32**, 919–928.
- Brochet, A.L., Guillemain, M., Gauthier-Clerc, M., Fritz, H. & Green, A.J. (2010a) Endozoochory of Mediterranean aquatic plant seeds by teal after a period of desiccation: determinants of seed survival and influence of retention time on germinability and viability. *Aquatic Botany*, **93**, 99–106.
- Brochet, A.L., Guillemain, M., Fritz, H., Gauthier-Clerc, M. & Green, A.J. (2010b) Plant dispersal by teal (*Anas crecca*) in the Camargue: duck guts are more important than their feet. *Freshwater Biology*, **55**, 1262–1273.
- Bromfield, W.A. (1837) A description of *Spartina alterniflora* of Loiseleur, a new British species. *Companion to the Botanical Magazine*, **2**, 254–263.
- Bromfield, W.A. (1850) A catalogue of the plants growing wild in Hampshire, with occasional notes and observation on some of the more remarkable species. *The Phytologist: a Popular Botanical Miscellany*, **3**, 1095–1098.
- Brongniart, M.A. (1829) *Phanérogamie*. Voyage autour du monde sur la corvette La Coquille, pendant les années 1822–1825, par MLI Duperrey. Bertrand A, Paris.
- Bryce, J. (1936) *Spartina townsendii* and *S. brasiliensis* in warm countries. *Bulletin of Miscellaneous Information (Royal Botanic Gardens, Kew)*, **1**, 21–34.
- Burkholder, P.R. (1956) Studies on the nutritive value of *Spartina* grass growing in the marsh areas of coastal Georgia. *Bulletin of the Torrey Botanical Club*, **83**, 327–334.
- Cagnoni, M. (1999) Espartillares de la costa bonaerense de la República Argentina. Un caso de humedales costeros. *Tópicos sobre humedales subtropicales y templados de Sudamérica* (ed. by A.I. Malvárez), pp. 55–69. MAB UNESCO, Montevideo, Uruguay.
- Callaway, J.C. & Josselyn, M.N. (1992) The introduction and spread of smooth cordgrass (*Spartina alterniflora*) in South San Francisco Bay. *Estuaries*, **15**, 218–226.
- Canepuccia, A.D., Escapa, M., Daleo, P., Alberti, J., Botto, F. & Iribarne, O.O. (2007) Positive interactions of the smooth cordgrass *Spartina alterniflora* on the mud snail *Heleobia australis*, in south western Atlantic salt marshes. *Journal of Experimental Marine Biology and Ecology*, **353**, 180–190.
- Canepuccia, A.D., Montemayor, D., Pascual, J., Farina, J.L. & Iribarne, O.O. (2011) A stem-boring moth drive detritus production in SW Atlantic marshes. *Marine Ecology Progress Series*, **442**, 1–9.
- Carlton, J.T. (1996) Biological invasions and cryptogenic species. *Ecology*, **77**, 1653–1655.
- Carlton, J.T. (2003) Community assembly and historical biogeography in the North Atlantic Ocean: the potential role of human-mediated dispersal vectors. *Hydrobiologia*, **503**, 1–8.
- Carlton, J.T. (2007) Ballast. *The Oxford encyclopedia of maritime history* (ed. by J.B. Hattendorf), pp. 249–251. Oxford University Press, Oxford, UK.
- Carlton, J.T. (2009) Deep invasion ecology and the assembly of communities in historical time. *Biological invasions in marine ecosystems* (ed. by G. Rilov and J.A. Crooks), pp. 13–56. Springer-Verlag, Berlin, Germany.
- Carlton, J.T. (2011a) The global dispersal of marine and estuarine crustaceans. *In the wrong place: alien marine crustaceans – distribution, biology and impacts* (ed. by B.S. Galil, P.F. Clark and J.T. Carlton), pp. 3–23. Springer, Dordrecht, Netherlands.
- Carlton, J.T. (2011b) Ballast. *Encyclopedia of biological invasions* (ed. by D. Simberloff and M. Rejmanek), pp. 43–49. University of California Press, Berkeley, USA.
- Chapman, V.J. (1960) *Salt marshes and salt deserts of the world*. Interscience Pub. Inc., New York.
- Chapman, V.J. (1977) *Wet coastal ecosystems*. Elsevier Scientific Publishing company, New York.
- Chapman, J.W. & Carlton, J.T. (1991) A test of criteria for introduced species: the global invasion by the isopod *Synidotea laevidorsalis* (Miers, 1881). *Journal of Crustacean Biology*, **11**, 386–400.
- Chapman, J.W. & Carlton, J.T. (1994) Predicted discoveries of the introduced isopod *Synidotea laevidorsalis* (Miers, 1881). *Journal of Crustacean Biology*, **14**, 700–714.
- Choi, C.Y., Nam, H.Y. & Chae, H.Y. (2010) Exotic seeds on the feathers of migratory birds on a stopover island in Korea. *Journal of Ecology and Field Biology*, **33**, 19–22.
- Civille, J.C., Sayce, K., Smith, S.D. & Strong, D.R. (2005) Reconstructing a century of *Spartina alterniflora* invasion with historical records and contemporary remote sensing. *Ecoscience*, **12**, 330–338.
- Clara, M. & Maneyro, R. (1999). Humedales del Uruguay. El ejemplo de los humedales del Este. *Tópicos sobre Humedales subtropicales y templados de Sudamérica* (ed. by A.I. Malvárez), pp. 68–80. MAB UNESCO, Montevideo, Uruguay.
- Clausen, P., Nolet, B.A., Fox, A.D. & Klaassen, M. (2002) Long-distance endozoochorous dispersal of submerged macrophyte seeds by migratory waterbirds in Northern Europe - a critical review of possibilities and limitations. *Acta Oecologica*, **23**, 191–203.
- Correa, M.N. (1998) *Flora Patagónica*, Tomo VIII. INTA, Buenos Aires.
- Costa, C.B. & Davy, A.J. (1992) Coastal saltmarsh communities of Latin America. *Coastal plant communities of Latin America* (ed. by U. Seeliger), pp. 179–212. Academic Press Inc, New York, USA.

- Costa, C.B., Marangoni, J.C. & Acevedo, A.G. (2003) Plant zonation in irregularly flooded salt marshes: relative importance of stress tolerance and biological interactions. *Journal of Ecology*, **91**, 951–965.
- Crooks, J.A. & Soulé, M.E. (1999) Lag times in population explosions of invasive species: causes and implications. *Invasive species and biodiversity management* (ed. by O.T. Sandlund, P.J. Schei and A.Å. Viken), pp. 103–125. Kluwer Academic Publishers, Dordrecht, the Netherlands.
- Cunha, S., Asmus, M. & Costa, C. (2005) Production dynamics of *Spartina alterniflora* salt marshes in the estuary of Patos Lagoon (RS, Brazil): a simulation model approach. *Brazilian Journal of Aquatic Science and Technology*, **9**, 75–85.
- Daehler, C.C. & Strong, D.R. (1996) Status, prediction and prevention of introduced cordgrass *Spartina* spp. invasions in Pacific estuaries, USA. *Biological Conservation*, **78**, 51–58.
- Davies, C.A. (1910) Salt marsh formation near Boston and its geological significance. *Economic Geology*, **5**, 623–639.
- Day, J.W. Jr, Hall, C.A.S., Kemp, W.M. & Yañez-Arancibia, A. (1989) *Estuarine ecology*, 1st edn. Wiley-Interscience Publication, John Wiley & Sons, New York.
- De Angelis, P. (1836) *Colección de obras y documentos relativos a la historia antigua y moderna de las provincias del Río de la Plata, ilustrados con notas y disertaciones*. Imprenta del Estado, Buenos Aires.
- Elliott, S. (1821) *A sketch of the botany of South Carolina and Georgia*. Schenck J.R., Charleston.
- Excoffon, A.C., Acuña, F.H. & Zamponi, M.O. (2004) Presence of *Haliplanella lineata* (Verrill, 1869) (Actiniaria, Haliplanellidae) in the Argentine Sea and the finding of anisorhize haploneme cnidocyst. *Physis*, **60**, 1–6.
- Faggi, A.M., Cagnoni, M. & Otero, P. (1997) *Mar Chiquito: nueva reserva de la Biosfera*. Actas del VI Encuentro de Geógrafos de América Latina, Buenos Aires, Argentina.
- Falkner, T. (1774) *A description of Patagonia, and the adjoining parts of South America: containing an account of the soil, produce, animals, vales, mountains, rivers, lakes, &c. of those countries; the religion, government, policy, customs, dress, arms, and language of the Indian inhabitants; and some particulars relating to Falkland's Islands*. Hereford, London.
- Fariña, J.M., Silliman, B.R. & Bertness, M.D. (2009) Can conservation biologists rely on established community structure rules to manage novel systems? ...Not in salt marshes. *Ecological Applications*, **19**, 413–422.
- Figuerola, J., Santamaria, L., Green, A.J., Luque, I., Alvarez, R. & Charalambidou, I. (2005) Endozoochorous dispersal of aquatic plants: does seed gut passage affect plant performance? *American Journal of Botany*, **92**, 696–699.
- Fortune, P.M., Schierenbeck, K., Ayres, D., Bortolus, A., Catrice, O., Brown, S. & Ainouche, M. (2008) The enigmatic invasive *Spartina densiflora*: a history of hybridizations in a polyploidy context. *Molecular Ecology*, **17**, 4304–4316.
- Frenkel, R.E. & Boss, T.R. (1988) Introduction, establishment and spread of *Spartina patens* on Cox Island, Siuslaw Estuary, Oregon. *Wetlands*, **8**, 33–49.
- Gedan, K.B., Silliman, B.R. & Bertness, M.D. (2009) Centuries of human-driven change in salt marsh ecosystems. *Annual Review of Marine Science*, **1**, 117–141.
- Giacobbo, E.O. & Boechat, S.C. (1988) O genero *Spartina* Schreber (Gramineae, Chloridoideae) no Rio Grande do Sul. *Iheringia Série Botânica*, **37**, 89–109.
- Gibert, E. (1873) *Enumeratio plantarum sponte nascentium agro Montevidensi cum synonymis selectis*. Asociación Rural del Uruguay, Montevideo.
- González Trilla, G. (2010) *Patrones de biomasa de Spartina spp. en dos marismas costeras de la Provincia de Buenos Aires*. Buenos Aires, Argentina. Doctoral Thesis, Universidad de Buenos Aires, Argentina.
- González Trilla, G., Kandus, P., Negrin, V., Vicari, R. & Marcovecchio, J. (2009) Tiller dynamic and production on a SW Atlantic *Spartina alterniflora* marsh. *Estuarine, Coastal and Shelf Science*, **85**, 126–133.
- González Trilla, G.G., Borro, M.M., Morandeira, N.S., Schivo, F., Kandus, P. & Marcovecchio, J. (2013) Allometric scaling of dry weight and leaf area for *Spartina densiflora* and *Spartina alterniflora* in two southwest Atlantic saltmarshes. *Journal of Coastal Research*, **29**, 1373–1381.
- Hauman, L. (1913) Etude phytogéographique de la region du Rio Negro inferieur. *Anales del Museo Nacional de Buenos Aires*, **24**, 19–442.
- Heiman, K.W., Vidargas, N. & Micheli, F. (2008) Non-native habitat as home for non-native species: comparison of communities associated with invasive tubeworm and native oyster reefs. *Aquatic Biology*, **2**, 47–56.
- Hicken, C.M. (1923) *Los estudios Botánicos. Evolución de las ciencias en la República Argentina*. CONI, Buenos Aires.
- Hooker, W.J. (1837) [On ballast from America as the vector for introduction of *Spartina alterniflora* to Europe]. *Companion to the Botanical Magazine*, **2**, 261 (footnote).
- Huiskes, A.H.L., Koutstaal, B.P., Herman, P.M.J., Beeftink, W.G., Markusse, M.M. & de Munck, W. (1995) Seed dispersal of halophytes in tidal salt marshes. *Journal of Ecology*, **83**, 559–567.
- Idaszkin, Y.L. & Bortolus, A. (2011) Does low temperature prevent *Spartina alterniflora* from expanding toward the austral-most salt marshes? *Plant Ecology*, **212**, 553–561.
- Idaszkin, Y.L., Bortolus, A. & Bouza, P.J. (2011) Ecological processes shaping Central Patagonian salt marsh landscapes. *Austral Ecology*, **36**, 59–67.
- Iribarne, O.O. (2001) *Reserva de Biosfera Mar Chiquita: Características físicas, biológicas y ecológicas*. Editorial Martin, Mar del Plata.
- Isacch, J.P., Costa, C.S.B., Rodríguez-Gallego, L., Conde, D., Escapa, M., Gagliardini, D.A. & Iribarne, O.O. (2006) Distribution of salt marsh plant communities associated with environmental factors along a latitudinal gradient on the southwest Atlantic coast. *Journal of Biogeography*, **33**, 888–900.
- Isla, F.I. & Gaido, E.S. (2001) Evolución geológica de la laguna Mar Chiquita. *Reserva de Biosfera Mar Chiquita: Características físicas, biológicas y ecológicas* (ed. by O.O.

- Iribarne), pp. 19–30. Editorial Martín, Mar del Plata, Argentina.
- Judziwicz, E.J. (1990) Poaceae (Gramineae). *Flora of the Guianas, Series A, Phanerogams* (ed. by A.R.A. Gorts-Van Rijn), pp. 602–604. Koeltz Scientific Books, Königstein, Germany.
- Kennish, M.J. (2001) Coastal salt marsh systems in the U.S.: a review of anthropogenic impacts. *Journal of Coastal Research*, **17**, 731–748.
- Kew Bulletin of Miscellaneous Information. (1907) *Mud binding grasses*. No 5, 190–197.
- Kupriyanova, E., Nishi, E., ten Hove, H. & Rzhavsky, A. (2001) Life history patterns in serpulimorph polychaetes: ecological and evolutionary perspectives. *Oceanography and Marine Biology: an Annual Review*, **39**, 1–101.
- Lacerda, L.D., Freixo, J.L. & Coelho, S.M. (1997) The effect of *Spartina alterniflora* Loisel on trace metals accumulation in inter-tidal sediments. *Mangroves and Salt Marshes*, **1**, 201–209.
- Li, B., Liao, C.H., Zhang, X.D., Chen, H.L., Wang, Q., Chen, Z.Y., Gan, X.J., Wu, J.H., Zhao, B., Ma, Z.J., Cheng, X.I., Jiang, L.F. & Chen, J.K. (2009) *Spartina alterniflora* invasions in the Yangtze River estuary, China: an overview of current status and ecosystem effects. *Ecological Engineering*, **35**, 511–520.
- von Linnaeus, C. (1753) *Species Plantarum, exhibentes plantas rite cognitatas, ad genera relatas, cum differentiis specificis, nominibus trivialibus, synonymis selectis, locis natalibus, secundum systema sexuale digestas*. Vol 1. Holmiae, Impensis Laurentii Salvii, Stockholm, Sweden.
- Lonsdale, W.M. (1999) Global patterns of plant invasions and the concept of invasibility. *Ecology*, **80**, 1522–1536.
- Marangoni, J.C. & Costa, C.S.B. (2012) Short- and long-term vegetative propagation of two *Spartina* species on a salt marsh in Southern Brazil. *Estuaries and Coasts*, **35**, 763–773.
- Marchant, C.J. (1967) Evolution in *Spartina* (Gramineae) I. The history and morphology of the genus in Britain. *Journal of the Linnean Society, Botany*, **60**, 1–24.
- Martyn, E.B. (1934) A note on the foreshore vegetation in the neighborhood of Georgetown, British Guiana, with special reference to *Spartina brasiliensis*. *Journal of Ecology*, **22**, 292.
- Mazzon, C., Pratolongo, P., Piovan, M.J. & Zapperi, G. (2012) *Direction and magnitude of recent changes in coastal wetlands of the Bahía Blanca Estuary (Argentina)*. Coastal and Estuarine Research Federation, Mar del Plata, Argentina.
- Mendelssohn, I.A. & McKee, K.L. (2000) Saltmarshes and mangroves. *North American terrestrial vegetation* (ed. by M. Barbour and W.D. Billings), pp. 501–536. Cambridge University Press, Cambridge, UK.
- Mendez, M.M. (2013) *El rol del cirripedio introducido *Balanus glandula* como ingeniero ecosistémico en intermareales de Patagonia, Argentina*. Doctoral Thesis, Universidad Nacional del Comahue, Argentina.
- Mitsch, W.J. & Gosselink, J.G. (2000) *Wetlands*, 3rd edn. John Wiley and Sons Inc, New York.
- Mobberley, D.G. (1956) Taxonomy and distribution of the genus *Spartina*. *Iowa State College Journal of Science*, **30**, 471–574.
- Molina, L.M., Valiñas, M.S., Pratolongo, P.D., Elias, R. & Perillo, G.M.E. (2009) First record of the sea anemone *Diadumene lineata* (Verrill 1871) associated to *Spartina alterniflora* roots and stems, in marshes at the Bahía Blanca estuary, Argentina. *Biological Invasions*, **11**, 409–416.
- Montemayor, D.I., Addino, M., Fanjul, E., Escapa, M., Alvarez, M.F., Botto, F. & Iribarne, O.O. (2011) Effect of dominant *Spartina* species on salt marsh detritus production in SW Atlantic estuaries. *Journal Sea Research*, **66**, 104–110.
- Montemayor, D.I., Addino, M., Valiñas, M., Fanjul, E., Alvarez, M.F. & Iribarne, O.O. (2014) Biomass dynamics of the two dominant SW Atlantic *Spartina* species and its implications on the saltmarsh organic matter accumulation/exportation. *Aquatic Botany*, **120**, 201–204.
- Mora-Olivo, A. & Valdés-Reyna, J. (2011) Nota sobre la presencia de *Spartina alterniflora* Loisel. (Poaceae: Chloridoideae: Cynodonteae) en humedales mexicanos. *Acta Botánica Mexicana*, **95**, 45–50.
- Morgan, V. & Sytsma, M. (2010) *Alaska Spartina prevention, detection and response plan*. National Marine Fisheries Service, Alaska Region, Juneau, USA.
- Negrin, V.L., de Villalobos, A.E., González Trilla, G.G., Botté, S.E. & Marcovecchio, J.E. (2012) Above- and belowground biomass and nutrient pools of *Spartina alterniflora* (smooth cordgrass) in a South American salt marsh. *Chemistry and Ecology*, **28**, 391–404.
- Negrin, V.L., González Trilla, G., Botté, S.E. & Mazzon, C. (2013) Ciclo de materia orgánica: producción primaria. *Producción en marismas. Procesos Químicos en Estuarios* (ed. by J.E. Marcovecchio and R.H. Freije), pp. 197–218. Editorial de la Universidad Nacional del Sur (EDIUNS), Bahía Blanca, Argentina.
- Olivier, S.R., Escofet, A.M., Penchaszadeh, P. & Orensanz, J.M. (1972) Estudios ecológicos de la región estuarial de Mar Chiquita (Buenos Aires, Argentina). 1. Las comunidades bentónicas. *Anales de la Sociedad Científica Argentina*, **193**, 237–262.
- Orensanz, J.M., Schwindt, E., Pastorino, G., Bortolus, A., Casas, G., Darrigran, G., Elías, R., López Gappa, J.J., Obenat, S., Pascual, M., Penchaszadeh, P., Piriz, M.L., Scarbino, F., Spivak, E.D. & Vallarino, E.A. (2002) No longer a pristine confine of the world ocean—a survey of exotic marine species in the Southwestern Atlantic. *Biological Invasions*, **4**, 115–143.
- Parodi, L.R. (1919) Las Chlorideas de la República Argentina. *Extracto de la revista de la Facultad de Agronomía y Veterinaria*, **2**, 233–335.
- Peterson, P.M., Romaschenko, K., Arrieta, Y.H. & Saarela, J.M. (2014a) A molecular phylogeny and new subgeneric

- classification of *Sporobolus* (Poaceae: Chloridoideae: Sporobolinae). *Taxon*, **63**, 1212–1243.
- Peterson, P.M., Romaschenko, K., Arrieta, Y.H. & Saarela, J.M. (2014b) 2332) Proposal to conserve the name *Sporobolus* against *Spartina*, *Crypsis*, *Poncaletia*, and *Heleo-chloa* (Poaceae: Chloridoideae: Sporobolinae). *Taxon*, **63**, 1373–1374.
- Pfauth, M., Sytsma, M. & Isaacson, D. (2003) *Oregon spartina response plan*. Oregon Department of Agriculture, Portland, USA.
- Pratolongo, P.D., Perillo, G.M.E. & Piccolo, M.C. (2010) Combined effects of waves and plants on a mud deposition event at a mudflat-saltmarsh edge in the Bahía Blanca estuary. *Estuarine, Coastal and Shelf Science*, **87**, 207–212.
- Pratolongo, P., Piovan, M.J., Zapperi, G., Negrin, V., González Trilla, G. & Botté, S. (2013) Humedales en estuarios. *Procesos Químicos en Estuarios* (ed. by J.E. Marcovecchio and R.H. Freije), pp. 84–108. Editorial de la Universidad Nacional del Sur (EDIUNS), Bahía Blanca, Argentina.
- Pratolongo, P., Mazzon, C., Zapperi, G., Piovan, M.J. & Brinson, M.M. (2014) Land cover changes in coastal wetlands of the Bahía Blanca Estuary (Argentina) during the past 40 years. *Estuarine, Coastal and Shelf Science*, **133**, 23–31.
- Pulle, A. (1906) *An enumeration of the vascular plants known from Surinam, together with their distribution and synonymy*. E.J. Brill Ltd, Leiden.
- Pyšek, P., Richardson, D.M., Pergl, J., Jarošík, V., Sixtová, Z. & Weber, E. (2008) Geographical and taxonomic biases in invasion ecology. *Trends in Ecology and Evolution*, **23**, 237–244.
- Qiu, J. (2013) China's cordgrass plan is “overkill”. *Nature*, **499**, 392–393.
- Raddi, G. (1823) *Agrostografia brasiliensis*. Memoria del Sig. Giuseppe Raddi. Socio corrispondente della R. Accademia Lucchese, Lucca, Italy.
- Redfield, A.C. (1972) Development of a New England salt marsh. *Ecological Monographs*, **42**, 201–237.
- Rousseau, J. (1945) Le folklore botanique de L'île Aux Coudres. *Contributions de l'Institut Botanique de l'Université de Montreal*, **55**, 75–111.
- Saarela, J.M. (2012) Taxonomic synopsis of invasive and native *Spartina* (Poaceae, Chloridoideae) in the Pacific Northwest (British Columbia, Washington and Oregon), including the first report of *Spartina* × *townsendii* for British Columbia, Canada. *PhytoKeys*, **10**, 25–82.
- Saint-Yves, A. (1932) Monographia Spartinarum. *Cyollea*, **5**, 19–100.
- San Martin, C., Contreras, D., San Martin, J. & Ramirez, C. (1992) Vegetation of salt marshes of south-central Chile. *Revista Chilena de Historia Natural*, **65**, 327–342.
- Sayce, K., Dumbauld, B. & Hidy, J. (1997) Seed dispersal in drift of *Spartina alterniflora*. *Proceedings of the Second International Spartina Conference* (ed. by K. Patter), pp. 27–31. Washington State University, Cooperative Extension, Olympia, USA.
- Schaeffer-Novelli, Y., Cintrón-Molero, G., Rothleder Adaime, R. & de Camargo, T.M. (1990) Variability of Mangrove Ecosystems along the Brazilian Coast. *Estuaries*, **13**, 204–218.
- Scheffer, T.H. (1945) The introduction of *Spartina alterniflora* to Washington with oyster culture. *Leaflets of Western Botany*, **4**, 163–164.
- Schomburgk, R. (1847) Description of some grasses and sedges from the east coast of Demerara, with remarks on the geographical distribution of the species. *Annals and Magazine of Natural History*, **20**, 396–409.
- Schomburgk, R. (1848) *Reisen in Britisch-Guiana in den Jairen 1840-1844*. Verlagsbuchhandlung von J. J. Weber. Leipzig, Germany.
- Schwindt, E., Bortolus, A., Idaszkin, Y.L., Savoya, V. & Mendez, M.M. (2009) Salt marsh colonization by a rocky shore invader: *Balanus glandula* Darwin (1854) spreads along the Patagonian coast. *Biological Invasions*, **11**, 1259–1265.
- Schwindt, E., López Gappa, J., Raffo, M.P., Tatián, M., Bortolus, A., Orensanz, J.M., Alonso, G., Diez, M.E., Doti, B., Genzano, G., Lagger, C., Lovrich, G., Piriz, M.L., Mendez, M.M., Savoya, V. & Sueiro, M.C. (2014) Marine fouling invasions in ports of Patagonia (Argentina) with implications for legislation and monitoring programs. *Marine Environmental Research*, **99**, 60–68.
- Seeliger, U. (1992) *Coastal plant communities of Latin America*, 1st edn. Academic Press Inc, New York.
- Settle, T., Mollock, G.N., Hinchman, R.R. & Negri, M.C. (1998) *Engineering the use of green plants to reduce produced water disposal volume*. Society of Petroleum Engineers. Inc. Devon Energy Corporation and Argonne National Laboratory, Oklahoma City, OK, and Argonne IL.
- Silliman, B. & Bortolus, A. (2003) Underestimation of *Spartina* production in western Atlantic marshes: marsh invertebrates eat more than just detritus. *Oikos*, **101**, 549–554.
- Silliman, B.R., Bertness, M.D. & Grosholz, E.D. (2009) *Human impacts on salt marshes. A global perspective*, 1st edn. University of California Press, Berkeley.
- da Silva Attolini, F., Flynn, M.N. & Tararam, A.S. (1997) Influence of *Spartina alterniflora* and tide level on the structure of polychaete associations in an euryhaline salt marsh in Cananéia lagoon estuary region (SE Brazil). *Revista Brasileira de Oceanografia*, **45**, 25–34.
- Smith, L.B., Wasshausen, D.C. & Klein, R.M. (1873) Gramineae. Géneros: 1. Bambusa até 44. Chloris. *Flora ilustrada Catarinense* (ed. by P. Reitz), pp. 3–435. Herbário Barbosa Rodrigues, Santa Catarina, Brasil.
- Spegazzini, C. (1905) *Flora de la Provincia de Buenos Aires*. Imprenta de M Biedma e hijo, Bolivar, Argentina.
- Spicher, D. & Josselyn, M. (1985) *Spartina* (Gramineae) in Northern California: distribution and taxonomic notes. *Madroño*, **32**, 158–167.
- Spivak, E. (2010) The crab *Neohelice* (= *Chasmagnathus*) *granulata*: an emergent animal model from emergent countries. *Helgoland Marine Research*, **64**, 149–154.

- Sprague, T.A. (1933) The Dates of Hooker's "Companion to the Botanical Magazine." *Bulletin of Miscellaneous Information (Royal Botanic Gardens, Kew)*, **7**, 362–364.
- Stapf, O. (1908) *Spartina townsendii*. *Gardeners' Chronicles: A Weekly Illustrated Journal of Horticulture and Allied Subjects*, **1099**, 33–35.
- Strong, D.R. & Ayres, D.A. (2009) *Spartina* introductions and consequences in salt marshes. *Human Impacts on Salt Marshes: a Global Perspective* (ed. by B.R. Silliman, M.D. Bertness and E.D. Grosholz), pp. 3–22. University of California Press, Berkeley, USA.
- Strong, D.R. & Ayres, D.R. (2013) Ecological and evolutionary misadventures of *Spartina*. *Annual Review of Ecology and Systematics*, **44**, 389–410.
- Stutz, S. (2001) Vegetación del área de la laguna mar chiquita. *Reserva de Biosfera Mar Chiquita: Características físicas, biológicas y ecológicas* (ed. by O.O. Iribarne), pp. 75–78. Editorial Martín, Mar del Plata, Argentina.
- Stutz, S. & Prieto, A.R. (2001) Historia de la vegetación de la laguna Mar Chiquita desde ca. 6000 ¹⁴C años A.P. *Reserva de Biosfera Mar Chiquita: Características físicas, biológicas y ecológicas* (ed. by O.O. Iribarne), pp. 67–73. Editorial Martín, Mar del Plata, Argentina.
- Takács, A., Schmotzer, A., Jakab, G., Deli, T., Mesterházy, A., Király, G., Lukács, B.A., Balázs, B., Perić, R., Eliáš, P.jun., Sramkó, G., Tökölyi, J. & Molnár, V.A. (2013) Key environmental variables affecting the distribution of *Elatine hungarica* in the Pannonian Basin. *Preslia*, **85**, 193–207.
- Tyler, A.C., Lambrinos, J.G. & Grosholz, E.D. (2007) Nitrogen inputs promote the spread of an invasive marsh grass. *Ecological Applications*, **17**, 1886–1898.
- Verling, E., Ruiz, G.M., Smith, L.D., Galil, B., Miller, A.W. & Murphy, K.R. (2005) Supply-side invasion ecology: characterizing propagule pressure in coastal ecosystems. *Proceedings of the Royal Society B*, **272**, 1249–1256.
- Vervoorst, F. (1967) *La vegetación de la República Argentina VII: las comunidades vegetales de la depresión del Salado (Prov. Buenos Aires)*. INTA-Serie Fitogeográfica, Buenos Aires.
- Vinci, M.A. (2004) Los humedales de la costa patagónica de la provincia de Río Negro. *Documentos del Curso-Taller Bases ecológicas para la clasificación e inventario de humedales en Argentina* (ed. by A.I. Malvarez), pp. 71–74. MAB-UNESCO, Buenos Aires, Argentina.
- Vivian-Smith, G. & Stiles, E.W. (1994) Dispersal of salt marsh seeds on the feet and feathers of waterfowl. *Wetlands*, **14**, 316–319.
- Wan, S., Qin, P., Liu, J. & Zhou, H. (2009) The positive and negative effects of exotic *Spartina alterniflora* in China. *Ecological Engineering*, **35**, 444–452.
- Wan, H., Wang, Q., Jiang, D., Fu, J., Yang, Y. & Liu, X. (2014) Monitoring the invasion of *Spartina alterniflora* using very high resolution unmanned aerial vehicle imagery in Beihai, Guangxi (China). *Scientific World Journal.*, **2014**, 1–7 doi: 10.1155/2014/638296.
- Weinstein, M.P. & Kreeger, D.A. (2000) *Concepts and controversies in tidal marsh ecology*, 1st edn. Kluwer Academic Publishers, Dordrecht.
- West, R.C. (1977) Tidal salt-marsh and mangal formation of Middle and South America. *Wet coastal Ecosystems* (ed. by V.J. Chapman), pp. 193–213. Elsevier, Amsterdam, the Netherlands.
- Willis, B. (1914) *Northern Patagonia, character and resources*. Scribner Press, New York.
- Xia, L., Zhao, H., Yang, W. & An, S. (2014) Genetic diversity, ecotype hybrid, and mixture of invasive *Spartina alterniflora* Loisel in coastal China. *Clean (Weinh)*, **42**, 1–10.
- Yin, S., An, S., Deng, Q., Zhang, J., Ji, H. & Cheng, X. (2015) *Spartina alterniflora* invasions impact CH₄ and N₂O fluxes from a salt marsh in eastern China. *Ecological Engineering*, **81**, 192–199.
- Zelege, J., Sheng, Q., Wang, J.-G., Huang, M.-Y., Xia, F., Wu, J.-H. & Quan, Z.-X. (2013) Effects of *Spartina alterniflora* invasion on the communities of methanogens and sulfate-reducing bacteria in estuarine marsh sediments. *Frontiers in Microbiology*, **4**, 1–13.
- Zuloaga, F. & Morrone, O. (1999) *Catálogo de las Plantas Vasculares de la República Argentina*. Missouri Botanical Garden, St. Louis.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Chronology of the earliest records of *Spartina alterniflora* in South America.

BIOSKETCHES

AB and ES are coastal ecologists focused on natural history, biogeography and biological invasions in southern South America and the south-western Atlantic Ocean and lead the GEAC research team (Facebook page: Grupo de Ecología en Ambientes Costeros Geac-Conicet). JTC is a marine biological invasions researcher, professor of marine sciences at Williams College and founding editor in chief of the international journal *Biological Invasions*. The authors of this article form an international academic consortium focused on the study of coastal marine bioinvasions, including workshops, teaching initiatives and research on ecology, taxonomy, biogeography and historical ecology (website in progress).

Author contributions: A.B. and J.T.C. conceived the idea. A.B. and E.S. led the study design and data searching. A.B. and J.T.C. led the writing.

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Appendix S1: Chronology of the Earliest records of *Spartina alterniflora* in South America and naturalistic details.

**Article: Reimagining South American coasts:
Unveiling the hidden invasion history of an iconic ecological
engineer**

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Running title: Reimagining South American Coasts

Appendix S1

First record in Brazil, 1817

Spartina alterniflora was first collected in South America in the intertidal zone in the vicinity of Rio de Janeiro, Brazil ("Reperitur in inundatis prope Rio-janeiro") and described by Raddi (1823) as a new species, *Spartina brasiliensis* (recognized by Parodi (1918) as a synonym of *S. alterniflora*; see also Mobberley, 1956 and Saarela, 2012). Raddi collected the specimens in 1817 (Longhi-Wagner *et al.*, 2010). Redescriptions as new species of introduced taxa already described earlier are also a common taxonomic and biogeographic phenomenon (Carlton, 2009). Botanical explorations of the coast of Brazil (Pires-O'Brien, 1993) began nearly 300 years prior to the first collections of *S. alterniflora*, suggesting that if this cordgrass had been present and common, it would have been collected.

First record in Suriname, 1838

Pulle (1906) reported (as *Spartina brasiliensis*) on Frederik Louis Splitgerber's collections of *S. alterniflora* in the Upper Commewyne district in Suriname in 1838; Splitgerber's material is in the National Herbarium of The Netherlands (referred to as "H.L.B." by Pulle, who noted one of the two herbarium sheets on file there). Pulle further reviewed the history of botanical surveys of Suriname, noting a number of collections from the 1750s to the early 1830s, none of which recovered *S. alterniflora*. Pulle himself collected in Suriname in 1902-1903, along the Saramacca River, to the north of the Commewijne region, but did not encounter *S. alterniflora*. That *S. alterniflora* was still rare at that time is further indicated by his description of the riverine vegetation: "The nearly bare mud banks which extend far into the sea, especially near the mouths of the rivers, pass on the side of the land into a typical mangrove vegetation, chiefly consisting of *Rhizophora mangle* and *Avicennia nitida*, mixed with *Conocarpus erectus*, *Bucida buceras*, *Laguncularia racemosa* and

Acrostichum aureum” (Pulle, 1906, p. 482). Moreover, there is no mention of smooth cordgrass in Linnaeus’ botanical catalogues of the flora of Suriname (Linnaeus, 1775) that included intertidal plants such as the red mangrove, *Rhizophora mangle* L., and the black mangrove, *Avicennia* sp.

First record in Guyana [British Guiana], 1844

Schomburgk (1847, p. 406) recorded *S. alterniflora* (as *S. fasciculata* Pal. de Beauv.) from British Guiana based on specimens “by no means abundant” collected in brackish water, apparently sometime between 1835 and 1844; we thus use 1844 as the latest possible date (Schomburgk, 1848; Roth, 1922).

First record in Uruguay, 1880

Spartina alterniflora was first reported in the Uruguay region *circa* 1880, by reference to the presence of a fungus (*Sclerotium*) growing on *S. brasiliensis* (= *S. alterniflora*) (Spegazzini, 1882). While Spegazzini reported the record as the "Bonaria" region, an older allusion to a broad region including Uruguay and the Buenos Aires province (see a contemporary discussion of this term in Hicken, 1910, pp. 6-7), it is clear that he was referring to collections from Uruguay, because he did not include *S. brasiliensis* in his Flora of the Buenos Aires province (Spegazzini, 1905). Arechavaleta (1894, pp. 317-318) next reported *S. alterniflora* in Uruguay based on observations (but without specific dates) of its inhabiting coastal marshes along the northern shore of the la Plata River: “Vive en lugares cenagosos de las orillas del Río de la Plata, en el espacio de las mareas ordinariamente, así están casi constantemente sumergidas por su base en el agua.”[“It lives in swampy places along the coast of the Río de la Plata, in the space of ordinary tides, and has their base almost constantly submerged in water.”]. This was 26 years before *S. alterniflora* was reported from the Argentinean shore of that river (Parodi, 1918, 1919). We find no valid records for *S. alterniflora* in Uruguay prior to 1880 (e.g., Gibert, 1873).

First record in Guiana [French Guiana] 1886

The first record of *S. alterniflora* in Guiana appears to be a collection in Cayenne in 1886, under the name of *Dactylis fasciculata* Lam. (labels with holotype in the Herbarium Lamarck: P00564318; type fragment deposited in 1935 at the U. S. National Herbarium: A865637). We find no valid records of *S. alterniflora* in Guiana prior to 1886 (e.g., Le Normand, 1859).

First record in Argentina, 1902

The first *S. alterniflora* specimens in Argentina were collected by the well-known Italian-Argentinean botanist Carolo Luigi Spegazzini in 1902 at Punta Alta (BAB #2353, Fig. 1), a major port area since 1898 located near the city of Bahía Blanca (southern part of Buenos Aires Province, Fig. 1). The specimen was identified as *S. alterniflora* by Cristóbal Maria Hicken (undated) and confirmed by Mobberley in 1953 (Mobberley, 1956). Parodi (1919, p.14, footnote) emphasized that the *S. alterniflora* included by Hicken (1910) in his *Chloris Platensis Argentina* was the only species he did not find in the Buenos Aires city area while working on the Chlorideas of the Argentinean Republic, reinforcing the probability that *S. alterniflora* was present in Uruguay but not in Buenos Aires (see above). Hauman (1913) collected *S. alterniflora* in Argentina in 1912 during his expedition to the Negro River estuary and San Blas Bay (BA 39394, Fig. 1), and noted its unmistakable presence at Punta Alta “près de Puerto Militar” [close to the Militar port”, p. 341) ignoring the existence of the specimens collected by Spegazzini ten years before, in that same location. Floral surveys in Argentina establish the earlier absence of *S. alterniflora*. Major botanical accounts made by those who travelled across the coast of Argentina during the 1800s never reported the existence of *S. alterniflora* (Berg, 1877; Hieronymus, 1880; Spegazzini, 1897; Macloskie, 1903; see also Willis, 1914; Hauman, 1926). The invalid reports of *S. alterniflora* at the Río Gallegos estuary (Fig. 1, West, 1977; Isacch *et al.*, 2006) are based upon a mistranslation by West (1977) of the Buenos Aires Province Flora of Angel Cabrera (compare West, 1977: p. 196, and Cabrera, 1970: pp. 387-388, see also Boelcke *et al.*, 1985) that presumably led West to mistakenly use a

synonym of *S. densiflora* as a synonym of *S. alterniflora* (Bortolus, 2001), thereby resulting in the wrong mention of *S. alterniflora* at the Gallegos River estuary, 10 latitudinal degrees south of its then southernmost limit (40° 43' S) at the Negro River (Hauman, 1913, 1926; Mobberley, 1956; Boelcke *et al.*, 1985; Nicora & Rúgolo, 1987; Correa, 1998; Bortolus *et al.*, 2009).

First record in Trinidad, pre-1936 and in Venezuela, 1996

Spartina alterniflora was collected sometime prior to 1936 in Trinidad (Hitchcock, 1936; Hitchcock *et al.*, 1939, p. 583). We have not yet located the source of this record, but presume it will be sometime later than the 1880s, and more likely in the early 1900s, since it remained unrecorded by all major botanical catalogues until 1917 (see Grisebach, 1864; Hitchcock & Chase, 1917). Colonnello (1999) noted it from a number of mainland locations in Venezuela based on 1996 collections. Despite the proximity of Trinidad to the continent, the first formal record from Venezuela is 1996 from an intertidal area at Capure, where *S. alterniflora* was found growing on sand and silt banks associated with seashore dropseed grass (*Sporobolus virginicus* (L.) Kunth), mangrove rubber vine (*Rhabdadenia* sp.) and an herb (*Crenea maritime* Aubl.) (Colonnello, 1999).

References

- Arechavaleta, J. (1894) *Las Gramíneas Uruguayas*. Establecimiento Tipo-Litográfico “Oriental”, Montevideo.
- Berg, C. (1877) Enumeración de las plantas europeas que se hallan como silvestres en la provincia de Buenos Aires y en la Patagonia. *Anales de la Sociedad Científica Argentina*, **3**, 183–204.
- Boelcke, O., Moore, D.M. & Roig, F.A. (1985) *Transecta botánica de la Patagonia Austral*. CONICET, Buenos Aires.
- Bortolus, A. (2001) *Interacciones ecológicas entre el cangrejo cavador Chasmagnathus granulata y los espartillares de Spartina densiflora, mesofauna asociada y características del sustrato en la laguna costera Mar Chiquita (Buenos Aires, Argentina)*. Doctoral Thesis, Universidad Nacional de Mar del Plata, Buenos Aires, Argentina.
- Bortolus, A., Schwindt, E., Bouza, P.J. & Idaszkin, Y.L. (2009) A characterization of Patagonian salt marshes. *Wetlands*, **29**, 772–780.
- Cabrera, A.L. (1970) *Flora de la Provincia de Buenos Aires. Parte II. Gramíneas*. Colección Científica del INTA, Buenos Aires.
- Carlton, J.T. (2009) Deep invasion ecology and the assembly of communities in historical time. *Biological Invasions in Marine Ecosystems* (ed. by G. Rilov and J.A. Crooks), pp. 13–56. Springer-Verlag, Berlin, Germany.

- Colonnello, G. (1999) *Spartina alterniflora* Loisel: primer registro para Venezuela. *Memoria (Fundación La Salle de Ciencias Naturales)*, **59**, 29–34.
- Correa, M.N. (1998) *Flora Patagónica*. Tomo VIII. INTA, Buenos Aires.
- Gibert, E. (1873) *Enumeratio plantarum sponte nascentium agro Montevidensi cum synonymis selectis*. Asociación Rural del Uruguay, Montevideo.
- Grisebach, A.H.R. (1864) *Flora of the British West Indian islands*. L. Reeve & Co., London.
- Hauman, L. (1913) Etude phytogéographique de la région du Rio Negro inférieur. *Anales del Museo Nacional de Buenos Aires*, **24**, 19–442.
- Hauman, L. (1926) Etude phytogéographique de la Patagonie. *Bulletin de la Société Royale de Botanique de Belgique*, **58**, 105–179.
- Hicken, C.M. (1910) *Chloris Platensis Argentina*. Imprenta y Casa Editora Juan A. Alsina, Buenos Aires.
- Hieronymus, J. (1880) *Sertum patagonicum*. *Boletín de la Academia de Córdoba*, **3**, 1–59.
- Hitchcock, A.S. (1936) *Manual of the grasses of the West Indies*. Miscellaneous Publication No. 243. United States Department of Agriculture. 439 pp.
- Hitchcock, A.S. & Chase, A. (1917) *Grasses of the West Indies*. Contribution from the US National Herbarium, vol 18 part 7, Washington Govt, Print Off.
- Hitchcock, A.S., Swallen, J.R. & Chase, A. (1939) North American Flora. (Poales) Poaceae (pars). *The New York Botanical Garden*, **17**, 543–638.
- Isacch, J.P., Costa, C.S.B., Rodríguez-Gallego, L., Conde, D., Escapa, M., Gagliardini, D.A. & Iribarne, O.O. (2006) Distribution of salt marsh plant communities associated with environmental factors along a latitudinal gradient on the southwest Atlantic coast. *Journal of Biogeography*, **33**, 888–900.
- Le Normand, M.R. (1859) Catalogue des plantes recueillies a Cayenne par M. Deplanche, chirurgien de l'avis à vapeur le Rapide. Extrait du 4^e volume du Bulletin de la Société Linnéenne de Normandie (CAEN A. Harel).
- Linnaeus, C. von (1775) *Plantae Surinamenses*. Upsalæ: Typis Edmannianis.
- Longhi-Wagner, H.M., Baldini, R.M. & Araujo, A.C. (2010) *Cyperacea Raddiana: a nomenclatural and taxonomic study of the Cyperaceae published in G. Raddi's Agrostografia brasiliensis*. *Kew Bulletin*, **65**, 449–461.
- Macloskie, G. (1903) *Flora patagonica, the flowering plants, spermatophyta or phanerogamia*. Reports of The Princeton University Expeditions to Patagonia, 1896-1899. Vol VIII. pp. 139–920.
- Mobberley, D.G. (1956) Taxonomy and distribution of the genus *Spartina*. *Iowa State College Journal of Science*, **30**, 471–574.
- Nicora, E.G., & Rúgolo, Z.E. (1987) *Los géneros de gramíneas de América Austral. Argentina, Chile, Uruguay y áreas limítrofes de Bolivia, Paraguay y Brasil*. Editorial Hemisferio Sur, Buenos Aires.
- Parodi, L.R. (1918) Notas preliminares sobre las Chlorideas de la República Argentina. *Physis*, **4**, 167-185.
- Parodi, L.R. (1919) Las Chlorideas de la República Argentina. *Extracto de la revista de la Facultad de Agronomía y Veterinaria*, **2**, 233–335.
- Pires-O'Brien, M.J. (1993) An essay on the history of natural history in Brazil, 1500–1900. *Archives of Natural History*, **20**, 37–48.
- Pulle, A. (1906) *An enumeration of the vascular plants known from Surinam, together with their distribution and synonymy*. Leiden – E.J. Brill Ltd.
- Raddi, G. (1823) *Agrostografia Brasiliensis*. Memoria del Sig. Giuseppe Raddi. Socio corrispondente della R. Accademia Lucchese.
- Roth, W.E. (1922) Richard Schomburgk's travels in British Guiana, 1840-1844. *Daily Chronicle*, p. 402.

- Saarela, J.M. (2012) Taxonomic synopsis of invasive and native *Spartina* (Poaceae, Chloridoideae) in the Pacific Northwest (British Columbia, Washington and Oregon), including the first report of *Spartina* × *townsendii* for British Columbia, Canada. *PhytoKeys*, **10**, 25–82.
- Schomburgk, R. (1847) Description of some grasses and sedges from the east coast of Demerara, with remarks on the geographical distribution of the species. *Annals and Magazine of Natural History*, **20**, 396–409.
- Schomburgk, R. (1848) *Reisen in Britisch-Guiana in den Jaiiren 1840-1844*. Leipzig, Verlagsbuchhandlung von J. J. Weber.
- Spegazzini, C. (1882) Fungi Argentini additis nonnullis brasiliensibus montevidensibusque. *Anales de la Sociedad Científica Argentina*, **13**, 60–64.
- Spegazzini, C. (1897) Plantae Patagoniae. *Revista de la Facultad de Agronomía y Veterinaria*, **30/31**, 579–580.
- Spegazzini, C. (1905) *Flora de la Provincia de Buenos Aires*. Imprenta de M. Biedma e hijo, Bolívar, Argentina.
- West, R.C. (1977) Tidal salt-marsh and mangal formation of Middle and South America. *Wet coastal Ecosystems* (ed. by V.J. Chapman), pp. 193–213. Elsevier, Amsterdam, Netherlands.
- Willis, B. (1914) *Northern Patagonia, character and resources*. Scribner Press, New York.