

Supporting *Spartina*: Interdisciplinary perspective shows *Spartina* as a distinct solid genus

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ABSTRACT

In 2014 a DNA-based phylogenetic study confirming the paraphyly of the grass subtribe *Sporobolinae* proposed the creation of a large monophyletic genus *Sporobolus*, including (among others) species previously included in the genera *Spartina*, *Calamovilfa*, and *Sporobolus*. *Spartina* species have contributed substantially (and continue contributing) to our knowledge in multiple disciplines, including ecology, evolutionary biology, molecular biology, biogeography, experimental ecology, biological invasions, environmental management, restoration ecology, history, economics, and sociology. There is no rationale so compelling to subsume the name *Spartina* as a subgenus that could rival the striking, global iconic history and use of the name *Spartina* for over 200 years. We do not agree with the subjective arguments underlying the proposal to change *Spartina* to *Sporobolus*. We understand the importance of both the objective phylogenetic insights and of the subjective formalized nomenclature and hope that by opening this debate we will encourage positive feedback that will strengthen taxonomic decisions with an interdisciplinary perspective. We consider that the strongly distinct, monophyletic clade *Spartina* should simply and efficiently be treated as the genus *Spartina*.

Key words: cordgrass, salt marsh, coastal ecology, botanical nomenclature, interdisciplinary decisions, integrative analysis

In 2014 a DNA-based phylogenetic study confirming the paraphyly of the grass subtribe *Sporobolinae* proposed the creation of a large monophyletic genus *Sporobolus*, including (among others) species previously included in the genera *Spartina*, *Calamovilfa*, and *Sporobolus* (Peterson et al. 2014*a,b*). This comprehensive phylogenetic research is an important contribution that provides critical insights into the evolutionary history of the *Sporobolinae*, encompassing its morphological, physiological and chromosome number evolution. It also provides a clear picture of the closest relative (sister) lineages of *Spartina*, which is of crucial importance for understanding the emergence of this polyploid clade which includes only tetraploid to dodecaploid species with a basic chromosome number of $x=10$ (Ainouche et al. 2009).

The rules for naming plant taxa are governed by the International Association for Plant Taxonomy and detailed in the International Code of Botanical Nomenclature (ICBN; Turland et al. 2018). The guiding principle in this nomenclature is *priority*, with a formal base date of 1753 (first publication of *Species Plantarum* by Linnaeus) for historical precedence. The name *Spartina* (*Spartina* Schreb., *Gen. Pl.* ed. 8[a]. 43. 1789) has historical priority over *Sporobolus* (*Sporobolus* R. Brown, *Prodr.* 169. 1810) and *Calamovilfa* (*Calamovilfa*, A. Gray), *Hack.*, *True Grasses* 113. 1890) under the ICBN rules. The newly combined monophyletic genus should retain the priority name *Spartina* first published in 1789, that predates recognition and description of *Sporobolus* in 1810. While Peterson et al. (2014*a*) recognized that the name *Spartina* had nomenclatural priority, they proposed conserving *Sporobolus* against *Spartina* as well as other genera. Their proposal was accepted by a Permanent Nomenclature Committee of the

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International Association for Plant Taxonomy. The authors argued that conserving the name *Sporobolus* would avoid taxonomic destabilization, noting that shifting all names to the senior name *Spartina* would necessitate many new binomial combinations and heterotypic synonyms. This proposal, however, presents major disadvantages including not only the creation of an extremely large genus that encompasses highly divergent clades (e.g. *Spartina* diverged from its sister clade sometimes 12-20 MYA; Rousseau-Gueutin et al. 2015), but also overlooking the long and well-rooted history of scientific, cultural and socio-economic relevance implicit in the name *Spartina*. The important criterion for rejection or conservation of botanical names is to avoid of “disadvantageous nomenclatural changes” (MacNeill et al. 2015). We do not agree with the rationale underlying the proposal to change *Spartina* to *Sporobolus*. We argue that this change will serve to undermine the legacy of significant advances achieved after decades of worldwide multidisciplinary efforts, often at immense cost.

The genus *Spartina* Schreb. is a morphologically well-circumscribed group of grasses (Mobberley 1956), representing a monophyletic clade (Baumel et al. 2002, Fortune et al. 2007, Peterson et al. 2014a). Its species are abundant and widely distributed on every continent except for Antarctica and are present on some of the most remote islands of the Atlantic, Pacific and Indian Oceans. Some *Spartina* species are among the most studied plant species (e.g., Pyšek et al. 2008) and the genus has contributed substantially (and it continues contributing) to our knowledge in multiple disciplines, including evolutionary biology, molecular biology, biogeography, experimental ecology, environmental management, restoration ecology, invasion ecology, history, economics, and sociology.

The smooth cordgrass *Spartina alterniflora*, for instance, is a well-known salt marsh plant on temperate and subtropical coasts. This iconic species has inspired some of the most insightful concepts and perspectives in modern ecology, including studies on the causal processes of plant zonation, debates on the dynamics of soil nutrients in marine and terrestrial ecosystems, the biodegradation of organic pollutants, the negative vs. positive interactions in community ecology, the global paradigm on outwelling-pulsing events in integrative ecology, the “connectivity” through trophic interactions including the nursery role hypothesis (Haines 1979, Valiela and Teal 1979, Mendelsohn et al. 1981, Weinstein and Kreeger 2000, Beck et al. 2001, Bruno et al. 2003), the functioning of environmental eutrophication and the paramount "top-down vs. bottom-up" processes debate in ecosystem ecology (Bertness et al. 2001, Mendelsohn and Morris 2001, Silliman and Bertness 2002, Silliman and Bortolus 2003, Valiela 2015). It has further fostered key advances in our understanding of the role of biotic resistance and legacy effects in invasion biology (Dethier and Hacker 2005, Hacker and Dethier 2006, 2009, Rilov and Crooks 2009) as well as advances in biogeomorphology (Morris et al. 2002). Species such as *S. alterniflora* figured prominently in agriculture and botany in the colonial Americas (Eliot 1821, Barlett 1908), as well as in pioneer works on coastal biogeography (Chapman 1960). In modern times *Spartina* species have played a major role in long-term studies of coastal environmental engineering, inspiring the “ecological mirages hypothesis” (Bortolus et al. 2015), and in conservation ecology relative to coastal accretion and marsh creation, as well as of linkages to primary and secondary production of fauna species worldwide (Costa and Davy 1992, Adam 1993, Bertness 1999, Gan et al. 2009, Silliman et al. 2009).

Other species of *Spartina* have also made critical contributions to scientific knowledge. *Spartina anglica*, known as common cordgrass, is a model of recent allopolyploid speciation (Ainouche et al. 2004). This species derived from genome doubling of the F1 hybrid *S. x townsendii* of the native European *S. maritima* and the introduced American *S. alterniflora* (Gray et al. 1991, Ainouche et al. 2009, Strong and Ayres 2013). This recent speciation event following hybridization and polyploidy makes this lineage a model system for studying the effects of recurrent genome merger and duplication in plants (Ainouche et al. 2004, 2012, Kueffer et al. 2013). *S. anglica* provided the evidence to reconstruct the long-term epidemic of the ergot fungus *Claviceps purpurea* (Raybould et al. 1998). It is also considered a key model species in the interdisciplinary field of “BioGeoMorphology”, demonstrating the crucial importance of organism traits in landscape formation (Bouma et al. 2005, 2013, Temmerman et al. 2007, Schwarz et al. 2018). This species is one of the “100 World's Worst Invasive Alien Species” and is widely regarded as an aggressive non-native species in Europe, the North American Pacific coast, South American Atlantic coast, China, New Zealand, Australia and South Africa. In fact, *S. alterniflora* and *S. anglica* are responsible for some of the largest continental-scale bioinvasion events ever recorded in Asia (Qiu 2013) and the Americas (Bortolus et al. 2015) having reshaped vast coastal-marine ecosystems and altered coastal geomorphology, biodiversity, and primary and secondary productivity. These invasions resulted in striking, cascading socio-economic impacts (Li et al. 2009, Strong and Ayres 2009, Wan et al. 2009, Saarela 2012, Luque et al., 2014, Yin et al. 2015).

The saltmeadow cordgrass *S. patens* has long been central to a number of important experiments in marine ecology, including foundational work designed to understand coastal plant zonation (Bertness 1991), microevolution of clonal plants (Silander 1979) and the physiological

mechanisms for the intra- and extra-cellular regulation in habitats where hypersaline conditions and the lack of oxygen can reach toxic levels for most species (Burdick and Mendelsohn 1987, Morris 1984, Pennings and Bertness, 2001). The prairie cordgrass *S. pectinata* is currently used in predictive models focusing on different genotypes for woody biomass production in bioenergy research, and in studies directed to identify stress tolerance genes, as well as in pollutant remediation projects (Carpita and Sage, 2015, Friesen et al. 2015). Manipulative experiments with *S. foliosa* and *S. densiflora* illustrate the major control that these species can exert on physical conditions and the consequences for native and introduced invertebrates along the North Pacific and the Southwestern Atlantic respectively (Levin et al. 2006, Whitcraft and Levin 2007, Sueiro et al. 2012, 2013). The austral cordgrass *S. densiflora* is described as a key dominant in a new type of coastal environment named “rocky marshes” (Bortolus et al. 2009). This species and its hybrids also permitted elucidation of the complex routes non-native species follow across oceans, with work in the USA and Spain showing that introduced species may lay fallow for decades before aggressively spreading at unprecedented rates (Bortolus 2006, Ayres et al. 2008, Fortune et al. 2008, Castillo et al. 2010, 2018). Substantial advances in understanding adaptations to soil anoxia, soil drainage, and soil chemistry, and how these processes influence plant growth, were achieved by studying *Spartina* species (Weinstein and Kreeger 2001).

Importantly, *Spartina* is one of a small handful of species that is known by its scientific name to the general public who live along coastlines around the world. In its native range it is beloved by environmentalists. In its introduced range, it is the focus of environmental action by citizen scientists. The USA Pacific coast, for instance, is commonly patrolled by volunteers called “*Spartina* Watchers” participating in early-detection activities to discover new non-native *Spartina* populations. This has been repeatedly acknowledged at the “International *Spartina*

Conference”, attended by professional scientists and environmental managers, and held regularly since 1990 in different countries to discuss the problems associated with this plant group, its increasing global distribution, the impacts on human society, and possible solutions.

While databases such as GenBank (<https://www.ncbi.nlm.nih.gov/genbank/>) and Tropicos (<https://www.tropicos.org/>) have unilaterally adopted *Sporobolus*, giving an illusory impression of broad consensus, changing *Spartina* to *Sporobolus* has not found support for nearly half a decade in the primary peer-reviewed scientific literature. On the contrary, Google Scholar (<https://scholar.google.com/>, accessed May 16, 2019) records 7,290 uses of "*Spartina alterniflora*" versus 11 (eleven) uses of "*Sporobolus alterniflorus*" since 2015. Web of Science shows no (zero) listings using *Sporobolus alterniflorus* in the title between 2015 and 2019, while *Spartina alterniflora* has 189 listings. Moreover, a search in Web of Science (accessed May 20, 2019) showed 4,626 papers under the Topic “*Spartina*”, while 690 papers were found using “*Sporobolus*” as a Topic. Given the number of species in each genus, 17 in *Spartina* and about 200 in *Sporobolus* (Peterson et al 2014a) this works out to 8x more papers per species on *Spartina* than *Sporobolus*. The discrepancy becomes more pronounced when the search term is used under the Title category: 1,507 for *Spartina* vs 184 for *Sporobolus* – almost 100x more papers per species have been written on *Spartina* than *Sporobolus*. While only a few examples are cited in this report, if this was a review article, the pages of an entire journal issue would be required to cite all the literature produced on *Spartina* since the genus was first described in 1789. The ultimate test of the value of a taxonomic revision is its acceptance and application by the international scientific community. Clearly, this is not the case with the change of *Spartina* for *Sporobolus*. As one final example, while this work was under review, two papers (Gallego- Tévar et al. 2019, Infante-Izquierdo et al. 2019) that include taxonomic updates on *Spartina* species

were peer reviewed and published by respected journals focused on plant systematics. Similarly, the “New Flora of the British Isles” published in 2019 retains the name *Spartina* after considering the case (Stace 2019). It is of no small concern that globally popular (digital open access websites) databases are likely to induce the acceptance of replacing *Spartina* for *Sporobolus*, while potentially restraining any further nomenclatural discussions and sound open debate.

Spartina is a deeply-nested, strongly supported clade (Peterson et al. 2014a,b). Peterson et al. (2014b) proposed retaining *Spartina* as a subgenus of *Sporobolus* ("A molecular phylogeny and new subgeneric classification..." (title of paper) and "A proposed classification of the *Sporobolinae* and subgeneric classification of *Sporobolus*" (Table 2 legend)). Whether a name is employed as a genus or subgenus does not change any conclusions about evolutionary relationships derived from molecular-based (or morphological-based) phylogenies. Decisions as to whether a name is used as a genus or subgenus are subjective; no commission, congress, or committee rules on this question. There is clearly no rationale so compelling to subsume the name *Spartina* as a subgenus that could rival the striking, global iconic history and use of the name *Spartina* for over 200 years. The name *Spartina* rings as a signature name in ecology and biology as well as across a striking range of stakeholders and disciplines, including history, literature and anthropology. Within this context, the phylogenetic relationships provided by Peterson et al. (2014b) supply good basis for (re)naming other *Sporobolinae* clades in agreement with other experts.

We unequivocally recognize the value of molecular work that may provide the basis for objective phylogenetic insights. This said, on this report we have focused on a subjective nomenclatural question, which we feel deserves critical attention. In this sense, we do not seek to stifle differing nomenclatural viewpoints but, rather, the contrary (see Bortolus 2008, 2012). Thus, our work should not be interpreted as a general argument for the systematic rejection of name changes — indeed, we fully understand the importance of both phylogenetic resolutions and of the resulting formalized nomenclature that may accompany such advances (Thomson et al. 2018). Given that scientific names are hypotheses, our hope is that by opening this debate we will encourage positive feedback that will strengthen taxonomic decisions. Few taxa, in botany or zoology, have ever provided such an immense impact in so many scientific and non-scientific fields as has *Spartina*, intimately linked to the initial recognition of the ecological importance of coastal salt marshes globally as well as contributing to our understanding of the top-five direct drivers of change in nature (IPBES 2019) with profound global impacts. The name *Spartina* has linked and should continue to link scientists, citizens and environmental managers across the globe. We, therefore, consider that the distinct well-knit clade designated as subgenus *Spartina* by Peterson et al. 2014a, should simply and efficiently be treated as the genus *Spartina*.

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Literature Cited

- Adam, P. 1993. Saltmarsh ecology. Cambridge Studies in Ecology. Cambridge University Press, Cambridge.
- Ainouche, M., A. Baumel, and A. Salmon. 2004. Biological relevance of polyploidy, ecology to genomics: *Spartina anglica* Schreb. a natural model system for analyzing early evolutionary changes that affect allopolyploid genomes. *Biological Journal of the Linnean Society* 82:475–484.
- Ainouche, M. L., P. Fortune, A. Salmon, C. Parisod, M. A. Grandbastien, K. Fukunaga, K. M. Ricou, and M.-T. Misset. 2009. Hybridization, polyploidy and invasion: Lessons from *Spartina* (Poaceae) *Biological Invasions* 11:1159–1173.
- Ainouche, M., H. Chelaifa, J. Ferreira De Carvalho, S. Bellot, A. Ainouche, and A. Salmon. 2012. Polyploid evolution in *Spartina*: Dealing with highly redundant hybrid genomes. Pages 225–244 in P. S. Soltis and D. E. Soltis, editors. *Polyploidy and Genome Evolution*. Springer, New York, USA.
- Ayres, D. R., E. K. Grotkopp, K. Zaremba, C. M. Sloop, M. J. Blum, J. P. Bailey, C. K. Anttila, and D. R. Strong. 2008. Hybridization between invasive *Spartina densiflora* (Poaceae) and native *S. foliosa* in San Francisco Bay, California, USA. *American Journal of Botany* 95: 713–719
- Barlett, 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.
- Baumel, A., M. Ainouche, R. J. Bayer, A-K. Ainouche, and M-T. Misset. 2002. Molecular Phylogeny of hybridizing species from the genus *Spartina* Schreb. (Poaceae). *Molecular Phylogenetics and Evolution* 22:303–3014.

- Beck, M. W., K. L. Heck, JR., K. W. Able, D. L. Childers, D. B. Eggleston, B. M. Gillanders, B. Halpern, C. G. Hays, L. Hoshino, T. J. Minello, R. J. Orth, P. F. Sheridan, and M. P. Weinstein. 2001. The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. *Bioscience* 51:633–641.
- Bertness, M. D. 1991. Zonation of *Spartina patens* and *Spartina alterniflora* in a New England salt marsh. *Ecology* 72:138–148.
- Bertness, M. D. 1999. *The Ecology of Atlantic shorelines*. Sinauer Associates, Sunderland, Massachusetts, USA.
- Bertness, M. D., S. D. Gaines, and M. E. Hay, editors. 2001. *Marine Community Ecology*. Sinauer Associates, Sunderland, Massachusetts, USA.
- Bortolus, A. 2006. The austral cordgrass *Spartina densiflora* Brong.: its taxonomy, biogeography and natural history. *Journal of Biogeography* 33:158–68.
- Bortolus, A. 2008. Error cascades in the biological sciences: the unwanted consequences of using bad taxonomy in ecology. *Ambio* 37:114–118.
- Bortolus, A. 2012. Guiding authors to reliably use taxonomic names. *Trends in Ecology and Evolution* 27:418.
- Bortolus, A., E. Schwindt, P. J. Bouza, and Y. L. Idaszkin. 2009. A characterization of Patagonian salt marshes. *Wetlands* 29:772–780.
- Bortolus, A., J. T. Carlton, and E. Schwindt. 2015. Reimagining South American coasts: Unveiling the hidden invasion history of an iconic ecological engineer. *Diversity and Distributions* 21:1267–1283.
- Bouma, T. J., M. B. De Vries, E. Low, G. Peralta, I. C. Tánzos, J. van de Koppel, and P. M. J. Herman. 2005. Trade-offs related to ecosystem engineering: A case study on stiffness of emerging macrophytes. *Ecology* 86:2187–2199.

- Bouma, T. J., S. Temmerman, L. A. van Duren, E. Martini, W. Vandenbruwaene, D. P. Callaghan, T. Balke, G. Biermans, P. C. Klaassen, P. van Steeg, F. Dekker, J. van de Koppel, M. B. de Vries, and P. M. J. Herman. 2013. Organism traits determine the strength of scale-dependent bio-geomorphic feedbacks: A flume study on three intertidal plant species. *Geomorphology* 180–181:57–65.
- Bruno, J. F., J. J. Stachowicz, and M. D. Bertness. 2003. Inclusion of facilitation into ecological theory. *Trends in Ecology and Evolution* 18:119–125.
- Burdick, D. M. and I. A. Mendelssohn. 1987. Waterlogging responses in dune, swale and marsh populations of *Spartina patens* under field conditions. *Oecologia*, 74:321-329.
- Carpita, N. and R. F. Sage. 2015. Plants and bioenergy. *Journal of Experimental Botany* 66:4093–4095.
- Castillo, J. M., D. R. Ayres, P. Leira-Doce, J. Bailey, M. Blum, D. R. Strong, T. Luque, and E. Figueroa. 2010. The production of hybrids with high ecological amplitude between exotic *Spartina densiflora* and native *S. maritima* in the Iberian Peninsula. *Diversity and Distributions* 16: 547–558.
- Castillo, J. M., S. Dréano, J. Castillo, B. Gallego-Tévar, E. Figueroa, B. Grewell, D. Vallet, H. Rousseau, J. Keller, O. Lima, S. Dréano, A. Salmon, and M. Ainouche. 2018. Low genetic diversity contrasts with high phenotypic variability in heptaploid *Spartina densiflora* populations invading the Pacific coast of North America. *Ecology and Evolution* 8:4992–5007.
- Chapman, V. J. 1960. Salt marshes and salt deserts of the world. Interscience Pub. Inc., New York, USA.

- Costa, C. B., and A. J. Davy. 1992. Coastal saltmarsh communities of Latin America. Pages 179–212 in U. Seeliger, editor. Coastal plant communities of Latin America. Academic Press, New York, USA.
- Dethier, M. N. and S. D. Hacker. 2005. Physical factors vs. biotic resistance in controlling the invasion of an estuarine marsh grass. *Ecological Applications* 15:1273–1283.
- Elliott, S. 1821. A sketch of the botany of South Carolina and Georgia. Schenck J.R., Charleston, USA.
- Fortune, P. M., K. Schierenbeck, D. Ayres, A. Bortolus, O. Clatrice, and M. L. Ainouche. 2008. The enigmatic invasive *Spartina densiflora*: a history of hybridizations in a polyploidy context. *Molecular Ecology* 17:4304–4316.
- Friesen, P. C., M. M. Peixoto, D. K. Lee, and R. F. Sage. 2015. Sub-zero cold tolerance of *Spartina pectinata* (prairie cordgrass) and *Miscanthus × giganteus*: candidate bioenergy crops for cool temperate climates. *Journal of Experimental Botany* 66: 4403–4413.
- Gallego- Tévar, B., Grewell, B.J., Rousseau H., Keller, J. Ainouche, A., Lima, O., Dréano, S., Salmon, A., Figueroa, E., Ainouche, M., Castillo, J.M. 2019. Genetic structure of *Spartina* hybrids between native *Spartina maritima* and invasive *Spartina densiflora* in Southwest Europe. *Perspectives in Plant Ecology, Evolution and Systematics* 37:26-38.
- Gan, X., Y. Cai, C. Choi, Z. Ma, J. Chen, and B. Li. 2009. Potential impacts of invasive *Spartina alterniflora* on spring bird communities at Chongming Dongtan, a Chinese wetland of international importance. *Estuarine, Coastal and Shelf Science* 83:211–218.
- Gray, A. J., D. F. Marshall, and A. F. Raybould. 1991. A century of evolution in *Spartina anglica*. *Advances in Ecological Research* 21:1–62.
- Hacker, S. D., and M. N. Dethier. 2006. Community modification by a grass invader has differing impacts for marine habitats. *Oikos* 113:279–286.

Hacker, S. D., and M. N. Dethier. 2009. Differing consequences of removing ecosystem-modifying invaders: significance of impact and community context to restoration potential. Pages 375–385 in G. Rilov and J. Crooks, editors. *Marine Bioinvasions: Ecology, Conservation and Management Perspectives*, Springer-Verlag, Berlin, Germany.

Haines, E. B. 1979. Interactions between Georgia salt marshes and coastal waters: A changing paradigm. Pages 35–46 in R. J. Livingston, editor. *Ecological Processes in Coastal and Marine Systems*. Plenum Press, New York, USA.

Infante-Izquierdo, M.D., Gallego-Tévar, B., Sanchez Gullon, E., Nieva, F. J. J., Grewell, B.J., Castillo, J.M., Munoz Rodriguez, A.F. 2019. Morphological and anatomical evidence supports differentiation of new interspecific hybrids from native *Spartina maritima* and invasive *S. densiflora* (Poaceae, subfamily Chloridoideae). *Plant Systematics and Evolution*.

<https://doi.org/10.1007/s00606-019-01591-5>

Kueffer, C., P. Pyšek, and D. M. Richardson. 2013. Integrative invasion science: model systems, multi-site studies, focused meta-analysis and invasion syndromes. *New Phytologist* 200:615–633.

Levin, L. A., C. Neira, and E. D. Grosholz. 2006. Invasive cordgrass modifies wetland trophic function. *Ecology* 87:419–432.

Li, B., C. H. Liao, X. D. Zhang, H. L. Chen, Q. Wang, Z. Y. Chen, X. J. Gan, J. H. Wu, B. Zhao, Z. J. Ma, X. I. Cheng, L. F. Jiang, and J. K. Chen. 2009. *Spartina alterniflora* invasions in the Yangtze River estuary, China: an overview of current status and ecosystem effects. *Ecological Engineering* 35:511–520.

Luque, G. M., C. Bellard, C. Bertelsmeier, E. Bonnaud, P. Genovesi, D. Simberloff, and F. Courchamp. 2014. The 100th of the world's worst invasive alien species. *Biological Invasions* 16:981–985.

McNeill, J., Redhead, S. A., and J. H. Wiersema. 2015. Guidelines for proposals to conserve or reject names. *Taxon* 64: 1-4.

Mendelssohn, I. A., K. L. McKee and W. H. Patrick. 1981. Oxygen deficiency in *Spartina alterniflora* roots: metabolic adaptation to anoxia. *Science* 214:439-441.

Mendelssohn, I. A., and J. T. Morris. 2000. Eco-physiological controls on the productivity of *Spartina alterniflora* Loisel. Pages 59–80 in M. P. Weinstein and D. A. Kreeger editors. *Concepts and Controversies in Tidal Marsh Ecology*. Kluwer Academic Publishers, Boston, Massachusetts, USA.

Mobberley, D. G. 1956. Taxonomy and distribution of the genus *Spartina*. *Iowa State College Journal of Science* 30:471–574.

Morris, J. T. 1984. Effects of oxygen and salinity on ammonium uptake by *Spartina alterniflora* Loisel and *Spartina patens* (Aiton) Muhl. *Journal of Experimental Marine Biology and Ecology* 78:87–98.

Morris, J. T., P.V. Sundareshwar, C.T. Nietch, B. Kjerfve, and D. R. Cahoon. 2002. Responses of coastal wetlands to rising sea level. *Ecology* 83:2869-2877.

McNeil, J., S. A. Redhead, and J. H. Wiersema. 2015. Guidelines for proposals to conserve or reject names. *Taxon* 64:1–4.

Pennings, S. C., and M. D. Bertness. 2001. Salt marsh communities. Pages 289–316 in M. Bertness, S. D. Gaines and M. E. Hay, editors. *Marine Community Ecology*. Sinauer Associates, Sunderland, Massachusetts, USA.

Peterson, P. M., K. Romaschenko, Y. Herrera Arrieta, and J. M. Saarela. 2014a. Proposal to conserve *Sporobolus* against *Spartina*, *Crypsis*, *Poncoletia*, and *Heleochloa* (*Poaceae: Chloridoideae: Sporobolinae*). *Taxon* 63:1373–1374.

- Peterson, P.M., K. Romaschenko, Y. Herrera Arrieta, and J. M. Saarela. 2014b. A molecular phylogeny and new subgeneric classification of *Sporobolus* (Poaceae: Chloridoidea: Sporobolinae). *Taxon* 63:1212–1243.
- Pyšek, P., D. M. Richardson, J. Pergl, V. Jarošík, Z. Sixtová, and E. Weber. 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.
- Raybould, A. F., A. J. Gray, and R. T. Clarke. 1998. The long-term epidemic of *Claviceps purpurea* on *Spartina anglica* in Poole Harbour: pattern of infection, effects on seed production and the role of *Fusarium heterosporum*. *New Phytologist* 138:497–505.
- Rilov, G., and J. Crooks, editors. 2009. *Marine Bioinvasions: Ecology, Conservation and Management Perspectives*. Springer-Verlag, Berlin, Germany.
- Rousseau-Gueutin, M., S. Bellot, G. E. Martin, J. Boutte, H. Chelaifa, O. Lima, S. Michon-Coudouel, D. Naquin, A. Salmon, A. K. Ainouche, and M. Ainouche. 2015. The chloroplast genome of the hexaploid *Spartina maritima* (Poaceae, Chloridoideae): Comparative analyses and molecular dating. *Molecular Phylogenetics and Evolution* 93:5–16.
- 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 x townsendii* for British Columbia, Canada. *PhytoKeys* 10:25–82.
- Schwarz, C., O. Gourgue, J. van Belzen, Z. C. Zhu, T. J. Bouma, J. van de Koppel, G. Ruessink, N. Claude, and S. Temmerman. 2018. Self-organization of a biogeomorphic landscape controlled by plant life-history traits. *Nature Geoscience* 11:672–677.
- Silander, J. A. 1979. Microevolution and clone structure in *Spartina patens*. *Science* 203:658–660.

Silliman, B. R., and M. D. Bertness. 2002. A trophic cascade regulates salt marsh primary production. *Proceedings of the National Academy of Sciences* 99:10500–10505.

Silliman, B., and A. Bortolus. 2003. Underestimation of *Spartina* production in western Atlantic marshes: marsh invertebrates eat more than just detritus. *Oikos* 101:549–554.

Silliman, B. R., M. D. Bertness, and E. D. Grosholz, editors. 2009. Human impacts on salt marshes. A global perspective. University of California Press, Berkeley, USA.

Stace, C. 2019. *New Flora of the British Isles* (4th Ed). Cambridge University Press, Cambridge, UK.

Strong, D. R., and D. A. Ayres. 2009. *Spartina* introductions and consequences in salt marshes: arrive, survive, thrive, and sometimes hybridize. Pages 3–22 in B. R. Silliman, M. D. Bertness, and E. D. Grosholz, editors. *Human Impacts on Salt Marshes: A Global Perspective*. Berkeley: University of California Press, California, USA.

Strong, D. R., and D. R. Ayres. 2013. Ecological and evolutionary misadventures of *Spartina*. *Annual Review of Ecology and Systematics* 44:389–410.

Sueiro M.C., A. Bortolus, and E. Schwindt, 2012. The role of the physical structure of *Spartina densiflora* Brong. in structuring macroinvertebrate assemblages. *Aquatic Ecology* 46:25–36.

Sueiro M.C., E. Schwindt, M.M. Mendez, and A. Bortolus. 2013. Interactions between ecosystem engineers: A native species indirectly facilitates a non-native one. *Acta Oecologica* 51:11–16.

Temmerman, S., T. J. Bouma, J. van de Koppel, D. D. van der Wal, M. B. De Vries, and P. M. J. Herman. 2007. Vegetation causes channel erosion in a tidal landscape. *Geology* 35:631–634.

Thomson, S. A., R. L. Pyle, S. T. Ahyong, M. Alonso-Zarazaga, J. Ammirati, J. F. Araya, et al. 2018. Taxonomy based on science is necessary for global conservation. *PLoS Biology* 16:e2005075.

Turland, N. J., Wiersema, J. H., Barrie, F. R., Greuter, W., Hawksworth, D. L., Herendeen, P. S.,

Knapp, S., Kusber, W.-H., Li, D.-Z., Marhold, K., May, T. W., McNeill, J., Monro, A. M.,

Prado, J., Price, M. J. & Smith, G. F. (eds.) 2018. International Code of Nomenclature for

algae, fungi, and plants (Shenzhen Code) adopted by the Nineteenth International Botanical

Congress Shenzhen, China, July 2017. Regnum Vegetabile 159. Glashütten: Koeltz Botanical

Books. DOI <https://doi.org/10.12705/Code.2018>

Valiela, I. 2015. Marine ecological processes. Springer-Verlag, New York, USA.

Valiela, I., and J. M. Teal. 1979 The nitrogen budget of a salt marsh ecosystem. *Nature* 280:652–656.

Wan, S., P. Qin, J. Liu, and H. Zhou. 2009. The positive and negative effects of exotic *Spartina alterniflora* in China. *Ecological Engineering* 35:444–452.

Weinstein, M. P., and D. A. Kreeger, editors. 2000. Concepts and Controversies in Tidal Marsh Ecology. Springer Netherlands, Netherlands.

Whitcraft C. R., and L. A. Levin. 2007. Light-mediated regulation of the sediment ecosystem by salt marsh plants. *Ecology* 88:904–917.

Yin, S., S. An, Q. Deng, J. Zhang, H. Ji, and X. Cheng. 2015. *Spartina alterniflora* invasions impact CH₄ and N₂O fluxes from a salt marsh in eastern China. *Ecological Engineering* 81:192–199.