PERSPECTIVES AND PARADIGMS

Exploring how non-native seagrass species could provide essential ecosystems services: a perspective on the highly invasive seagrass *Halophila stipulacea* in the Caribbean Sea

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Abstract The loss of biodiversity by the replacement of invasive species could lead to the loss of functional traits that maintain certain ecosystem services (ES). The ES method provides a conceptual framework to value changes of functional traits related to this loss of biodiversity. The Caribbean Sea offers a multifaceted seascape to evaluate this approach as native seagrass species (*Thalassia testudinum*, *Syringodium filiforme* or *Halodule wrightii*) cohabit this region together with the invasive seagrass *Halophila stipulacea*, native to the Indian Ocean. The functional traits of native seagrass species in the Caribbean are compared to different traits of *H. stipulacea* observed worldwide with the aim of evaluating the dimensions of this change in terms of the ES that seagrass meadows provide in the Caribbean. Under a changing seascape due to climate change and anthropogenic pressures that have driven the disappearance of most seagrass meadows in the Caribbean, we explore how this invasive seagrass could play a role in restoration attempts as a pioneer species where native species have been lost. The potential unintended consequences of the presence of *H. stipulacea* to replace services of native species are also noted.

Keywords *Halophila stipulacea* · Caribbean Sea · Pioneer species · Functional traits · Facilitative interactions

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Introduction

Since the late 1970s, the concept of ecosystems services (ES) has been gaining increased traction within biodiversity conservation planning, environmental policy-making, and valuation of ecosystems (Costanza et al. 1997, 2017). Using the lens of ES, we question the relevance of understanding diverse impacts of invasive species by focusing on their traits and related functions that can, in turn, be positive, particularly in the context of ecosystem degradation.

In exploring how particular invasive species could potentially provide valued and less visible forms of ES, we draw on a more expansive definition of the concept proposed by de Groot et al. (2002) as "the capacity of natural processes and components to provide goods and services that satisfy human needs, directly or indirectly." As an interdisciplinary concept, ES can be combined with traits analysis, thereby providing an indicator of the ecosystem's functioning (Diaz and Cabido 2001). Understanding ecosystem functioning as the overall performance of ecosystems (Jax 2005), we define a specific ecosystem function as a process that links different structural elements of the community together (e.g., transfer of energy through the food web). Most of these functions are shared among many of the organisms present in the community (Duarte 2000) and are sustained by the specific traits that the species possess (Suppl. Fig. 1). By adopting a functional approach, species are classified according to functional traits, rather than relying on traditional taxonomic definitions. This is particularly useful for the evaluation of ES where service delivery can be independent of the species identity (Storkey et al. 2013).

Seagrass beds provide beneficial ecosystems functions and services to humans, organisms and other ecosystems (Moberg and Rönnbäck 2003; Barbier et al. 2011). The services and functions are directly correlated to traits of the seagrass species (Bremner 2008; Kilminster et al. 2015). ES and functions of Caribbean seagrass meadows can be also classified according to the type of traits that sustain them; they can be divided into three levels of traits: eco-physiological, morphological and growth, and community structure (Suppl. Fig. 1).

The Caribbean islands offer a good scenario to monitor potential interactions between native and invasive species. Native island ecosystems are vulnerable to impacts of invasive species because of small population size, diversity of indigenous species, and evolutionary effects of isolation (Kairo and Ali 2003). The population and economies of most Caribbean islands have grown in the last 50 years, leading to extensive development of which much has occurred without adequate planning. This, together with rapid urbanization and the growth of tourism, has led to the destruction and degradation of marine habitats, transforming the coastal landscape of many islands. This loss of seagrass beds can lead to a decrease in ES (Orth et al. 2006), such as the increase in particulate sediments in the water column that might negatively affect coral reefs (Gillis et al. 2014) or the loss of commercially important fish species.

For many marine invasive species, the potential for new introductions has grown in recent years through the increase in international trade, tourism, and transport links. As an empirical example for coupling ES with functional traits in the native and invasive species in the Caribbean, we draw on the case of *Halophila stipulacea* as a recent invasive seagrass species in this region. The contemporary presence of *H. stipulacea* is the most widespread in the Eastern Caribbean, particularly the Lesser Antilles (Maréchal et al. 2013). *H. stipulacea* has been noted across the Caribbean Sea for over a decade (Willette et al. 2014) with its near- and long-term effects on complex, intertwined socio-ecological systems remain largely unknown.

Better studied is the spread of *H. stipulacea* as an invasive species in the Mediterranean; however, we argue that its successful colonization was largely a result of the relative absence of native seagrasses (Rogers et al. 2014) making it difficult to compare to the Caribbean. Regardless, while the far-reaching ecological and socio-economic consequences relating to the spread and growth of *H. stipulacea* in the Caribbean seascape remain highly uncertain, its traits and ES documented in other regions of the world may prove valuable in future scenario-mapping and the determining of its management strategies—as both a non-native and invasive species. This perspective adopts a three-tiered approach: i) we ask what is currently known about the ecosystem traits (and thus ES) of *H. stipulacea* based on the literature in their native and invasive ranges; ii) focusing on the Caribbean scenario, we question whether the substitution of *H. stipulacea* can provide services or functions that have been lost due to ecosystem degradation; and finally iii) we explore how this invasive seagrass could be useful in restoration attempts as pioneer species where native species have been lost.

Native seagrasses in the Caribbean: threats and traits

The tropical coastal seascape in the Caribbean has traditionally been comprised of mangrove forests, seagrass beds, and coral reefs (Ogden and Gladfelter 1983). Seagrass beds being in shallow coastal areas at this midpoint, between mangroves and coral reefs, allow them to have reciprocal interconnections (Gillis et al. 2014), that is, providing direct services to both ecosystems (Suppl. Table 1). Seagrass traits supporting these services change across species; therefore, positive connections to two ecosystems may be altered if seagrass composition changes.

For example, seagrass species such as *Thalassia testudinum* reduce wave attenuation via their biomass and leaf length, allowing the establishment of mangrove seedlings, which require calm wave conditions (Table 1). Additionally, the seagrass leaves and roots also bind and stabilize the sediment allowing for clear water for coral reefs (Table 1 and Suppl. Table 1). The ability of seagrasses to uptake nutrients by below-ground biomass is also related to a higher biomass, as a large proportion of the microbial community (diazotrophic bacterium) might be directly attached to the roots and rhizome surfaces (Table 1). Furthermore, *T. testudinum* rhizomes modify sediment redox conditions around their rhizosphere, oxygenating the sediment (Enríquez et al. 2001), thereby providing a more favorable environment for sediment-dwelling organisms (Table 1).

Additionally, the complexity of the seagrass bed habitat provides a sheltered nursery area for juvenile reef fish and invertebrates (e.g., Nagelkerken et al. 2002; Abed-Navandi and Dworschak 2005; Dromard et al. 2017). High plant biomass, the density of seagrass leaves, as well as the leaf width and length features, conceal juveniles from predators (Nagelkerken et al. 2000; Peterson and Heck 2001; Dorenbosch et al. 2007).

While the importance of native seagrasses in Caribbean ecosystems has been widely researched across the natural sciences, there are fewer studies within the marine social sciences (Cullen-Unsworth et al. 2014). Native Caribbean seagrass species are providers of ES to humans, specifically related to recreation, food, tourism, and research (Nordlund et al. 2016). Yet unlike in the Indo-Pacific region, the medicinal or other socio-economic uses, such as housing construction, have barely been documented.

Native seagrass cover in the Caribbean has declined due to the increased human populations and their associated activities (Linton and Fisher 2004; van Tussenbroek et al. 2014). Direct stressors from increasing sediment loads from construction and tourism have affected seagrass resilience and health in sites as Cuba and Belize (Linton and Fisher 2004; Koltes and Opishinski 2009; van Tussenbroek et al. 2014). Boat anchoring has also caused direct physical disturbance in seagrass meadows in US Virgin Islands (Rogers and Beets 2001), whilst snorkelers have affected the physical structure of *T. testudinum* in the Mexican Caribbean by re-suspending sediments and ripping off seagrass leaves (Herrera-Silveira et al. 2010). Finally, increasing nutrient inputs from ground or wastewater have led to eutrophication, as was seen along the Caribbean Mexican coast (Szmant and Forrester 1996; Carruthers et al. 2005).

Anthropogenic impacts of human development can combine with indirect consequences of climate change. For example, Glenn et al. (2015) observed a 30-year warming trend in the Caribbean, and positive trends have been found in annual total precipitation (Stephenson et al. 2014). Regardless, no direct relation has yet been established between climate change and seagrass loss in the Caribbean (Murdoch et al. 2007; van Tussenbroek et al. 2014).

Ecosystem services and functional traits of *H. stipulacea* in their native and Mediterranean and Caribbean invasive ranges: What is known?

Halophila stipulacea is native of the tropical Indo-Pacific bioregion, being restricted to the East coast of Africa, Southeast coast of India, and the Red Sea (Short et al. 2007). From the Red Sea, this species invaded the Mediterranean Sea towards the end of the nineteenth century, after the opening of the Suez Canal. In the early twenty-first century, *H. stipulacea* spread to the Caribbean, likely on anchors of recreational vessels sailing between the Mediterranean and Caribbean Seas (Ruiz and Ballantine 2004; Willette and Ambrose 2009). The recent arrival of *H. stipulacea* to the Caribbean Sea explains the lower number of studies that have yet examined the species'

Table 1 Overview showing native seagrass species in the Caribbean (*Thalassia testudinum*, *Tt*; *Syringodium filiforme*, *Sf*; *Halodule wrightii*, *Hw*), their type of function and associated ecosystem services, the traits that control the function, the value associated with this trait, and the reference

Function (service)	Trait (specific trait)	Species	Value	References
Current wave attenuation (coastal protection)	Community structure (biomass), morphological (leaf length)	*T. testudinum*	Density (m^{-2}): 210–2500, leaf length (m): 0.14–0.8	Weitzman et al. (2015)
Oxygenating the sediment (erosion control)	Community structure (root density), morphological (root length)	*T. testudinum*, *S. filiforme*	Rhizome density (g DW m^{-2}): 125–765 (*Tt*), 11.8–195 (*Sf*); root density (g DW m^{-2}): 11.8–195 (*Tt*), 18.3–79.5 (*Sf*)	Enríquez et al. (2001)
Nitrogen fixation (nutrient source)	Eco-physiological (microbial community)	*T. testudinum*	Nitrogen fixation (mg N m^{-2} day^{-1}): 5.1–140	Welsh (2000)
Food for shrimps (nutrient source)	Eco-physiological (C:N ratio, nutrient content)	*T. testudinum*, *S. filiforme*	C:N ratio: 20.17–29.91 (*Tt*), 20.17–29.91 (*Sf*); N content (%): 0.54–1.42 (*Tt*), 0.84–1.35 (*Sf*)	Abed-Navandi and Dworschak (2005)
Food for parrot fish/damsel fish (nutrient source)	Eco-physiological (C:N ratio)	*T. testudinum*	C:N ratio: 19.7–23.8	Tribble (1981) and Dromard et al. (2017)
Food for turtles (nutrient source)	Eco-physiological (C:N ratio)	*S. filiforme*	C:N ratio: 23	Moran and Bjorndal (2005) and Fourqurean et al. (2010)
Food for gastropods[a] (nutrient source)	Eco-physiological (C:N ratio)	*T. testudinum*, *S. filiforme*, *H. wrightii*	C:N ratio: 16.1–21.8 (*Tt*)	Holzer et al. (2011)
Nursery area for coral reef fish (fisheries)	Community structure (biomass), morphological (leaf length)	*T. testudinum*	Density (m^{-2}): 59.2–93.4; leaf length (m): 0.29–0.30	Nagelkerken et al. (2000) and Dorenbosch et al. (2007)
Mussel habitat (fisheries)	Community structure (biomass), morphological (leaf characteristics)	*T. testudinum*	Above-ground biomass (g DW m^{-2}): 76–240.9; below ground biomass (g DW m^{-2}): 127–1171; leaf length (m): ≈ 0.19; leaf width (m): 0.073–0.075; leaves per shoot: ≈ 2.75–3	Peterson and Heck (2001)

[a]This snail species can feed on many different types of seagrass species including, pioneer species

functional traits as compared to the Mediterranean and Red Sea (Suppl. Table 2).

H. stipulacea is present in different depths. It has adapted to different conditions in its native range, being found at depths from < 1 to 50 m (Sharon et al. 2011). While in its invasive range, the seagrass was dredged from a depth of 145 m off at Cyprus (Lipkin 1975), making it the deepest report of a seagrass worldwide (Short et al. 2007). The ability to perform chloroplast clumping to one part of the cytoplasm of the epidermis may provide this adaptation to different light irradiance scenarios (Sharon and Beer 2008).

The colonization strategy of *H. stipulacea*, as found in other invasive species (Sakai et al. 2001) is based on a rapid growth and a high leaf turnover rate (Wahbeh 1984). Despite the limiting nutrient conditions, *H. stipulacea* can maintain high-density meadows in the nutrient-limited carbonate sediments where it grows (Lipkin 1979). The high production of *H. stipulacea* is sustained by the high uptake rates of

ammonium both in the leaves and the roots (Alexandre et al. 2014). Also, nitrogen fixation, provided by a stable microbiome, might supply this seagrass with enough nitrogen to sustain growth (Suppl. Table 2). The high uptake efficiency developed in the different plant parts allows them to reduce energy transport within the shoots and along the ramet (Suppl. Table 2). These eco-physiological traits may provide advantages in nitrogen cycling and filtering. This also enables *H. stipulacea* to take advantage of sites with high nutrient loading (van Tussenbroek et al. 2016), where other species may eventually not survive because of eutrophication. Finally, *H. stipulacea* has comparable shoot densities in both its native and invasive ranges, which is an important trait that helps sustain diverse invertebrate and fish populations (Suppl. Table 2).

Among marine social sciences, *H. stipulacea* is considered a valuable good in its native range in the Indo-Pacific. The use of *Halophila* species has been recorded as a medicine against malaria and for skin diseases (de la Torre-Castro and Rönnbäck 2004). The potential for antibacterial use against human pathogens has also been demonstrated (Kannan et al. 2010).

H. stipulacea colonization of the Caribbean Sea: Can this invasive species replace the traits and services of the native seagrass ecosystems?

Once in the Caribbean, *H. stipulacea* quickly spread to over 19 islands in the Eastern and Southern Caribbean and to Venezuela's mainland during the 16 years since its discovery at a rate of ~ 35 km year^{-1} (Willette, unpublished data) (Fig. 1). The dispersal of *H. stipulacea* to islands such as Martinique and across the Lesser Antilles appear to be strongly influenced by inter-island marine transportation, particularly associated with heightened tourist activity in the region (Ruiz and Ballantine 2004; Willette and Ambrose 2009).
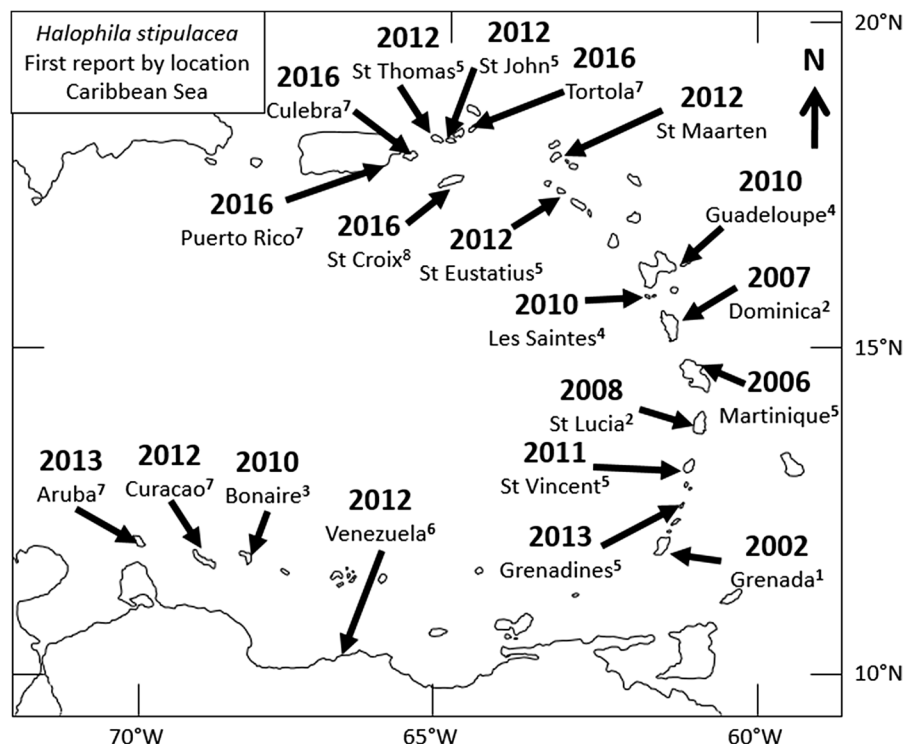
The rapid and widespread colonization of *H. stipulacea* in the Caribbean may be in part attributed to its propensity to break and reproduce via highly dispersive fragments (Willette and Ambrose 2012) that easily detached, float, and are able to quickly root when close to the sediment (Smulders et al. 2017). Only recently, sexual reproductive structures (flowers and fruits) have been seen for *H. stipulacea* both in the

Caribbean and Mediterranean Sea (Chiquillo et al. 2018). This observation may possibly be a consequence of greater surveillance, but it could also potentially be in response to a changing marine environment (Gambi et al. 2009; Georgiou et al. 2016).

Ecologically, *H. stipulacea* in the Caribbean grows both within existing seagrass meadows and in bare sand. Notably, the seagrass grows within the typical bare 'sand halo' characteristic of Caribbean coral reefs, a boundary between a reef and meadow void of vegetation due to high herbivore activity from reef-dwelling organisms (Steiner and Willette 2014). In Dominica, the expansion of *H. stipulacea* has more than doubled the island's seagrass habitat, primarily via the replacement of bare sand with mono-specific invasive stands (Steiner and Willette 2015). Recent studies have identified that *H. stipulacea* has outcompeted native seagrass species. Between 2011 and 2015, *H. stipulacea* increased from 6 to 20% whilst *T. testudinum* decreased from 53 to 33% (Smulders et al. 2017). This was attributed to green turtle grazing, which creates patches in the *T. testudinum* beds, allowing *H. stipulacea* to replace the native seagrass species in these gaps due to its fast growth and colonization rates (Smulders et al. 2017; Christianen et al. 2019). However, this process could also occur in other areas due to other disturbances-such as storms, anchor or propeller damage from boats, or bioturbation from other grazers-which create gaps for *H. stipulacea* to colonize. Steiner and Willette (2015) found that a high frequency of storms facilitated this process in Dominica, where *H. stipulacea* replaced most of *Syringodium filiforme* and *Halodule wrightii* in depths below 4 m. Furthermore, *H. stipulacea* in the Caribbean occurs under a broad range of stressors, including in highly disturbed and eutrophic harbors, freshwater river outfalls, wave-swept shorelines, shallow and protected bays, and deep waters of > 30 m, all areas where native seagrasses are sparse or absent (Willette et al. 2014; Steiner and Willette 2015).

Generally, the research of invasive species is lacking regarding their interactions with ES (Pejchar and Mooney 2009). To date, scientific research has focused largely on predicting invasibility, comparing invader and native species, and assessing environmental impacts, particularly on biodiversity (Charles and Dukes 2008). An assessment from a trait-based

Fig. 1 Distribution of *H. stipulacea* in the Caribbean Sea by location and year of first observation ([1]Ruiz and Ballantine 2004, [2]Willette and Ambrose 2009, [3]Debrot et al. 2012, [4]Kerninon 2012, [5]Willette et al. 2014, [6]Vera et al. 2014, [7]Ruiz et al. 2017, [8]Ellis 2016). Modified from Willette et al. (2014)

approach would help to better understand the impacts on the ES, and, in turn, the implications for humans. Therefore, here we ask if the colonization of *H. stipulacea* can provide services that have been lost when other seagrass species have disappeared (Suppl. Fig. 1).

Data comparing traits of the two dominant Caribbean species (*S. filiforme* and *T. testudinum*) versus *H. stipulacea* shows that there is some overlap in some key traits that may control essential services (Fig. 2). Although the literature is limited, we have found specific examples of traits, that control ES. As an example, *H. stipulacea* has a higher density of plants and leaves (Fig. 2c), but this trait does not equate to greater wave attenuation, as the biomass, leaf length, and width are smaller than *T. testudinum* (Fig. 2b). Wave energy reduction has been shown to decrease by 40% when the seagrass leaf length is the
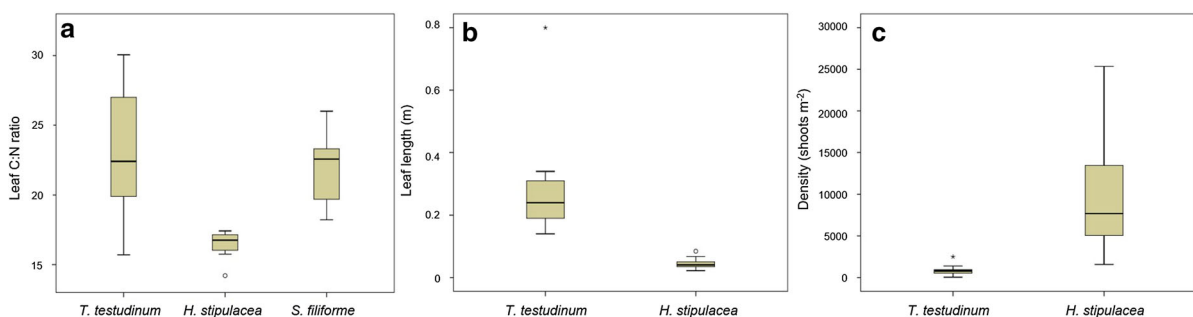

Fig. 2 Box plots showing the range of values for one selected trait of the three different levels of biological organization (according to Suppl. Fig. 1) in *H. stipulacea* and two of the main Caribbean seagrass species, *Thalassia testudinum and Syringodium filiforme*. Leaf C:N ratio, eco-physiological traits (**a**); leaf length (m), morphological traits and growth (**b**); and density (leaves m^{-2}), community structure traits (**c**). The boxes represent the interquartile range and the line within the box, the median value. The stars and circles represent the values at least 1.5 times lower or higher than the interquartile range. Data used correspond to the specific references cited in Table 1 and Suppl. Table 2

same as the depth (Fonseca and Cahalan 1992). For instance, where *H. stipulacea* has colonized shallow areas, the seagrass may indeed have an impact, but this effect will be less pronounced in deeper areas. The density, width, and length of the plants may still be used as a nursery area for juvenile species of coral reef fish, although the communities are altered (Olinger et al. 2017). This may be especially true in locations where *H. stipulacea* grows up to the margin of coral reefs (Steiner and Willette 2014), an area that does not normally have seagrasses, in effect, creating a new nursery or foraging area (Jackson et al. 2001).

To date, however, fish studies have found lower juvenile fish abundance and diversity in Caribbean *H. stipulacea* beds compared to native seagrass beds (Willette and Ambrose 2012; Hylkema et al. 2015). On the other hand, in terms of invertebrate species, *H. stipulacea* beds appear to provide a favorable new habitat for the sea star *Oreaster reticulatus* in addition to large sessile filter feeders such as bivalves or sponges (Scheibling et al. 2018). Likewise, leaf-dwelling crustaceans were significantly more abundant on *H. stipulacea* than native Caribbean seagrass meadows (Willette and Ambrose 2012), although this seagrass's potential to restructure the invertebrate community is unknown at this time, as are the consequences of such community-level changes. Indeed, history has shown that well-intentioned introductions can have disastrous consequences.

To assess secondary producers' food preferences, the C:N ratios of native and invasive seagrasses can be compared. In several species of grazers (damsel, parrot fish, turtles, and shrimps), the C:N ratio of *H. stipulacea* (16.8–17.2) was lower than the normal feeding preference (*T. testudinum* 18.2–26 and *S. filiforme* 19.7–30.1) (Fig. 2a), although the N content of the *H. stipulacea* leaves was within acceptable ranges (Schwarz and Hellblom 2002). Monitored fish traps placed in *H. stipulacea* beds captured larger fish and a higher diversity of species than traps in native seagrass beds (Willette and Ambrose 2012), indicating that these high C:N ratios may be a preference but not a prerequisite for fish species. Green turtles in the Caribbean were observed grazing on *H. stipulacea*, although a preference for native species was recorded (Becking et al. 2014; Christianen et al. 2019). Conversely, recent research also showed that colonizing *H. stipulacea* actually reduced fish species

biomass, as food availability in the seagrass bed was lower than in the mudflat (Lee and Park 2008).

The discussion above indicates there is no clear-cut answer to the question: Can invasive seagrass provide functions to replace the native species' ES? The answer would strongly depend on physical dynamics, the characteristics of the adjacent ecosystems, as well as the specific species being investigated. Yet, could *H. stipulacea* have other positive aspects?

Are invasive species always bad? *H. stipulacea*'s role as a pioneer species

Invasive species are widely accepted as one of the leading direct causes of biodiversity loss. Much of the evidence for this contention is based on simple correlations between exotic dominance and native species decline in degraded systems (Didham et al. 2005). From this starting point of the Caribbean deteriorated seascape (see "Native seagrasses in the Caribbean: threats and traits" section), we ask if *H. stipulacea* is growing in areas where the native seagrasses are not able to grow any longer, as *H. stipulacea* has colonized bare sediment areas where native seagrasses had disappeared from (Steiner and Willette 2015).

The functional traits associated with *H. stipulacea* that make this species a fast-establishing invasive species (Suppl. Table 2) also render it a pioneer species (Kilminster et al. 2015). Pioneer species are normally opportunistic, with fast growth rates, fast shoot turnover, and well-developed reproduction strategies. These characteristics give these species the ability to rapidly recover after a disturbance due to their high resilience and low physiological resistance (Kilminster et al. 2015). It can be then argued that there already exist native pioneer species in the Caribbean, namely *Halophila decipiens* and *H. wrightii*. These species, however, have been shown to be susceptible to replacement by *H. stipulacea* (Steiner and Willette 2015), likely due to the highly successful colonization rate and asexual reproduction of *H. stipulacea* (Rogers et al. 2014). This difference might give *H. stipulacea* a greater advantage as a successful pioneer species.

Sharp changes in temperature, light conditions due to terrestrial run-off and eutrophication, or increasing nutrient concentrations in the water column and

sediment led to the disappearance of seagrass meadows. Caribbean seagrass meadows have not only to recover from pulse disturbances but also to adapt to this new environmental scenario. In this respect, ecosystem engineers, including *T. testudinum*, have on one side a high capacity to physiologically adapt to disturbances, but they also have a slower ability to recover and a narrower tolerance range (Kilminster et al. 2015). Therefore, after an ecosystem is disrupted, pioneer species are the first colonizers, beginning the ecological succession that will eventually lead to a more diverse habitat when the environmental conditions are better or the impact of increasing human populations is controlled (Fig. 3). For example, van Tussenbroek et al. (2016) related the appearance of denser growth forms of *H. stipulacea* with high nitrogen content in seagrasses and sediment; they suggest that this species might have an advantage under this environment with high nutrient concentrations.

Plant–plant interactions change depending on environmental conditions, shifting from competition to facilitation when the stress is high. The "facilitative role" of invasive species has been widely described in terrestrial and freshwater ecosystems, with fewer examples within the marine environment (Rodriguez 2006). The notable resilience of invasive species, competitive success, comparative vigor in stressed systems, and capacity to provide at least some beneficial services combine to suggest some invasive species may have a useful role in the management of coastal ecosystems (Hershner and Havens 2008). For instance, it has been reported that habitat modification is a frequent mechanism where invasive species facilitate native species in grasslands (Hershner and Havens 2008; Jordan et al. 2008). For instance, *H. stipulacea* shows high uptake rates both from the leaves and the roots, removing increasing nutrients from the water column. Furthermore, their seagrass structure (above- and below-ground tissues) promotes
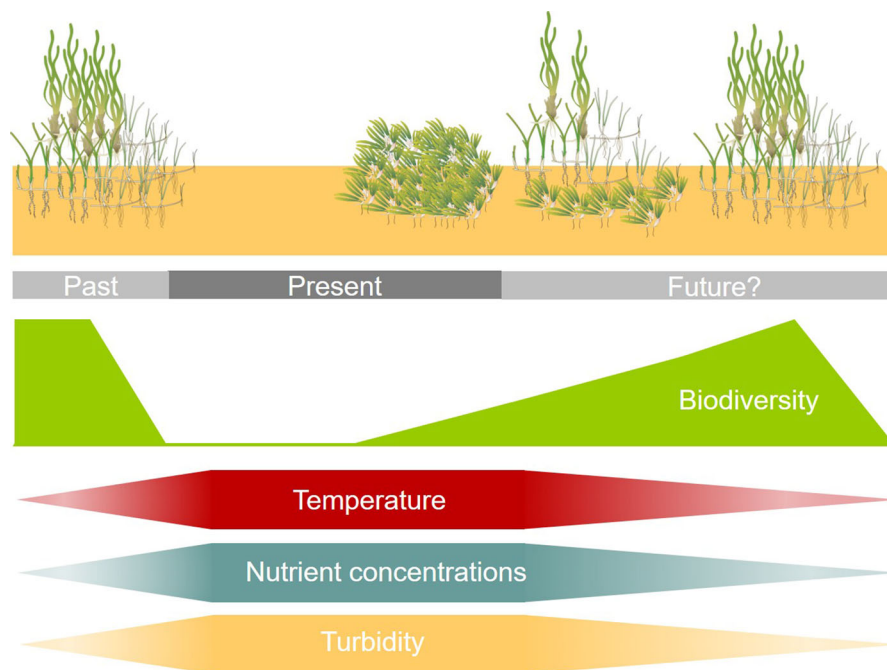

Fig. 3 Conceptual diagram showing the disappearance of seagrass meadows and loss of biodiversity in the Caribbean (*Thalassia testudinum*, *Syringodium filiforme* and *Halodule wrightii*) and potentially associated environmental (temperature) and human-associated drivers (nutrient concentrations and turbidity) that are causing the changes in the seagrass meadows. From that current scenario, it is hypothesized how *H. stipulacea* could act as pioneer species facilitating a future settlement of the native seagrass species if the environmental conditions are eventually balanced, going back to less disturbed scenarios, both because of the sustainable development of coastal areas (reducing anthropogenic inputs) and the facilitative role of *H. stipulacea*. Seagrass symbols is courtesy of the Integration and Application Network (ian.umces.edu/symbols/)

sediment stabilization in bare sand habitats (Potouroglou et al. 2017).

Whether or not invasive species are drivers or merely passengers of change has been questioned (MacDougall and Turkington 2005). This work in deteriorated grassland systems reveals that competitive ability alone cannot always explain the high abundance of invasive species or changes to the composition and diversity of invaded plant communities. Interacting factors relating to competition, dispersal limitation, environmental conditions, and disturbance determine community structure, including dominance. The authors conclude the invasive species were primarily "passengers", proliferating under conditions where perennial grasses are naturally abundant but easily displaced by repeated disturbance.

Nevertheless, *H. stipulacea*'s facilitative role as a pioneer species would only make sense if environmental conditions are within the range of the native seagrass species' tolerance in a future scenario (Fig. 3). Temperature perturbations are dependent on management policies at a global scale and thus out of the control of local resource managers. Direct physical damage due to boat anchoring or terrestrial run-off, on the other hand, can be addressed by raising awareness of the societal importance of the ES that seagrass meadows in the Caribbean provide ("Native seagrasses in the Caribbean: threats and traits" section). Over the last decades, the scientific community has responded by developing research and monitoring programs and initiatives that have gathered baseline data on seagrass beds, therefore improving restoration and conservation of seagrasses (Orth et al. 2006). For example, managing the entire catchment area (including urban areas and agriculture lands) to reduce nitrogen and phosphorus concentrations has proven highly effective in Chesapeake Bay where nitrogen concentrations have reduced by 23%, corresponding to an increase in seagrass cover to 17,000 ha (Lefcheck et al. 2018).

It is now widely accepted that successful restoration of native seagrass species means overcoming critical physical thresholds and enhancing self-sustaining feedbacks (van Katwijk et al. 2016; Maxwell et al. 2017). Consequently, ensuring that environmental conditions are within the thresholds of native species should be a priority. This effort should be combined with initiatives that focus on increasing the level of public awareness and a broader understanding of the

conservation biopolitics of labelling *H. stipulacea* as an invasive species by policymakers (Biermann and Anderson 2017).

In summary, we note that *H. stipulacea* introductions would not match the current biodiversity of seagrass beds in the Caribbean if native seagrass meadows are lost; and that perils associated with this community changes are still unknown. Nevertheless, if the potential advantages of having *H. stipulacea* as a pioneer species in this changing scenario outweigh the losses, then it is prudent to investigate this possible 'good' invasive species in this natural experiment now underway. However, we emphasize that further baseline data—on all Caribbean seagrass species, ecosystems, and potential unintended consequences—are needed, before managers can make informed decisions.

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