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Battle for the mounds: Niche competition between upside-down jellyfish and invasive seagrass

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Text

In tropical ecosystems, autotroph organisms are continuously competing for space, with some plant species benefiting from disturbances such as fire, grazing, or bioturbation that clear habitat (Pulsford et al. 2016). These disturbances can open up layers of vegetation, thereby promoting colonization of opportunistic species that would have been competitively inferior without disturbance (Castorani et al. 2018). Opportunistic fast-growing species also include often invasive species that are therefore also likely to increase in dominance after disturbance (Altman and Whitlatch 2007). In seagrass meadows in the southern Caribbean, we observed that the marine invasive plant *Halophila stipulacea* uses bioturbation mounds, created by burrowing infauna such as sea cucumbers and shrimp (see Suchanek 1983), to colonize new habitats (Figure 1a, b). On Bonaire and Curaçao, in habitats with ~100% native *Thalassia testudinum* cover, invasive *H. stipulacea* often at first only occurred on bioturbation mounds that smothered native *T. testudinum* seagrass, likely due to fragmentation and subsequent settlement (Smulders et al. 2017). These observations suggest that bioturbation mounds serve as starting points for further invasion (Fig. 1c).

These bioturbation mounds add a different kind of disturbance as a mechanism to free up space to settle and expand from than previously described for invasive marine plants (e.g. Christianen et al. 2019, Hernández-Delgado et al. 2020). This interaction between invasive marine plants and burrowing organisms could disrupt the natural balance between opportunists and climax species within the ecosystem. Invasive species may compete with native weak competitors in newly created niches after disturbance (Peltzer et al. 2009). This can lead to co-existence or declines of native species when these are weak competitors and are being pushed out by the invasive species (Altman and Whitlatch 2007, Hobbs et al. 2009). In this paper, we

report evidence of a novel ecological interaction in a tropical seagrass ecosystem, between two autotroph species, the invasive seagrass *H. stipulacea* and the native upside-down jellyfish *Cassiopea* spp. We discuss the ecological implications and suggest future directions for research.

After our first observation, our curiosity increased as we saw that, on Curaçao, the bioturbation mounds often became occupied by a combination of upside-down jellyfish and shoots of *H. stipulacea* (Fig. 1d) that seem to occupy the same niche. Upside-down jellyfish belonging to the genus *Cassiopea* (hereafter referred to as *Cassiopea*) have photosynthesizing dinoflagellates as symbionts and have a benthic lifestyle associated with Caribbean mangrove, seagrass, and coral ecosystems (Niggl and Wild 2010). To quantify the preference of invasive seagrass and *Cassiopea* for bioturbation mounds in seagrass meadows and to study potential niche competition we conducted a pilot experiment on Curaçao. We monitored ten natural bioturbation mounds, five artificial bioturbation mounds, and five vegetated plots without bioturbation every three days for 45 days. All treatments were situated between 1 and 2.3 m depth and randomized over space with at least 2 m in between plots, which resembled the average natural mound density in the larger area. The artificial bioturbation mounds were made of sediment collected nearby the study site and mimicked the average dimensions of the natural bioturbation mounds (diameter 40 cm; maximum height 20 cm). For each treatment, plots of 0.5 x 0.5 m were marked with PVC poles. Within each plot, a circle (40 cm diameter) was marked with six bamboo skewers, and all seagrass shoots (*T. testudinum* and *H. stipulacea*) and *Cassiopea* individuals within this circle were counted at each sampling moment. The plots were all situated in a mixed seagrass meadow dominated by *T. testudinum* with a sparse *H. stipulacea* understory.

The results from our pilot experiment suggest that *H. stipulacea* and *Cassiopea* both prefer niches where most bare sediment is available. *H. stipulacea* shoot development was 1.9 ± 0.3 shoots day^{-1} on artificial mounds compared to 1.6 ± 0.5 shoots day^{-1} on natural bioturbation mounds and 1.0 ± 0.4 shoots day^{-1} on vegetated plots (One-way ANOVA, $F(2,17) = 0.624$, $p = 0.55$). For *Cassiopea*, we found an average occurrence of 9.5 ± 5.0 individuals on natural bioturbation mounds, followed by 5.6 ± 1.6 individuals on artificial mounds and 1.4 ± 3.3 individuals in vegetated plots (Kruskal-Wallis, $H(2) = 4.118$, $p = 0.13$). Additionally, we observed that *Cassiopea* individuals spent less time in vegetated seagrass habitat (~1 day), and stayed longer on bare (artificial) bioturbation mounds (> 10 days), suggesting that the individuals are mostly passing through habitats with high seagrass cover selecting open spaces to settle (corresponding to findings of Niggl and Wild 2010). Average ($\pm$ SE) *Thalassia testudinum* shoot growth was low in each treatment (0.04 ± 0.02 shoots day^{-1}). Therefore, the data from this pilot experiment confirmed our observations that both *Cassiopea* and *H. stipulacea* prefer open habitats created by bioturbation activity and are in niche competition. Both the photosynthetic invertebrate and invasive seagrass are likely competing because of their similar requirements for light and space. Our next question was which species will win this competition, or is co-existence possible?

To explore the relationship between the presence of *Cassiopea*. and *H. stipulacea* and their potential competitive exclusion or co-existence, we pooled the artificial and natural bioturbation plots and visualized the average number of *H. stipulacea* and *Cassiopea* individuals over time (Fig. 2a). Densities of *H. stipulacea* steadily increased over time, while *Cassiopea* showed a peak halfway and decreasing densities towards the end of the experiment. To further visualize the differences in dynamics between plots, we compared the species composition at the

end of the experiment (based on the ratio of *H. stipulacea* shoots:*Cassiopea* individuals) (Fig. 2b). After 45 days, *H. stipulacea* was dominant in 80% (= 12 out of 15) of the plots. In the remaining 20% of the plots, no shoots of *H. stipulacea* were observed during the whole experimental period and only *Cassiopea* was present at the end of the experiment. Therefore, in all plots where at least one *H. stipulacea* shoot started growing, the invasive seagrass became dominant relative to *Cassiopea* within 1.5 months. This is a different outcome of seagrass-*Cassiopea* interaction as was suggested by Stoner et al. (2014), who discussed that high densities of *Cassiopea* may negatively impact seagrass cover through shading or other processes. Additionally, 27% of the plots were exclusively covered with *H. stipulacea* at the end of the experiment, while all plots had *Cassiopea* individuals present at some point during the experiment. This corresponded with our observations in the field: when the bioturbation mounds gradually became invaded by invasive seagrass, the *Cassiopea* individuals were seen leaving the plots with the last individuals remaining positioned themselves vertically between the leaves (Fig. 2c).

We report a novel interaction between an invertebrate with photosynthetic symbionts and an invasive plant after natural disturbance through bioturbation activity. We hypothesize that the arrival of the invasive *H. stipulacea* likely shifts patch dynamics in the seagrass ecosystem and thereby niche competition between seagrasses and *Cassiopea*. Within the native seagrass community dominated by *T. testudinum*, bioturbators are limited by strong root-rhizome networks (Bernard et al. 2019). These open habitats are thus created at a low frequency but remain stable for considerable time because *T. testudinum* does not quickly recover after disturbance (O'Brien et al. 2018). Native *Cassiopea* can therefore stay for a long period of time in the open habitat created by bioturbators. After introduction of the invasive seagrass,

bioturbation mounds are quickly covered by invasive shoots. In time, as the cover of invasive seagrass increases, we predict that the bioturbation frequency will go up (Fig. 1c). Biannual seagrass monitoring in Lac Bay, Bonaire since seagrass invasion started (2011), provides the opportunity to explore this relationship.

Previously we have shown that cross-sections of this bay reflect a gradient of invasion history through time (Smulders et al. 2017, Christianen et al. 2019). Based on this monitoring data, we compared the number of invasive *H. stipulacea* shoots and bioturbation mounds in habitats that have been recently invaded to habitats that have been invaded for a longer time within 12 transects along the invasion gradient on Bonaire. Each transect consisted of 4 to 6 monitoring points (1 m^2), which were at least 20 m apart, and each point along the transect was situated either in a long-term or recently invaded habitat. Seagrass and bioturbation data were collected in February and March 2022, first averaged per habitat per transect and then compared between habitats (N = 12). We found that there was a significantly higher number of bioturbation mounds (paired t-test, t(11) = 2.983, p = 0.012) as well as *H. stipulacea* shoots (paired Wilcoxon rank-sum test, V = 64, p = 0.007) in areas that had been invaded for a longer time (2.8 ± 0.2 mounds m^{-2}, 767.0 ± 245.6 shoots m^{-2}) compared to recently invaded areas (1.6 ± 0.2 mounds m^{-2}, 140.6 ± 55.1 shoots m^{-2}). We hypothesize that this trend can be explained by the fact that plant species with colonizing traits such as *H. stipulacea* have a shallow and low biomass root system. This provides a more favorable habitat for burrowing animals, just like has been found for squirrel mounds that show a higher density in areas with more invasive cheatgrass which is structurally less complex (Blank et al. 2013). Therefore, there will likely be a more frequent creation of bare habitats, but these habitats do not persist as the invasive seagrass *H. stipulacea* can quickly cover the bioturbation mounds. *Cassiopea* will thus have to increase its moving

frequency between these mounds, which alters its metabolic costs and may potentially impact its survival.

Our preliminary data suggests that there is competition between the native opportunist species, the photosynthesizing *Cassiopea* spp., and the fast-growing invasive seagrass *H. stipulacea* within niches created by bioturbation activity. A suggestion for future work would be to monitor the bioturbation frequency and reproductive success of *Cassiopea* over time in invaded ecosystems. It is recommended to test if invasive seagrass generally wins this competition as our preliminary data suggests, or under which conditions co-existence may be possible (*cf.* Valladares et al. 2015). Overall, the detected pattern involving invasive seagrass, native jellyfish, and bioturbating ecosystem engineers has the potential to drive patch dynamics within these vegetated marine ecosystems.

Conflict of interest

All authors affirm that they have no conflicts of interest to declare

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Figure 1. Bioturbation activity in native *Thalassia testudinum* seagrass meadows creates an opportunity for the colonization and expansion of invasive seagrass *Halophila stipulacea* as observed on (a) Bonaire and on (b) Curaçao. (C) Seagrass meadows on Bonaire that have been invaded for more than a decade have higher densities of both *H. stipulacea* and bioturbation mounds compared to Curaçao (pers. obs. F.O.H. Smulders & N. Slikboer). (D) On Curaçao, both invasive seagrass and upside-down jellyfish *Cassiopea* spp. were observed occupying bioturbation mounds. Picture (a) and (c) taken by F.O.H. Smulders in Lac Bay, Bonaire on 19th November 2021, pictures (b) and (d) taken by N. Slikboer in Spanish Water Bay, Curaçao on 15th of November and 27th of December 2020 respectively.

Figure 2. Interactions between presence of *H. stipulacea* and *Cassiopea.* (A) Time series of the average number ± SE of *H. stipulacea* shoots and *Cassiopea* individuals on artificial and natural bioturbation mounds pooled together (N = 15). (B) The percentage of plots with a certain species composition as measured at the end of the experiment (day 45). We calculated the ratio of *H. stipulacea*:*Cassiopea*, plots with a ratio >1 were defined as *H. stipulacea* dominated, while plots below 1 were defined as *Cassiopea* dominated. At the end point, there were no mixed plots with *Cassiopea* dominance. Plots where only *Cassiopea* was present (mono *Cassiopea*) are labelled stadium I, mixed plots with *H. stipulacea* dominance are labelled stadium II, and plots where only *H. stipulacea* was present (mono *H. stipulacea*) are labelled stadium III. (C) Diagram based on our observations and pilot data of the development of species composition over time on newly created bioturbation mounds. Without *H. stipulacea* presence, the mound can stay in stadium I, providing habitat for *Cassiopea*. However, when *H. stipulacea* shoots start growing (stadium II)

it is likely that *Cassiopea* gets pushed out of its habitat and decreases in number while *H. stipulacea* steadily increases (stadium III).

(a)

(b)

(c)