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Citation for published version (APA):

Smulders, F. O. H., Slikboer, N., Christianen, M. J. A., & Vonk, J. A. (2023). Battle for the mounds: Niche competition between upside-down jellyfish and invasive seagrass. *Ecology*, *104*(4), Article e3980. https://doi.org/10.1002/ecy.3980

THE SCIENTIFIC NATURALIST

ECOLOGY
ECOLOGICAL SOCIETY OF AMERICA

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

Fee O. H. Smulders[1] | Naomi Slikboer[1] | Marjolijn J. A. Christianen[1] |
Jan Arie Vonk[2]

[1]Wageningen University & Research Aquatic Ecology and Water Quality Management Group, Wageningen, The Netherlands

[2]Department of Freshwater and Marine Ecology (FAME), Institute for Biodiversity and Ecosystem Dynamics (IBED), University of Amsterdam, Amsterdam, The Netherlands

Correspondence
Fee O. H. Smulders
Email: fee.smulders@wur.nl

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 habitats (Pulsford et al., 2016). These disturbances can open up layers of vegetation, thereby promoting the 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 & Whitlatch, 2007). In seagrass meadows in the southern Caribbean, we observed that the invasive marine 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 to be due to fragmentation and subsequent settlement (Smulders et al., 2017). These observations

suggest that bioturbation mounds serve as starting points for further invasion (Figure 1c).

These bioturbation mounds add a different kind of disturbance as a mechanism to free up space to settle and expand 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 the co-existence or decline of native species when these are weak competitors and are being pushed out by the invasive species (Altman & 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.
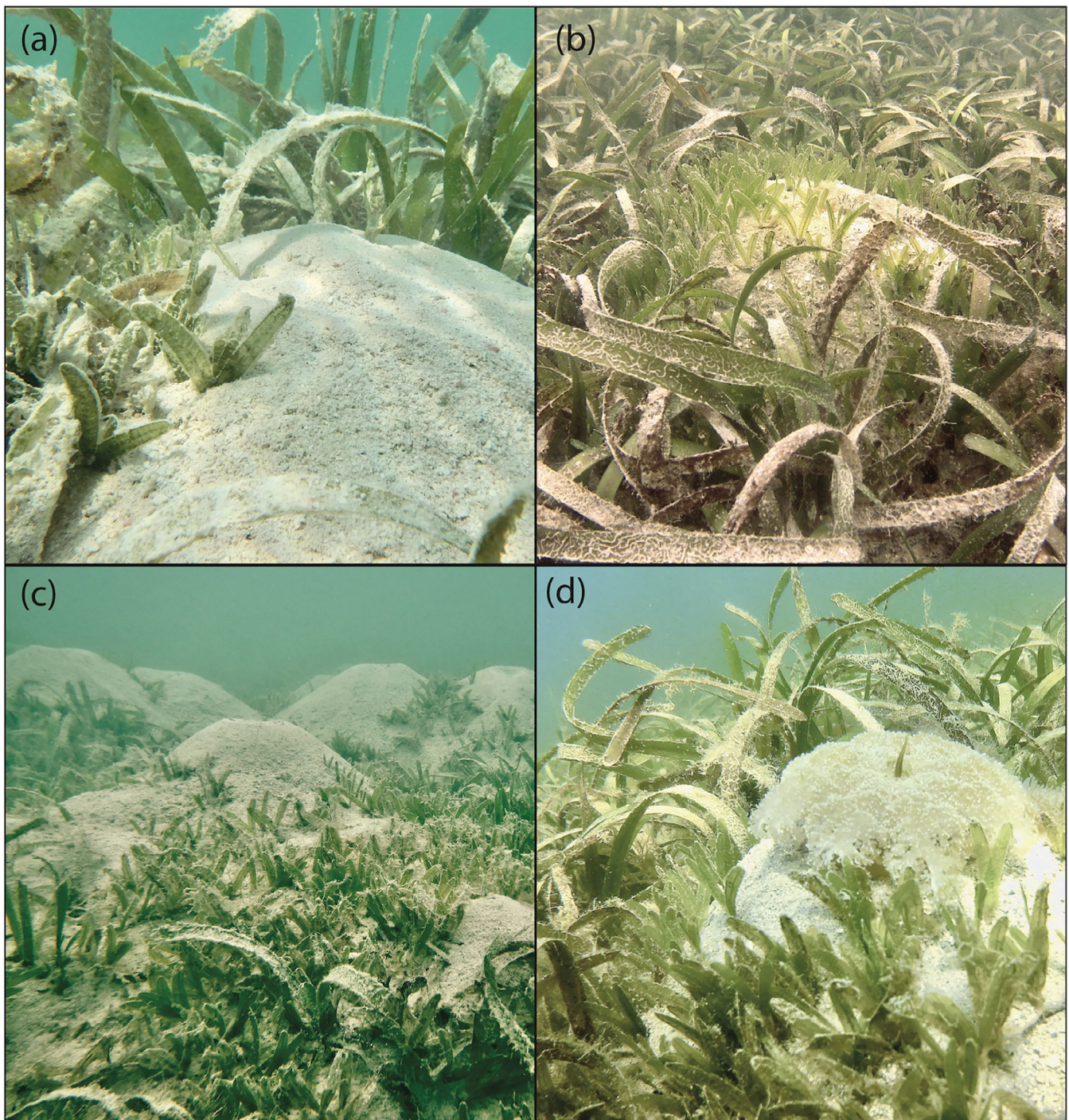
FIGURE 1 Bioturbation activity in native *Thalassia testudinum* seagrass meadows creates an opportunity for the colonization and expansion of invasive seagrass *Halophila stipulacea* as observed on (a) Bonaire and on (b) Curaçao. (c) Seagrass meadows on Bonaire that have been invaded for more than a decade have higher densities of both *H. stipulacea* and bioturbation mounds compared with Curaçao (F. O. H. Smulders and N. Slikboer, personal observation, October, 2020). (d) On Curaçao, both invasive seagrass and upside-down jellyfish *Cassiopea* spp. were observed occupying bioturbation mounds. Photographs (a) and (c) were taken by F. O. H. Smulders in Lac Bay, Bonaire on 19 November 2021; photographs (b) and (d) were taken by N. Slikboer in Spanish Water Bay, Curaçao on 15 November and 27 December 2020 respectively.

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 jelly-fish and shoots of *H. stipulacea* (Figure 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 & 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 10 natural bioturbation mounds, five artificial bioturbation mounds, and five vegetated plots without bioturbation every 3 days for 45 days. All treatments were situated between 1 and 2.3 m in 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 0.5×0.5 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 with 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 & 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 to be 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 (Figure 2a). Densities of *H. stipulacea* steadily increased over time, while *Cassiopea* showed a peak halfway and decreasing densities toward 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) (Figure 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 for the seagrass–*Cassiopea* interaction 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 remaining individuals positioning themselves vertically between the leaves (Figure 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* is likely to shift 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 a 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 the 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 increase (Figure 1c). Biannual seagrass monitoring in Lac Bay, Bonaire since the 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 (Christianen et al., 2019; Smulders et al., 2017). Based on this monitoring data, we compared the number of invasive *H. stipulacea* shoots and bioturbation mounds in habitats
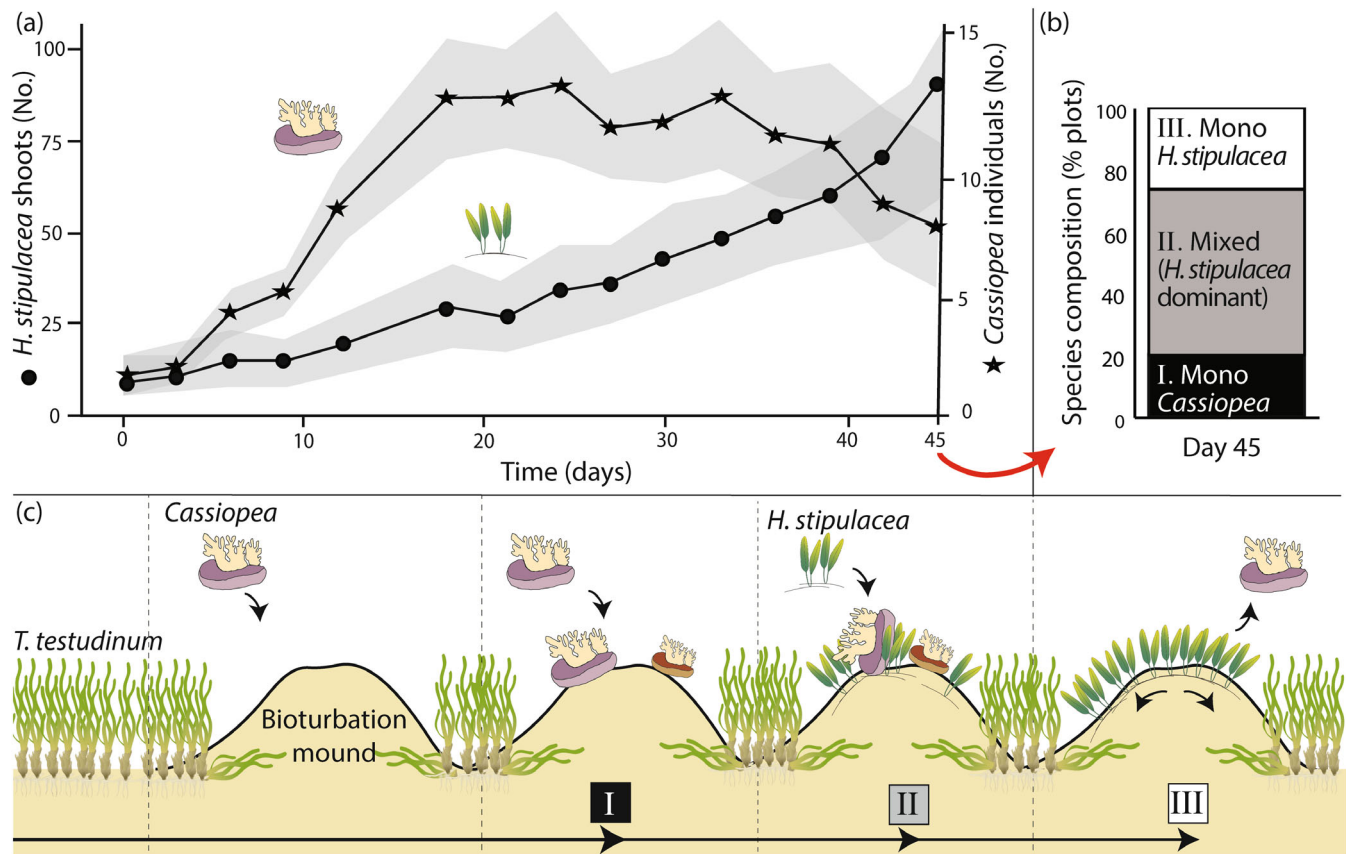
FIGURE 2 Interactions between the presence of *H. stipulacea* and *Cassiopea*. (a) Time series of the average number $\pm$ SE of *H. stipulacea* shoots and *Cassiopea* individuals on artificial and natural bioturbation mounds pooled together ($N = 15$). (b) The percentage of plots with a certain species 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 labeled stadium I, mixed plots with *H. stipulacea* dominance are labeled stadium II, and plots where only *H. stipulacea* was present (mono *H. stipulacea*) are labeled 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* will be pushed out of its habitat and decrease in number while *H. stipulacea* steadily increases (stadium III).

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 four to six monitoring points (1 m²), 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, as 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 is likely to 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 suggest 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. Tests to determine if invasive seagrass generally wins this competition, as our preliminary data suggest, or under which conditions co-existence may be possible, are recommended (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 STATEMENT
All authors affirm that they have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT
Data (Smulders et al., 2023) are available in 4TU. Researchdata at https://doi.org/10.4121/21803667.

ORCID
Fee O. H. Smulders https://orcid.org/0000-0003-4124-8355
Marjolijn J. A. Christianen https://orcid.org/0000-0001-5839-2981
Jan Arie Vonk https://orcid.org/0000-0002-8803-1148

REFERENCES
Altman, S., and R. B. Whitlatch. 2007. "Effects of Small-Scale Disturbance on Invasion Success in Marine Communities." *Journal of Experimental Marine Biology and Ecology* 342: 15–29.

Bernard, G., J. Gammal, M. Järnström, J. Norkko, and A. Norkko. 2019. "Quantifying Bioturbation across Coastal Seascapes: Habitat Characteristics Modify Effects of Macrofaunal Communities." *Journal of Sea Research* 152: 101766.

Blank, R. R., T. Morgan, C. D. Clements, and B. E. Mackey. 2013. "*Bromus tectorum* L. Invasion: Changes in Soil Properties and Rates of Bioturbation." *Soil Science* 178: 281–90.

Castorani, M. C. N., D. C. Reed, and R. J. Miller. 2018. "Loss of Foundation Species: Disturbance Frequency Outweighs Severity in Structuring Kelp Forest Communities." *Ecology* 99: 2442–54.

Christianen, M. J. A. A., F. O. H. H. Smulders, M. S. Engel, M. I. Nava, S. Willis, A. O. Debrot, P. J. Palsbøll, J. A. Vonk, and L. E. Becking. 2019. "Megaherbivores May Impact Expansion of Invasive Seagrass in the Caribbean." *Journal of Ecology* 107: 45–57.

Hernández-Delgado, E. A., C. Toledo-Hernández, C. P. Ruíz-Díaz, N. Gómez-Andújar, J. L. Medina-Muñiz, M. F. Canals-Silander, and S. E. Suleimán-Ramos. 2020. "Hurricane Impacts and the Resilience of the Invasive Sea Vine, *Halophila stipulacea*: A Case Study from Puerto Rico." *Estuaries and Coasts* 43: 1263–83.

Hobbs, R. J., E. Higgs, and J. A. Harris. 2009. "Novel Ecosystems: Implications for Conservation and Restoration." *Trends in Ecology & Evolution* 24: 599–605.

Niggl, W., and C. Wild. 2010. "Spatial Distribution of the Upside-Down Jellyfish *Cassiopea* sp. within Fringing Coral Reef Environments of the Northern Red Sea: Implications for its Life Cycle." *Helgoland Marine Research* 64: 281–7.

O'Brien, K. R., M. Waycott, P. Maxwell, G. A. Kendrick, J. W. Udy, A. J. P. Ferguson, K. Kilminster, et al. 2018. "Seagrass Ecosystem Trajectory Depends on the Relative Timescales of Resistance, Recovery and Disturbance." *Marine Pollution Bulletin* 134: 166–76.

Peltzer, D. A., P. J. Bellingham, H. Kurokawa, L. R. Walker, D. A. Wardle, and G. W. Yeates. 2009. "Punching above their Weight: Low-Biomass Non-native Plant Species Alter Soil Properties during Primary Succession." *Oikos* 118: 1001–14.

Pulsford, S. A., D. B. Lindenmayer, and D. A. Driscoll. 2016. "A Succession of Theories: Purging Redundancy from Disturbance Theory." *Biological Reviews* 91: 148–67.

Smulders, F. O. H., N. Slikboer, M. J. A. Christianen, and J. A. Vonk. 2023. "Data Underlying Publication: Battle for the Mounds: Niche Competition between Upside-Down Jellyfish and Invasive Seagrass." 4TU.ResearchData. Dataset. https://doi.org/10.4121/21803667.

Smulders, F. O. H., J. A. Vonk, M. S. Engel, and M. J. A. Christianen. 2017. "Expansion and Fragment Settlement of the Non-native Seagrass *Halophila stipulacea* in a Caribbean Bay." *Marine Biology Research* 13: 967–74.

Stoner, E. W., L. A. Yeager, J. L. Sweatman, S. S. Sebilian, and C. A. Layman. 2014. "Modification of a Seagrass Community by Benthic Jellyfish Blooms and Nutrient Enrichment." *Journal of Experimental Marine Biology and Ecology* 461: 185–92.

Suchanek, T. H. 1983. "Control of Seagrass Communities and Sediment Distribution by Callianassa (Crustacea, Thalassinidea) Bioturbation." *Journal of Marine Research* 41: 281–98.

Valladares, F., C. C. Bastias, O. Godoy, E. Granda, and A. Escudero. 2015. "Species Coexistence in a Changing World." *Frontiers in Plant Science* 6: 866.

> **How to cite this article:** Smulders, Fee O. H., Naomi Slikboer, Marjolijn J. A. Christianen, and Jan Arie Vonk. 2023. "Battle for the Mounds: Niche Competition between Upside-Down Jellyfish and Invasive Seagrass." *Ecology* 104(4): e3980. https://doi.org/10.1002/ecy.3980