RESEARCH ARTICLE

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Propagule composition regulates the success of an invasive seaweed across a heterogeneous seascape

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Abstract

1. Propagule pressure is acknowledged as a key determinant of invasion success. Nonetheless, the role of morphological or physiological attributes of propagules (i.e. their quality) in regulating invader establishment has been little explored. In particular, no study has investigated how the presence of propagules differing in quality within an inoculum influences establishment across heterogeneous landscapes.

2. We experimentally tested the hypothesis that the quality (+Fronds+Rhizoids; +Fronds−Rhizoids; −Fronds+Rhizoids) and the diversity (1, 2 and 3 fragment types) of vegetative fragments of the seaweed *Caulerpa taxifolia* determine their establishment success across seascapes consisting of bare sediments and patches of the seagrass *Zostera muelleri* exposed to different disturbance intensities (control, seagrass canopy clipping and total removal).

3. After 6 weeks, seaweed biomass, stolon and frond length, frond and rhizoid number were generally greater in unvegetated habitats (bare sediments and total seagrass removal) than full or reduced seagrass canopies. The type and the diversity of types of fragments inoculated had significant effects on the final biomass and morphological features of *C. taxifolia* only in vegetated habitats. In control plots, inocula of fragments retaining both fronds and rhizoids achieved higher biomass, developed longer stolons and more fronds. In canopy clipping plots, mixed inocula of +Fronds+Rhizoids and −Fronds+Rhizoids fragments had the greatest biomass and stolon length.

4. *Synthesis*. Assessing how propagules differing in quality perform in different habitats might be not sufficient to draw a comprehensive picture of invasion risk, as their establishment can be modulated by both negative and positive interactions among them. Propagule composition should be, therefore, considered as a further dimension of propagule pressure. Our results also suggest that the relevance of specific propagule traits for invader establishment decreases from intact to degraded habitats. Considering propagule size in terms of amount of competent propagules, rather than an absolute measure, would refine our ability of predicting invasion risk across habitats differing in biotic or abiotic conditions.

Fabio Bulleri, Ezequiel M. Marzinelli and Paul E. Gribben contributed equally to this study.

1 | INTRODUCTION

Biological invasions are a key component of global changes in biodiversity (Mack et al., 2000; Simberloff et al., 2013). Concerns over the impact of non-native species on the functioning of native ecosystems and their ability to provide goods and services have stimulated research seeking to identify the mechanisms underpinning their establishment and spread. A large body of research has brought compelling evidence that invasion success is regulated by a complex set of factors, including biotic and abiotic features of recipient systems, disturbance regimes, invader life traits and associated propagule pressure (D'Antonio & Vitousek, 1992; Davis, Grime, & Thompson, 2000; Levine & D'Antonio, 1999; Lockwood, Hoopes, & Marchetti, 2013; Sol et al., 2012; Stachowicz, Fried, Osman, & Whitlatch, 2002). Nonetheless, predicting community invasibility remains challenging due to interactions among the different factors at play.

Disturbance and propagule pressure have been long identified as primary determinants of invasion success (Davis et al., 2000; Lockwood et al., 2013). Dominance by native species that are very efficient in exploiting resources can deter invasion (Emery & Gross, 2007; Wardle, 2001). For example, intact canopies formed by a single or very few native plants can reduce the establishment of non-native species in both aquatic and terrestrial environments (Ceccherelli, Pinna, Cusseddu, & Bulleri, 2014; Prevey, Germino, & Huntly, 2010; Scheibling & Gagnon, 2006; Song, Hogan, Brown, Cao, & Yang, 2017; South & Thomsen, 2016; Valliere, Irvine, Santiago, & Allen, 2017). Thus, disturbances reducing the biomass of dominant native species can provide windows of opportunity for invaders (Davis et al., 2000; Lockwood et al., 2013). Decline of foundation species (Dayton, 1972) due to climate change is expected to further facilitate weedy species, including non-natives (Diez et al., 2012; Doubleday & Connell, 2018; Smale et al., 2019; Thomsen et al., 2019).

Resistance to invasion can be, however, swamped at high propagule pressure (Hollebone & Hay, 2007; Von Holle & Simberloff, 2005). Likewise, positive effects of increased resource availability following a disturbance event or external input on invasion can be dependent upon a high availability of invader propagules (Clark & Johnston, 2009). While some aspects of propagule pressure, such as the number of individuals introduced, the number of introductions and their frequency have been widely explored, others have received less attention. Relatively, few studies have investigated morphological or physiological attributes of propagules (i.e. their quality) despite their potential to influence their establishment success (Lockwood et al., 2013; Verling et al., 2005; Watanabe, Metaxas, & Scheibling, 2009; Wright & Davis, 2006). For example, colonies of the bushy bryozoan, *Bugula neritina* – a non-native species in many regions of the world (Ryland et al., 2011) – that were generated by larger larvae had greater survivorship and faster growth and reproduced earlier than colonies generated by smaller larvae (Marshall, Bolton, & Keough, 2003).

Vegetative reproduction is a trait often associated with high invasiveness in clonal plants (Kolar & Lodge, 2001; Lloret et al., 2005). Establishment ability varies, however, among vegetative propagules that differ in morphological characteristics (i.e. their quality). For example, establishment success of rhizome fragments of the invasive cogongrass, *Imperata cylindrica*, increased with fragment size (Estrada, Wilson, NeSmith, & Flory, 2016). Similarly, shoot height and survival of the invasive giant cane, *Arundo donax*, in Southern California riparian habitats were positively correlated with the weight of transplanted rhizomes (Quinn & Holt, 2008).

Although less explored, fragment characteristics underpinning establishment success of clonal plants are unlikely to be universal, but rather dependent upon the biotic and abiotic conditions of the recipient system. For example, fragments of the clonal seaweed, *Caulerpa cylindracea*, lacking rhizoids performed as well as intact fragments and better than fragments lacking fronds, but only when sediments were enriched in organic matter (Bulleri et al., 2018). Likewise, in the cogongrass, positive effects of increased fragment size on tiller production and growth were modulated by light levels (Estrada et al., 2016). As a consequence of disturbance, land- or seascapes often consist of mosaics of habitats differing in environmental conditions and resource availability. For example, forest canopies are generally punctuated with gaps opened by a variety of disturbances, including, fires, wind storms and insect outbreaks (Muscolo, Bagnato, Sidari, & Mercurio, 2014). Likewise, in marine environments, mechanical disturbances, such as storms, boating activities or trawling and herbivore grazing generate patchiness in seagrass meadows (Short & Wyllie-Echeverria, 1996). Propagule traits fostering invasion success are likely to vary across a land- or seascape consisting of different habitats. Under these circumstances, mixed inocula including propagules differing in quality can be expected to enhance establishment success across these heterogeneous land- or seascapes.

Clonal seaweeds belonging to the genus *Caulerpa* are among the worst marine invaders (Williams & Smith, 2007). The success of these species in the introduced range is favoured by vegetative reproduction through fragments and morphological plasticity (Ceccherelli & Cinelli, 1999; Ceccherelli & Piazzi, 2001; Smith & Walters, 1999; Wright, 2005). Morphological features of vegetative fragments conferring invasive *Caulerpa* spp. high ability of establishment can be expected to vary among habitats characterized by different biotic and abiotic conditions. Upright fronds are important for light harvesting but also for photoprotection (Cebrian & Ballesteros, 2009; Ceccherelli & Cinelli, 1998; Collado-Vides & Robledo, 1999). The presence of rhizoids could be relevant in

wave-swept environments where rapid re-attachment is critical for establishment, in particular, on topographically simple surfaces, such as bare sediments, where fragments cannot be entangled in the extant vegetation. The role of rhizoids for anchoring appears instead less relevant in wave-sheltered sedimentary habitats (Wright & Davis, 2006). Recent studies also demonstrate that establishment success of transplants of *C. taxifolia* and *C. cylindracea* is greater on sediments previously colonized by conspecifics than native seagrasses, suggesting that below-ground processes may play an important role in invasion success (Gribben et al., 2017, 2018). As documented for roots of terrestrial plants (Cipollini, Rigsby, & Barto, 2012; Hu et al., 2018; van der Putten, Klironomos, & Wardle, 2007), the rhizoids of invasive *Caulerpa* spp. promote a microbial community that alters sediment biochemical processes (e.g. sulphur cycling) and/or may release metabolites that benefit their own performance to the detriment of their native competitors (Gribben et al., 2017, 2018; Rizzo, Pusceddu, Stabili, Alifano, & Fraschetti, 2017). Thus, seaweed fragments with high rhizoid numbers could overcome biotic resistance. More generally, according to the biomass proportion allocated to different structures (i.e. their quality), fragment establishment success might be high in some habitats and low in others. Under these circumstances, inocula including fragments differing in morphological traits should improve establishment success across heterogeneous seascapes.

Another aspect of propagule pressure that has received little attention is interactions among propagules. Intra-specific competition among early settling stages has been documented in introduced plants and macroalgae (Blank, 2010; Steen, 2003; Uyà, Bulleri, & Gribben, 2018). Interactions among invader propagules differing in key life traits across habitats with contrasting biotic and abiotic features are, however, yet to be explored. The direction and magnitude of interactions among propagules of different qualities can be expected to vary according to local conditions. Indeed, fragments differing in quality may influence each other positively; for example, *Caulerpa* fragments with a high rhizoid density may alter sediment microbial community and biogeochemistry and facilitate the establishment and growth of fragments lacking rhizoids.

In a wave-sheltered estuarine embayment, we experimentally tested the hypothesis that the quality (+fronds+rhizoids; +fronds−rhizoids; −fronds+rhizoids; hereafter referred to as fragment type) and diversity (1, 2 and 3 fragment types) of vegetative fragments of the seaweed *Caulerpa taxifolia* determine their success across seascapes consisting of bare sediments and experimental patches of the seagrass *Zostera muelleri* exposed to different intensities of disturbance (control, canopy clipping to simulate leaf grazing by herbivores and total removal of above- and below-ground biomass to simulate more intense disturbances such as those from human activities, for example, boating/anchoring; hereafter referred to as habitats). We predicted that fragment establishment success would be generally low under full canopies and increase with the intensity of the disturbance applied to the seagrass. Indeed, intact fragments (i.e. with both fronds and rhizoids) should be the only type able to establish and grow under full seagrass canopies. However, we also expected establishment success in areas exposed to different disturbance intensity to vary among fragment types. For instance, establishment and growth of fragments lacking fronds were expected to be greater in bare sediments or total removal plots than clipped seagrass canopies. Likewise, the lack of rhizoids should be less relevant for establishment in bare sediments not previously colonized by the seagrass than in those from which the seagrass was shortly removed (i.e. seagrass total removal). Although rhizoid regeneration is rapid, newly regenerated rhizoids are unlikely to carry the same bacterial community of sediments from which they were collected and, hence, be efficient in sediment priming. Given such variation in the ability of the different fragment types to establish and grow in areas exposed to disturbances of different intensity, inocula made of different types of fragments should sustain seaweed success across different habitats. For the same reason, seaweed biomass stability at the sea-scape level (i.e. across habitats) should increase with the number of fragments types within an inoculum. In addition, by generating different combinations of two-fragment type inocula, we assessed how the success of each type of fragment varied when interacting with similar versus different quality fragments.

2 | MATERIALS AND METHODS

2.1 | Species and study site

This study was carried out in Pittwater, a sheltered embayment flanking Sydney's northern beaches (NSW, Australia; Lat. −33.6152°, Long. 151.3253°). Shallow subtidal sediments (20–30 cm below MLLW) in the study area are dominated by *Zostera muelleri*, a common seagrass in estuaries and coastal lagoons of tropical and temperate Australia, and colonized by the invasive green seaweed, *Caulerpa taxifolia*. In Pittwater, mean above- and below-ground dry weight biomass of shallow subtidal *Z. muelleri* are 400 and 1,000 g/m^2, respectively, with a mean leaf length close to 300 mm (Nicastro & Bishop, 2012; Nicastro, Onoda, & Bishop, 2013). *C. taxifolia*, first detected in NSW in 2000, has become a common component of soft-bottom assemblages in several estuaries and coastal lakes (Glasby, 2013). Drifting fragments of either shoots or stolons as small as 1 cm can regenerate rhizoids and re-attach, sustaining the spreading potential of this species (Smith & Walters, 1999). At our study site, the presence of *C. taxifolia* is mostly restricted to the inner part of the bay, where it forms dense stands in unvegetated sediment patches and extends into less dense *Z. muelleri* canopies.

2.2 | Experimental set-up

Between 30 January and 1 February 2018, 105 plots, 0.5 × 0.5 m^2 in size, were randomly selected in an area covered by *Z. muelleri*, but largely devoid of *C. taxifolia* and marked at their corners with numbered plastic tags. In all, 35 plots were assigned to each of the following treatments, simulating different intensities of seagrass

disturbance (referred to as habitats): seagrass total removal (STR), canopy clipping (hereafter referred to as seagrass partial removal: SPR) and control (SC). STR was performed by manually uprooting plants, paying attention to the complete elimination of belowground structures (Figure 1); SPR was performed using gardening scissors, cutting seagrass leaves about 3 cm above the rhizome. In addition, 35 plots were randomly selected and marked within bare sediment patches (BS) not colonized by either seagrass or *C. taxifolia*, which naturally occur interspersed among the seagrass bed. Five plots of each type of habitat were assigned to each of the seven types of *C. taxifolia* inocula generated by all the possible 1-, 2- and 3-fragment type combinations obtained using fragments with both fronds and rhizoids (+F+R), with fronds and without rhizoids (+F−R), without fronds and with rhizoids (−F + R) (Figure 1). Thus, each experimental plot was inoculated with either six fragments of the same type, three fragments of each of two types or two fragments of each of three types.

Before the start of the experiment, we measured the weight of 50 fronds and that of fifty 2-cm long stolons collected at the same study site, to standardize the mass of the different fragment types. On average, there were three fronds per 10 cm of stolon and the mean weight of one frond (*Mean ± SE* = 0.074 ± 0.003) was about twice the mean weight of a 2-cm long stolon (*Mean ± SE* = 0.036 ± 0.002). The weight of rhizoid filaments was very low and their removal did not influence the overall fragment weight. Therefore, to maintain biomass even across fragment types, +F+R and +F−R fragments equally consisted in 10-cm long stolons with 3 fronds, while −F+R fragments consisted in 22-cm long stolons. After 7 weeks following, the creation of the different experimental seagrass habitats, *C. taxifolia* was collected from the study site and brought to the laboratory in plastic containers filled with seawater. On the same day, fronds and rhizoid filaments were cut in the laboratory using scissors. Wound healing in *C. taxifolia* is very rapid (i.e. tens of minutes) (Williams & Schroeder, 2004) and our manipulation was, therefore, very unlikely to affect fragment health or fitness. Although to a different extent, all fragment types (including +F+R) were exposed to the same cutting procedure. Fragments were stored overnight in the dark in seawater maintained at the same temperature recorded in the field and
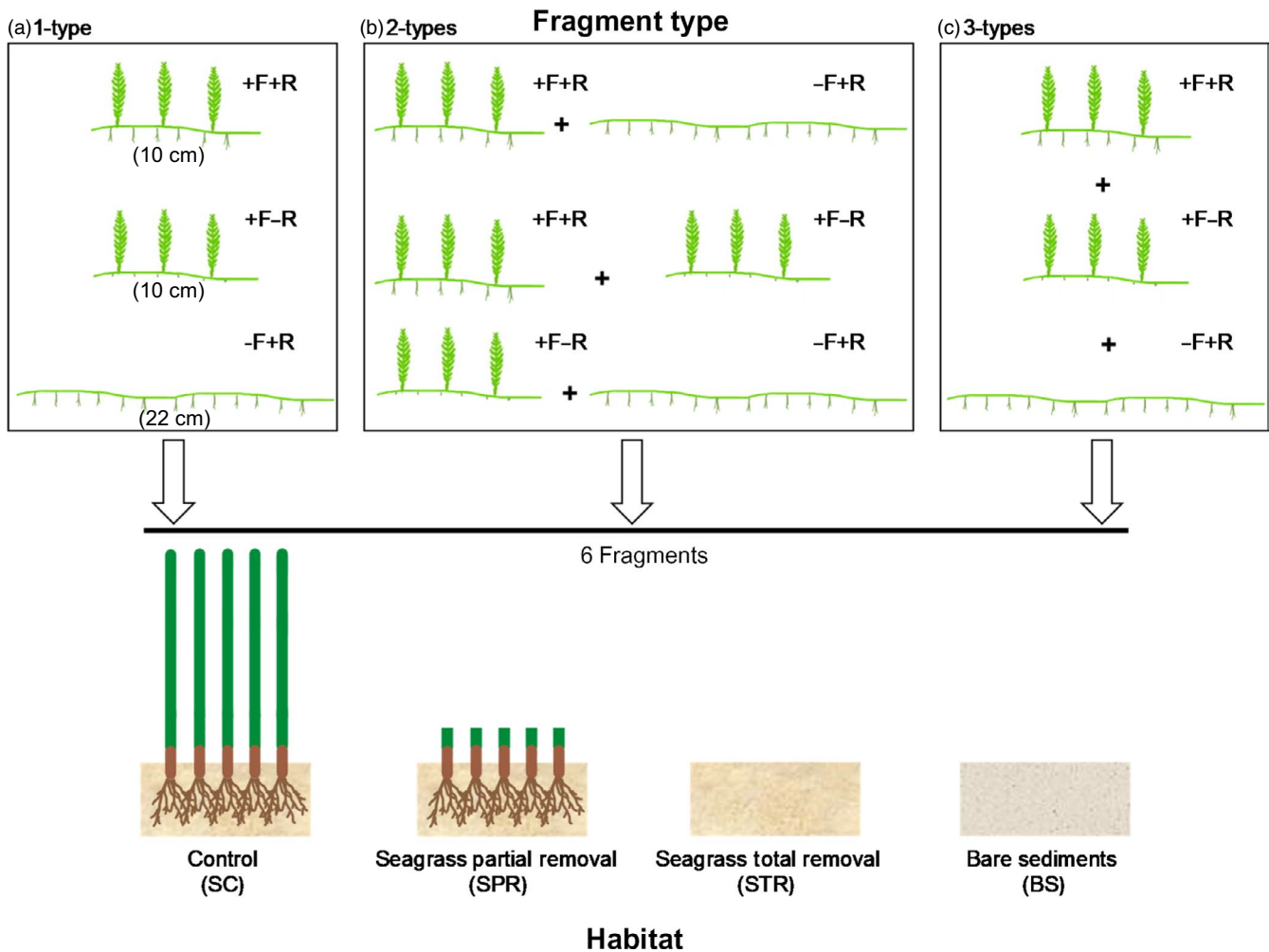

FIGURE 1 Schematic representation of the experimental design. An inoculum of six fragments of *Caulerpa taxifolia* was transplanted into each of the five replicate plots of each of the different habitats. The six-fragment inoculum was composed by either (a) one type of fragments (+F+R vs. +F−R vs. −F+R); (b) two types of fragments generated by the possible pair-wise combinations (+F+R/−F+R vs. +F+R/+F−R vs. +F−R/−F+R) or c) three types of fragments (+F+R/+F−R/−F+R). *F* = fronds; R = rhizoids [Colour figure can be viewed at wileyonlinelibrary.com]

transplanted into experimental plots the following day (22 March 2018). Each fragment was held in the centre of an experimental plot using two U-shaped metal wire pins, a widely used transplant technique (Ceccherelli & Piazzi, 2001; Piazzi, Balata, Ceccherelli, & Cinelli, 2005; Wright & Davis, 2006). Importantly, establishment and growth of *C. taxifolia* in Lake Conjola (NSW, Australia) have been previously shown not to differ between fragments deployed loose on sediments or maintained in place by means of U-shaped wire pins (Wright & Davis, 2006), suggesting that this technique does not impinge on our comparison of fragment establishment across habitats. The same authors have demonstrated no artefact of pins on *C. taxifolia* survivorship and growth. Seagrass leaves in SPR plots were re-clipped before transplanting fragments.

Six weeks after the addition of the fragments to plots (1 May 2018), a lapse of time long enough time for fragments to respond to experimental conditions (Ceccherelli & Cinelli, 1999; Gribben et al., 2018; Uyà et al., 2018), *C. taxifolia* was manually retrieved from each experimental plot and brought to the laboratory in separate plastic bags filled with seawater. Fresh fragments were immediately photographed while lying flat on a white plastic surface, including a scale bar. Total stolon length, number of rhizoid and fronds as well as the length of each frond were measured from each picture using video image analysis (ImageJ). Samples were then dried in a muffle furnace at 60°C for 30 hr and the biomass estimated as dry weight using a precision scale.

2.3 | Statistical analyses

All response variables measured were analysed by means of an asymmetrical ANOVA including habitat and fragment type, treated as fixed and crossed factors. To test for the effects of interaction terms relevant to our hypothesis, the factor fragment type was partitioned in the contrast '3 types' versus 'Other types', resulting in an asymmetrical design (Underwood, 1991). The term 'Other types' was then further partitioned into the contrasts 2 Types versus 1 Type, Among 2 Types and Among 1 Type to test for the effects of fragment type diversity and identity. Denominators for *F*-ratios were identified following the logic of Beyond-BACI designs (Underwood, 1991). Cochran's test was used to assess variance heterogeneity and data were log transformed when necessary. SNK tests were used for a posteriori comparisons of the means (as recommended by Underwood, 1997). Analyses were performed using the functions in the R package GAD (Sandrini-Neto & Camargo, 2014). In all, 11 plots, evenly distributed among treatments, could not be found at the end of the experiment. In addition, two image files were damaged preventing the acquisition of morphometric data. Missing data were replaced with the mean value of the treatment they belonged to, to maintain a balanced design; degrees of freedom in the residuals were adjusted accordingly (Underwood, 1997).

Stability of *C. taxifolia* biomass at the sea-scape level was assessed by calculating the coefficient of variation (CV), an inverse measure of stability (Tilman, 1996), calculated as the ratio of the standard deviation to the mean for each fragment type across habitats. CV values were compared among fragment types by means of a modified signed-likelihood ratio test (M-SLR test) using the function mslr_test implemented in the CVEQUALITY R package (Marwick & Krishnamoorthy, 2019). This package handles unbalanced designs and, therefore, there was no need of replacing missing replicates with treatment means. This test is generally more powerful than the asymptotic test (Feltz & Miller, 1996) and has lower rates of type I error.

3 | RESULTS

There was a general trend for higher values of the response variables in unvegetated habitats, both bare sediments (BS) and total seagrass removal (STR), compared to full (SC) and reduced canopy (SPR) plots (Figures 2 and 3). Except for rhizoid clusters, for which numbers increased from full canopy to bare sediment plots (SNK test: BS > STR > SPR = SC) regardless of fragment type, variations among habitats in the other response variables were dependent upon the characteristics of fragment inocula (Tables 1 and 2 and Supporting Information Tables S1–S4). Importantly, the type and type diversity of fragments inoculated had significant effects on the final biomass and morphological features of *C. taxifolia* in vegetated (either with intact or reduced canopies), but not unvegetated habitats (Figures 2 and 3). Seaweed biomass in vegetated habitats differed between plots inoculated with 2 types and 1 type of fragments (Table 1) and a similar trend was evident for stolon length and frond number (interaction H × 2 types vs. 1 type, .05 < *p* < .06; Table 2 and Tables S1 and S3). In control plots (SC), *C. taxifolia* achieved a higher biomass, developed longer stolons and more fronds when inocula were made of 1 type of fragment (Figures 2 and 3). This pattern was mainly due to intact fragments (+F+R) performing better than other fragment types (significant interaction Habitats × Among 1 Type, Tables 1 and 2). A similar trend was evident also for frond length (Figure 2).

In seagrass partial removal plots (SPR), although differences between 2 types and 1 type of fragment were not significant (SNK tests), mixed inocula made of +F+R and −F+R fragments had the greatest biomass and stolon length. Indeed, this combination of fragment types developed a higher biomass and stolon length than the other two-type combinations, consistently across habitats (significant main effect of the factor Among 2 Types; Tables 1 and 2 and Table S1).

There was no significant difference in CV among fragments types (M-SLRT = 4.406, *p* = .575), suggesting that seaweed biomass stability across habitats did not change according to the characteristics of the fragment inoculum (Figure 4).

4 | DISCUSSION

The ability of fragments of the invasive seaweed, *C. taxifolia*, to establish and grow was markedly lower in seagrass control and
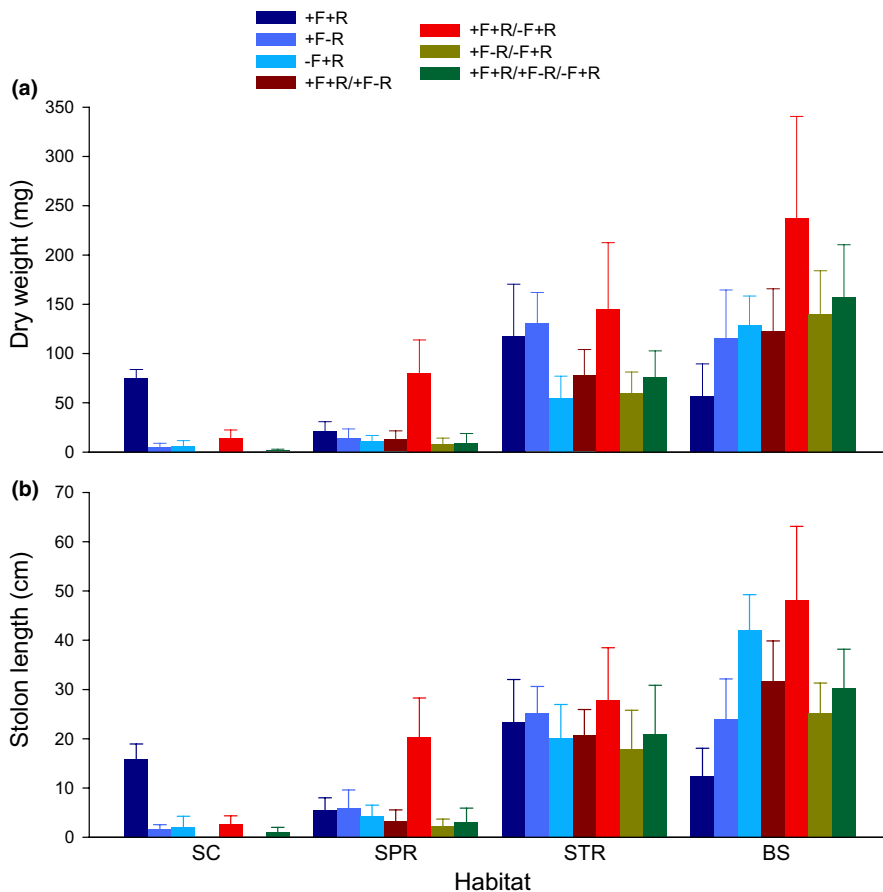
FIGURE 2 (a) final Biomass (mg dw) and (b) total stolon length (cm) of *Caulerpa taxifolia* in different habitats (SC = seagrass control, SPR = seagrass partial removal, STR = seagrass total removal, BS = bare sediments) produced by inocula of one fragment type (+F+R vs. +F−R vs. −F+R), two fragment types generated by the possible pair-wise combinations (+F+R/−F+R vs. +F+R/+F−R vs. +F−R/−F+R) or three fragment types (+F+R/+F−R/−F+R). *F* = fronds; R = rhizoids. Data are means ± *SE*, *n* = 5. Results of SNK tests for final biomass and total stolon length are reported in Table 1 and Table S1, respectively [Colour figure can be viewed at wileyonlinelibrary.com]

partial removal (SC and SPR) than in unvegetated plots (BS and STR), suggesting that both above- and below-ground seagrass biomass sustain resistance to invasion. These results are in accordance with previous studies from marine (Ceccherelli et al., 2014; Glasby, 2013; Mulas & Bertocci, 2016; Scheibling & Gagnon, 2006; South & Thomsen, 2016; Thomsen et al., 2019; Valentine & Johnson, 2003) and terrestrial habitats (D'Antonio & Vitousek, 1992; Diez et al., 2012; Hobbs & Huenneke, 1992) showing that invasive macrophytes are often opportunistic species that rely on native community disruption for establishment and spread. Such opportunistic behaviour of invaders does not imply weak effects on natives; in fact, once established, invasive species can trigger novel positive feedback mechanisms that facilitate their persistence at the expense of native habitat-formers and associated species (Bauer, 2012; Bulleri, Benedetti-Cecchi, Ceccherelli, & Tamburello, 2017; Gaertner et al., 2014).

In general, *C. taxifolia* fragments achieved a low biomass also in seagrass partial removal (SPR) plots, indicating that resistance to invasion is not sustained exclusively by the canopy. As widely demonstrated in terrestrial environments (Kowalski et al., 2015; van der Putten et al., 2007), below-ground processes under microbial control can regulate the establishment and growth of non-native species also in marine sediments (Gribben et al., 2017, 2018). The microbial metabolism (e.g. sulphur cycling) differs between sediments colonized by *Z. muelleri* versus *C. taxifolia*, likely because of variations in oxygen content, quantity and quality of

plant detritus (Gribben et al., 2017). Importantly, below-ground processes could sustain seagrass resistance to invasion in the face of increased leaf grazing due to the decline of top predators and poleward expansion of tropical herbivore fishes (Hyndes et al., 2016; Östman et al., 2016).

Recent studies have experimentally shown a limited growth of fragments of *C. taxifolia* in seagrass sediments and that sediment processes remain active post-canopy disturbance, at least in the short term (Gribben et al., 2017, 2018). Our results suggest that such microbial-mediated processes remained somewhat efficient also after the removal of both above- and below-ground biomass of *Z. muelleri*. This mechanism may explain the greater ability of −F+R fragments in regenerating fronds in bare sediments, but not on sediments from which both below- and above-ground *Z. muelleri* structures were recently removed. This hypothesis would be substantiated by the fact that the overall biomass (i.e. across the different fragment type inocula) achieved by *C. taxifolia* in STR (95.0 ± 15.4) was about 30% lower than BS (139.2 ± 24.2).

Few studies have investigated how the establishment and growth of different types of propagules vary according to external biotic or abiotic conditions. Nonetheless, those that have indicate that the effects of propagule quality on invasion success are context dependent. For example, in terrestrial environments, larger fragments (rhizome segments >3 nodes in length) of the cogongrass, *Imperata cylindrica*, had more tillers and exhibited enhanced growth, but only when exposed to full sun light (Estrada et al., 2016).

FIGURE 3 (a) final number of rhizoids, (b) number of fronds and (c) length of fronds of *Caulerpa taxifolia* in different habitats (SC = seagrass control, SPR = seagrass partial removal, STR = total seagrass removal, BS = bare sediments) produced by inocula of one fragment type (+F+R vs. +F−R vs. −F+R), two fragment types generated by the possible pair-wise combinations (+F+R/−F+R vs. +F+R/+F−R vs. +F−R/−F+R) or three fragment types (+F+R/+F−R/−F+R). *F* = fronds; *R* = rhizoids. Data are means ± *SE*, n = 5. Results of SNK tests are reported in Table S2 for the final number of rhizoids, in Table S3 for the number of fronds and in Table S4 for the mean length of fronds [Colour figure can be viewed at wileyonlinelibrary.com]
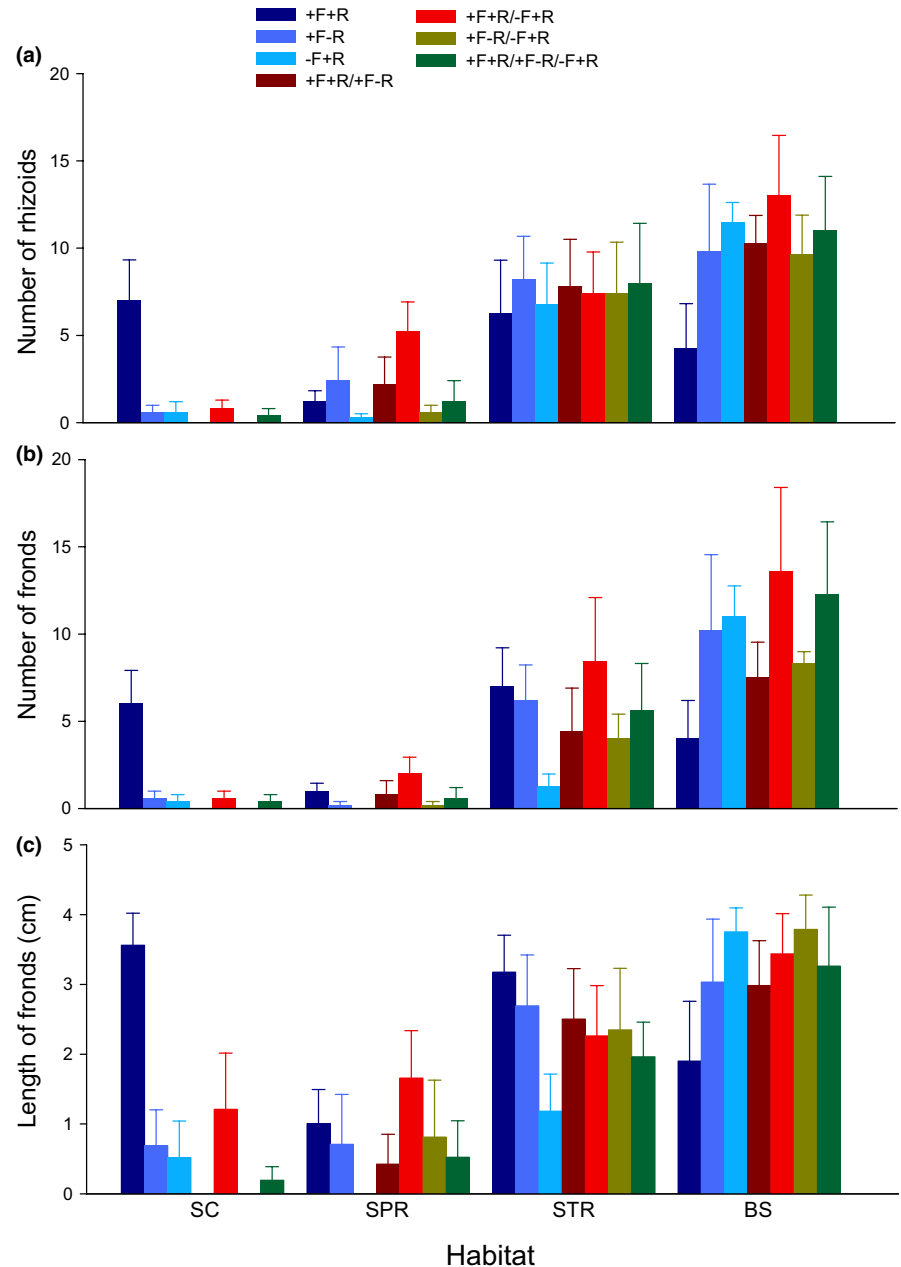
In marine environments, variation in survival and growth among different fragment types of *C. cylindracea* was found to be dependent upon the physical characteristics of sediments (organic matter loading; Bulleri et al., 2018) and to the intensity of the disturbance applied to the native canopy (Uyà et al., 2018). Our study expands these findings by showing that the relevance of seaweed fragment traits allowing a more efficient exploitation of resources appears reduced in unvegetated habitats lacking of native competitors. Irrespective of their traits, different types of fragments were able to establish in both bare sediments (BS) and seagrass total removal (STR) and develop a comparable biomass, following a growth form characterized by a relatively large number of long fronds. *C. taxifolia* fragments were transplanted at the centre of experimental plots and, in BS and STR treatments, they were unlikely to be shaded by the relatively short canopy of surrounding *Z. muelleri* plants. Thus, a

growth form characterized by tightly packed, long fronds may represent a plastic response to adverse environmental conditions, such as excessive solar irradiance, that characterize shallow subtidal sand flats (Collado-Vides & Robledo, 1999).

Fragments initially lacking rhizoids were able to regenerate them when transplanted in unvegetated habitats. Sediment anoxic conditions in the absence of seagrasses have been shown to facilitate establishment and growth in both *C. taxifolia* and *C. cylindracea* (Gribben et al., 2017, 2018). These seaweeds can quickly regenerate rhizoids from both fronds and stolon fragments, suggesting that the lack of these structures does not impair establishment where abiotic conditions are suitable and resources freely available to allow for regeneration without a cost to other structures (Bulleri et al., 2018; Gribben et al., 2017; Smith & Walters, 1999; Uyà et al., 2018).

Source of variation	df	MS	F	p
Habitat = H	3	83.349	28.05	.000
Fragment type = FT	6	5.161	1.74	.119
3 types versus Other types	1	5.980	2.01	.159
Among other types	5	4.998	1.68	.146
2 types versus 1 type	1	0.967	0.33	.567
Among 2 types	2	8.884	2.99	.055
Among 1 type	2	3.127	1.05	.354
H × FT	18	5.014	1.69	.053
H × 3 types versus Other types	3	0.905	0.30	.825
H × Among other types	15	5.835	1.96	.026
H × 2 types versus 1 type	3	9.306	3.13	.029
H × Among 2 types	6	1.316	0.44	.850
H × Among 1 type	6	8.619	2.90	.012
Residual	101	2.971		

SNK tests

Among 2 types	Habitat × Among 1 type
+F+R/−F+R > +F+R/+F−R = +F−R/−F+R	SC: +F+R > +F−R = −F+R
Habitat × 2 Types versus 1 Type	BS: −F+R = +F−R = +F+R
SC: 1 Type > 2 Types	SPR: +F+R = −F+R = +F−R
BS: 2 Types = 1 Type	STR: +F−R = +F+R = −F+R
SPR: 2 Types = 1 Type	+F+R: STR = SC = BS = SC
STR: 1 Type = 2 Types	+F−R: STR = BS > SPR = SC
1 Type: STR = BS > SC = SPR	+F−R: n.a.h. (BS > SC; BS > SPR; STR > SC)
2 Types: BS = STR > SPR > SC	

TABLE 1 Asymmetrical ANOVA on the effects of the Habitat and Fragment type on the biomass of *C. taxifolia*. Analysis on log (x + 1) transformed data; Cochran's test = 0.08; *p* > .05. SNK tests are reported for significant main effects or interaction terms. The residual has been corrected for missing replicates (*n* = 11); n.a.h. = no alternative hypothesis. *F* = fronds, R = rhizoids, SC = seagrass control, BS = bare sediments, SPR = seagrass partial removal, STR = seagrass total removal

Response variable	Source of variation						
Total stolon length	Habitat (H)		H × Among other types		H × Among 1 type		
Transf. log (x + 1)	MS	F	MS	F	MS	F	
	44.013	29.49***	2.724	1.82*	4.177	2.80*	
	Among 2 types		H × 2 types versus 1 type				
	MS	F	MS	F			
	4.497	3.01[†]	3.859	2.59[†]			
Rhizoid number	Habitat (H)						
Transf. None	MS	F					
	618.53	25.17***					
Frond number	Habitat (H)		H × FT		H × Among 1 type		
Transf. log (x + 1)	MS	F	MS	F	MS	F	
	23.823	37.88***	1.115	1.77*	2.401	3.82**	
	H × 2 types versus 1 type						
	MS	F					
	1.631	2.59[†]					
Frond length	Habitat (H)		H × Among other types		H × Among 1 type		
Transf. None	MS	F	MS	F	MS	F	
	47.801	23.51***	4.001	1.97*	6.717	3.30**	

TABLE 2 Summary table reporting significant main effects or interactions between factors included in the analyses of total stolon length, number of rhizoids, number of fronds and mean length of fronds. *p < .05; **p < .01; ***p < .001; [†]0.05 < p < .06. Full details of the analyses are reported in Tables S1–S4
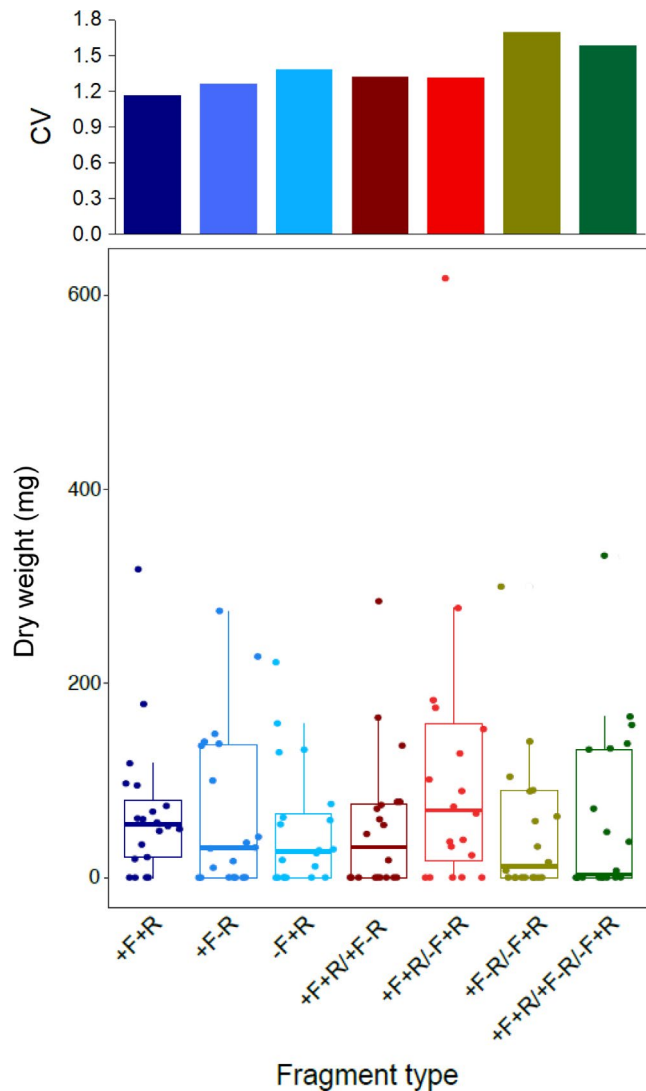
FIGURE 4 Boxplot of the final biomass (mg dw) achieved by different combinations of *Caulerpa taxifolia* fragment types across habitats. Horizontal lines show the median, boxes indicate the middle two quartiles, vertical lines indicate the first and fourth quartiles. Data points are reported to enhance visualization of dispersion. The top graph reports the CV values in the different fragment type treatments [Colour figure can be viewed at wileyonlinelibrary.com]

Pinning may have facilitated fragment establishment on bare sediment flats (BS and STR) where they are not entrapped by extant vegetation and, hence, more susceptible to dislodgement by waves and currents. Although we cannot exclude such an effect of fragment pinning in unvegetated habitats, a previous study (Wright & Davis, 2006) has reported no difference in the biomass of *C. taxifolia* between plots in which stolon fragments were left loose on the surface of the sediments or fixed by means of U-shaped pins. Our study was conducted within the inner part of an estuarine embayment, where both wave action and tidal currents are weak. Thus, reduced dragging due to hydrodynamic forces, along with the rapidity of fragment re-attachment (i.e. within 2 days; Walters, 2009), should

have minimized potential positive effects of pinning on fragment establishment. In addition, poor development of rhizoids by +F−R fragments transplanted in both seagrass canopy clipping (SPR) and control (SC) plots suggests a control of rhizoid regeneration by biotic and abiotic characteristics of recipient habitats.

Intact (+F+R) were the only type of fragment to perform well in seagrass control plots, suggesting that the presence of both rhizoids and fronds is necessary to establish and grow under seagrass canopies. These results are in accordance with those of Uyà et al. (2018) who found that only intact fragments of *C. cylindracea* could establish and grow underneath the canopy of the native seagrass, *Posidonia oceanica*. Intact *C. taxifolia* fragments developed long fronds, likely as a response to light limitation (Ceccherelli & Cinelli, 1998). This suggests that allocation of resources to frond elongation may represent a plastic response also to competition from native macrophytes.

In contrast, the success of +F+R was quite poor in SPR plots. Clipping of the canopy may have altered the carbon budget of plants and, thereby, sediment chemistry. For example, experimental leaf clipping of the tropical seagrass, *Thalassia hemprichii*, resulted in a reduction of organic carbon and THAA (total hydrolysable amino acids) in surficial sediment layers (Dahl et al., 2016). Reduced organic content in sediments has been, in turn, shown to reduce the success of fragments of the congeneric species, *C. cylindracea* (Bulleri et al., 2018).

Two-type inocula made of +F+R and −F+R fragments achieved a greater biomass and developed longer stolons than other fragment type treatments in SPR plots. To the best of our knowledge, this is the first study documenting facilitative effects between propagules of different quality. The success of both types of fragments in this habitat was rather poor when transplanted in single-type inocula. Unfortunately, it was not possible to monitor each single fragment and it is not, therefore, possible to establish if the greater biomass obtained in mixed inocula is the result of −F+R facilitating +F+R fragments, the opposite or both. Positive effects of −F+R on +F+R could be explained by below-ground processes, which have so far received little regard in the success of marine macrophytes in marine sediment systems, despite them being some of the most invasive species in the world (but see Gribben et al., 2017; Gribben et al., 2018). In Caulerpales, rhizoids are root-like structures associated with specific bacteria that enhance carbon, nitrogen (including amino acids) and phosphorous uptake from the substratum (Arnaud-Haond et al., 2017; Chisholm, Dauga, Ageron, Grimont, & Jaubert, 1996; Rizzo et al., 2017). Thus, 22-cm long −F+R fragments, by virtue of their high number of rhizoid clusters, may have enhanced the success of +F+R fragments allowing a more rapid conditioning of the sediment microbiota without, at least in the first stages of establishment, reducing light levels. By contrast, we do not currently envision plausible mechanisms that could underpin facilitation of −F+R by +F+R fragments.

Contrary to our expectations, the most diverse fragment inocula (three fragment types) did not enhance seaweed biomass stability across the seascape. Three-fragment type inocula only performed

well in unvegetated habitats where, as previously discussed, fragment type seems to have little effect on the establishment and growth of *C. taxifolia*. On the other hand, in SPR plots, two-fragment type inocula made of +F+R and −F+R achieved a greater biomass and developed longer stolons than other fragment type treatments. Thus, replacing one +F+R and one −F+R fragment with two +F−R fragments strongly reduced invasion success. Lower success of +F+R and −F+R in three-fragment type inocula could be due to the decrease in their relative density and a subsequent reduction in the total number of rhizoids in the plots, or, alternatively, to negative effects of +F−R fragments. Due to logistic constraints, we could not replicate fragment type treatments at different densities and we cannot, therefore, distinguish between these two alternative models.

The quality of propagules has been often investigated in terms of their size (Estrada et al., 2016; Lin, Alpert, & Yu, 2012; Quinn & Holt, 2008; Smith & Walters, 1999; Watanabe et al., 2009). For example, the number of nodes in stems or rhizomes in fragments of several invasive, clonal plants (e.g. *Ipomaea aquatica*, *Arundo donax* and *Imperata cylindrica*) was found to influence their survivorship and growth (Estrada et al., 2016; Lin et al., 2012; Quinn & Holt, 2008). Likewise, individuals of the bryozoan, *Bugula neritina*, developed from larger larvae had a better performance (Marshall et al., 2003). However, beyond size variation, propagules of invasive species can also differ in key life traits (Smulders, Vonk, Engel, & Christianen, 2017; Uyà et al., 2018; Wright & Davis, 2006). For example, drifting fragments of the non-native seagrass, *Halophila stipulacea*, in a Carribean Bay, had a number of shoots, leaves and roots varying between 3 and 15, 5 and 28 and 2 and 0, respectively (Smulders et al., 2017). Such differences may explain the large variation in fragment production of new shoots, leaves, roots and biomass (Smulders et al., 2017). Likewise, in vitro experiments demonstrated that branch tips of *Kappaphycus alvarezii*, a red seaweed intentionally introduced world-wide for cultivation, can develop new shoots faster than sections from older branches because they host apical cells with high regenerative potential (Luhan & Mateo, 2017). Our study, maintaining biomass even across fragment types, clearly suggests that propagule quality in clonal macrophytes is not limited to their size, but extends to their life traits.

In addition, our study suggests that the relevance of specific propagule traits for invader establishment and growth decreases when moving from intact to degraded habitats. High invasibility of disturbed habitats is currently thought to be mainly the result of reduced competition from native species (Davis et al., 2000; Levine & D'Antonio, 1999). However, due to reduced propagule trait requirements necessary for establishment, a propagule batch of a given size would exert a greater pressure on degraded than intact recipient habitats. Under these circumstances, considering propagule size in terms of the amount of competent propagules, rather than an absolute measure, would refine our ability of predicting invasion risk across habitats differing in biotic or abiotic conditions. In particular, it appears as paramount to predict

invasion risk in pristine environments, those generally given priority in conservation strategies.

Finally, we demonstrate that interactions among invader propagules differing in quality are not necessarily negative (Blank, 2010; Steen, 2003; Uyà et al., 2018). Although further experimental work is needed to identify the underpinning mechanisms, our study provides novel evidence that facilitation among different types of propagules may allow an invader to overcome the biotic resistance of native habitats. The large variability of propagule quality documented in nature (Lange & Marshall, 2016; Smulders et al., 2017; Verling et al., 2005) indicates that single quality propagule inocula are unlikely. Hence, assessing how propagules differing in quality perform in different habitats might be not sufficient to draw a comprehensive picture of invasion risk, as their establishment and spread can be modulated by both negative and positive interactions among them. For this reason, propagule composition should be considered as a further dimension of propagule pressure.

AUTHORS' CONTRIBUTIONS

F.B., P.E.G. and E.M.M. conceived the ideas and methodology. P.E.G., F.B., E.M.M. and S.E.V. collected the data. P.E.G. F.B. analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.44j0zpc8x (Bulleri, Marzinelli, Voerman, & Gribben, 2019).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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