Species richness effects on the vegetative expansion of transplanted seagrass in Indonesia

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Abstract: Seagrass restoration is necessary to provide the critical ecosystem functions that are being lost with seagrass decline. Seagrass restoration of mixed species seagrass beds, especially in the Indo-Pacific Ocean, is poorly understood. Here, we transplanted random combinations of 1, 2, 4 and 5 seagrass species common in Indonesia to determine the effect of multispecies plantings on expansion of rhizomes. We measured seagrass vegetative expansion outside of the transplantation plots after 1 year post-transplantation for 5 months. The expansion rate increased with species richness. This result indicates that a multispecies approach to seagrass restoration in Indonesia would benefit restoration efforts. Further, for multispecies restoration we suggest using five-species combinations because they expanded the fastest of all species richness levels by the end of the experiment (on average 15.4 cm^2 day^{-1}).

Keywords: biodiversity; Indonesia; multispecies restoration; rhizome expansion; seagrass.

Introduction

Seagrass ecosystems provide food, nursery, and spawning ground for organisms (Dorenbosch et al. 2006), support epiphyte and macrophyte communities (Harlin 1975), stabilize sediments, and can sequester carbon (Duarte 2002, Fourqurean et al. 2012). In addition, these ecosystems are able to reduce exposure to pathogenic bacteria, which threaten human life and marine organisms (Lamb et al. 2017). The rate of seagrass decline before 1990 has been approximately 7% year^{-1} worldwide (Waycott et al. 2009). In line with this decline, 10 out of 72 seagrass species on Earth are at risk of extinction (Short et al. 2011). These conditions are driven by increasing human activity in coastal areas, including boating activity (Walker et al. 1989, Demers et al. 2013), destructive fishing and marine debris (Sheavly and Register 2007), construction and eutrophication (Burkholder et al. 2007).

To mitigate these declines, various approaches have been taken, such as legislation or conservation activities like restoration (Hotaling et al. 2011). To date, a literature review by van Katwijk et al. (2016) cited 1786 restoration trials that have been conducted in many places. These trials used different planting techniques and response variables to assess success. Restoration has been practised mainly in temperate regions (Phillips 1974, Paling et al. 2001, Bastyan and Cambridge 2008, Bell et al. 2008, Ganassin and Gibbs 2008, Hotaling et al. 2011, Bourque and Fourqurean 2014, Tanner 2014, Greiner et al. 2016) whereas restoration in tropical regions is still being developed (Vermaat et al. 1995, Lanuru 2011, Ooi et al. 2011, Williams et al. 2017).

Indonesia is one of the Southeast Asia countries in which seagrass restoration activity is lacking, despite the high loss of seagrass in this area due to anthropogenic factors (Nadiarti et al. 2011). Indonesia has very high seagrass biodiversity and typically at least eight out of 15 species grow together in the seagrass beds (Short et al. 2007). However, in Indonesia and other regions where seagrasses grow in mixtures, a monospecific planting technique is typically used, as commonly done in temperate regions (Bastyan and Cambridge 2008, Ganassin and Gibbs 2008, Williams et al. 2017). In this study we assessed the role of species richness in the vegetative expansion of rhizomes, which is related to how rapidly seagrass transplants can colonize new areas. The assessment was conducted in an experimental transplantation of six species of Indonesian seagrass both individually and also in mixtures (Williams et al. 2017). Our hypothesis was that seagrass would expand faster when planted in mixtures as opposed to single species.

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Materials and methods

Site location and experimental restoration technique

An experimental restoration was conducted beginning in August 2014 and was located in northeast Badi Island, Spermonde Archipelago, Indonesia (S 4°57′56.32″ –4°57′58.18″, E 119°17′17.03″–119°17′19.63″). The experimental restoration consisted of planting six common species found in the waters: *Enhalus acoroides* (Linneaus f.) Royle, *Thalassia hemprichii* (Ehrenberg) Ascherson, *Halodule uninervis* (Forsskål) Ascherson, *Syringodium isoetifolium* (Ascherson) Dandy, *Cymodocea rotundata* Ascherson *et* Schweinfurth, and *Halophila ovalis* (R. Brown) J.D. Hooker (Kuo and den Hartog 2001). Each species was planted with intact rhizomes, roots, meristems and shoots. The standard rhizome length was 15 cm for each species and included a few leaf shoots except for *Enhalus acoroides* (single shoot). Each plot (60 cm × 60 cm) was planted with sixteen seagrass units at four levels of species richness. The species richness levels were single species (monoculture; one for each species), two-species (10 combinations), four-species (10 combinations) and five-species combinations (all six possible combinations of five out of six species; see Williams et al. 2017, Supporting Information Table S1). The two- and four-species combinations were selected randomly from all six available species. There were three replicates for each species combination with a total of 96 plots. Plots were spread randomly in an unvegetated area with at least 1 m between plots.

Expansion area measurement

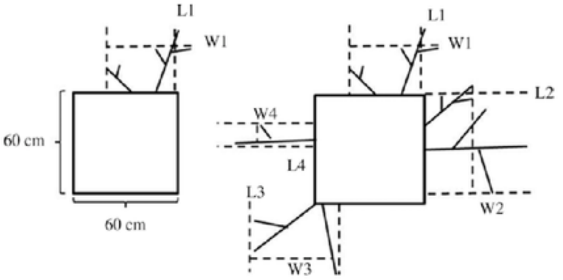

Figure 1: Method to measure elongation of rhizomes growing outside the plot boundary.
The dotted lines represent the maximum length (L) and width (W) of rhizome expansion beyond the plot.

Expansion area data were collected fortnightly starting 1 year after the seagrasses were transplanted and had established well at all the species richness levels from September 2015 to January 2016. We measured the maximum length and width of rhizomes that expanded outside of the plot (60 cm × 60 cm) using a meter tape. The expansion area was defined as a rectangle formed by the maximum length of a rhizome expanding beyond the plot edge and the distance of maximum spread along the plot edge from the point where the rhizome expanded outside of the plot and the rhizome or rhizome branch meristem (Figure 1). The expansion area for each plot was the sum of all the individual rectangles around the plot edge. The expansion rate was calculated as the expansion area at the end of the experiment divided by the number of days (490) after transplantation. The rate was stable over the 5-month monitoring period. The R^2 values from linear regressions of the extension area versus time over the monitoring period ranged from 0.003 to 0.604 across richness treatments.

Data analysis

Data were analysed in R-Studio (https://repo.bppt.go.id/cran/). The ggplot and plotly packages were used for graphical analysis and the ANOVA function was used to analyse the variance among species richness levels, among monocultures, and among five species combinations. The mean of the three replicate plots (except for two treatments in which one replicate plot was lost at the end of the experiment, i.e. only 94 out of 96 plots) for each species combination was the response variable in the ANOVAs. Tukey's HSD *post hoc* test was used to determine differences among species richness levels. Log response ratios were calculated to test for transgressive overyielding (Cardinale et al. 2006, 2011). LR_{mean} is a ratio of the most diverse mixtures compared to the average monoculture response and indicates non-transgressive overyielding if >1. LR_{max} is the transgressive overyielding log response ratio, which if >1 indicates that the most diverse polycultures are different from the monoculture treatment having the highest expansion rate. The hypothesis that each LR was equal to zero was tested using t-tests. To test for the contribution of each species to the expansion rate, a general linear model multiple regression was performed in which the predictor variables were species richness and the initial proportion of each of the six species in the plots (Kirwan et al. 2009).

Table 1: Comparison of expansion rate among species richness levels (n = 94) using ANOVA, among the five-species combinations (n = 3 plots), and among the six species grown in monoculture (n = 3 plots, except *Halodule uninervis* with n = 2 plots).

Source of variation	SS	*df*	MS	*F*	p-Value
Among species richness levels					
Between groups	9,95,043	3	331681	4.226	0.014
Within groups	21,97,381	28	78478		
Total	31,92,424	31			
Among five-species combinations					
Between groups	2146	5	429.196	1.450	0.276
Within groups	3553	12	296.090		
Total	5699	17			
Among monoculture species					
Between groups	120	5	244	0.698	0.636
Within groups	377	11	34		
Total	497	16			

Results

The rate of expansion was significantly different among richness levels (Table 1; Figure 2, Tukey HSD; $F_{3,28} = 4.226$, p = 0.014). The expansion rate was fastest in the five species treatment (15.4 cm^2 day^{-1}), almost four times faster than the slowest rate for the monocultures (3.8 cm^2 day^{-1}). The average expansion areas at the end of the experiment were 1852 ± 598 cm^2 SE for monocultures, 3688 ± 686 cm^2 SE for two species, 2649 ± 675 cm^2 SE for four species, and 7550 ± 2393 cm^2 SE for five species. There were no detectable differences in the expansion rates among all of the possible combinations of the six species (Figure 3; Table 1; one-way ANOVA: $F_{5,12} = 1.449$, p = 0.276). LR_{mean} was not significantly different from zero ($t = 1.729$, $df = 17$, p = 0.102). LR_{max} was not different from zero ($t = 0.168$, $df = 17$, p = 0.869) indicating that the mixtures did not expand as fast as the best monoculture (*Halodule uninervis*) and thus the response ratio did not support transgressive overyielding.

The rate of expansion in the monoculture was highest for *Halodule uninervis* (7.4 ± 7.4 cm^2 day^{-1} SE), followed by *Syringodium isoetifolium* (6.7 ± 4.3 cm^2 day^{-1} SE, *Cymodocea rotundata* (4.6 ± 4.6 cm^2 day^{-1} SE), *Thalassia hemprichii* (2.6 ± 1.6 cm^2 day^{-1} SE) and *Halophila ovalis* (1.3 ± 1.3 cm^2 day^{-1} SE) (Figure 4). Although *Enhalus acoroides* survived well, it did not expand outside the plots during the experiment. The analysis of variance indicated that the rates did not differ between species (Table 1; one-way ANOVA: $F_{5,11} = 0.698$, p = 0.636). Although richness was a significant predictor of the extension rate in the multiple linear regression, none of the coefficients corresponding to each species was significant, which further supported the lack of differences among species (Table 2).

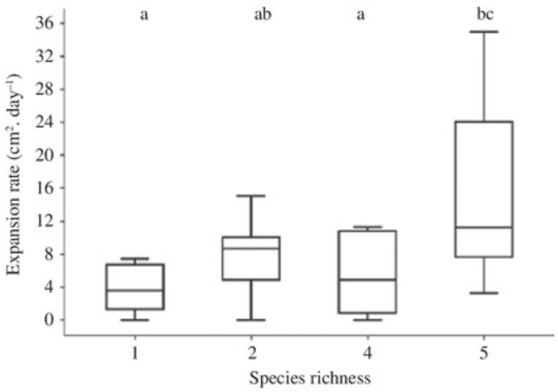

Figure 2: Median expansion rates at levels of species richness, the first and fourth quartiles and the "whiskers" indicate the lowest and highest values. n = 6 for 1 and 5 species, and n = 10 for 2 and 4 species.
Treatments that did not differ are indicated by the same letter above the bar (Tukey HSD test, p > 0.05).

Discussion

Species richness has a positive effect on the expansion of seagrass transplantations. Both the rate of expansion

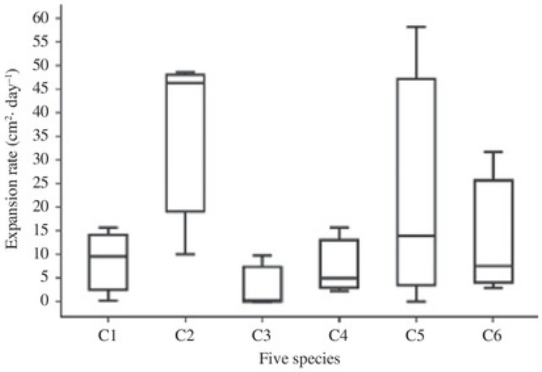

Figure 3: Expansion rates among five-species combinations.
C1: *Enhalus acoroides + Thalassia hemprichii + Cymodocea rotundata + Syringodium isoetifolium + Halodule* univervis; C2: *E. acoroides + T. hemprichii + C. rotundata + S. isoetifolium + Halophila ovalis*; C3: *E. acoroides + T. hemprichii + S. isoetifolium + H. univervis + H. ovalis*; C4: *E. acoroides + T. hemprichii + C. rotundata + H. univervis + H. ovalis*; C5: *E. acoroides + S. isoetifolium + C. rotundata + H. univervis + H. ovalis*; C6: *T. hemprichii + S. isoetifolium + C. rotundata + H. univervis + H. ovalis*. n = 3

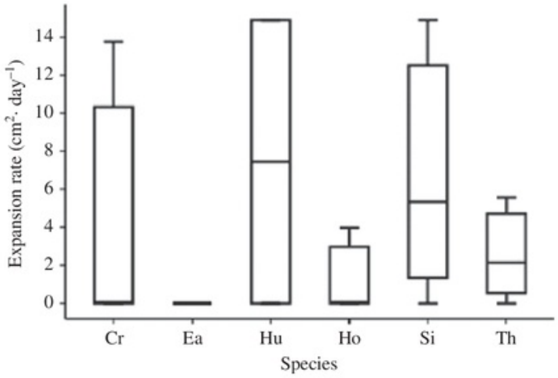

Figure 4: Expansion rates in monocultures of six species. Cr, *Cymodocea rotundata*; Ea, *Enhalus acoroides*; Hu, *Halodule uninervis*; Ho, *Halophila ovalis*; Si, *Syringodium isoetifolium*; Th, *Thalassia hemprichii*. n = 3 except *Halodule uninervis* n = 2. The expansion area of *Enhalus acoroides* was zero and it is not shown.

and the area covered by seagrasses increased, especially in the five species combination (Figure 2, Tables 1 and 2). Our results were similar to the effect of species richness on the survival and increase in % cover within transplanted plots (Williams et al. 2017). Monocultures expanded more slowly than mixtures in this experiment. These results indicate that a change from the common practice of planting a single species in seagrass restorations in Indonesia and other tropical regions to planting multiple species could improve restoration success, if the goal is to vegetate new areas as fast as possible.

Although the expansion rates and areas did not differ statistically among monocultures, the largest species (*Enhalus acoroides*) did not expand from the plots during the experiment and *Thalassia hemprichii*, another large species, expanded more slowly than the smaller species. This result is consistent with a previous study in which the strategies for rhizome elongation were related to the size of the seagrass species (Rollon et al. 1998). One difference between our study and other studies (Calumpong and Fonseca 2001, Duarte 2002) is that the small species *Halophila ovalis* did not expand fast in our experiment, despite being known as a colonizer species. Instead, although *Halophila ovalis* expanded fast, it was also fragile and easily broke or was uprooted, leading to a lower mean expansion. Regardless, the result that planting more than a single species led to the faster vegetative propagation is more important for seagrass restoration than the monoculture results.

The positive effect of species richness on the expansion of transplanted seagrasses is consistent with many other studies demonstrating the relationship between biodiversity and ecosystem functions and services (Gustaffson and Boström 2011, Duffy et al. 2017). Many other studies of seagrass intraspecific (genetic) diversity and species diversity within seagrass beds have contributed to this understanding (Duffy 2006, Duffy et al. 2003, 2015, Worm et al. 2006, Hughes and Stachowicz 2004, 2009). Although the mechanism for the positive effect of species richness in our experiment is a subject for future research, there was no evidence that a single species was driving the effect (Table 2). The most parsimonious hypothesis is that because the mixtures had the highest survival and rate of change in coverage, they had accrued sufficient resources to also expand the fastest. Williams et al. (2017) speculated that facilitation was occurring in that the larger, slower growing species offer protection from photoinhibition, hydrodynamic stress, and/or grazing, to the smaller faster growing ones. The small fast growers possibly stabilized the sediments more quickly and reduced advective loss of nutrients.

Our results, in combination with results on the survival and increase in % cover in mixed species transplantations (Williams et al. 2017), indicate that a multispecies approach to seagrass restoration in Indonesia would lead to faster colonization of unvegetated areas and the development of restored seagrass beds as compared to a monospecies approach. Practically speaking, any combination of the six species used in this experiment would lead to

Table 2: Coefficients from the general linear model for extension rate predicted by species richness and the proportion of each species transplanted in the plots.

Effect	Coefficient	Standard error	Standardized coefficient	*t*	p-Value
Richness	1.814	0.870	0.233	2.084	0.040
H. ovalis	64.10	109.5	1.236	0.586	0.560
H. uninervis	60.75	109.5	1.046	0.555	0.581
E. acoroides	63.24	110.1	1.315	0.574	0.567
T. hemprichii	57.51	109.6	1.078	0.525	0.601
S. isoetifolium	64.61	109.7	1.240	0.589	0.558
C. rotundata	67.68	109.6	1.373	0.617	0.539

enhanced vegetative propagation and, thus, the species that are most expedient to transplant could be selected. Also, the six species in our experiment represent only about half of the species that grow in the Indo-Pacific region, although they are common in mixed species seagrass beds. It is possible that species not tested in this experiment would lead to different results. Because the recommendation to transplant a mixed species assemblage is very different from the single species approach practised in Indonesia (Lanuru 2011, Ambo-Rappe and Yasir 2015), it will be important to test the effect of increasing species richness in other tropical regions where species grow together in mixtures (Tomasko et al. 1993, Bach et al. 1998, Lee et al. 2016).

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Bionotes

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Nenni Asriani is a doctoral student at Hasanuddin University. She studies the assessment of seagrass restoration success. She has been interested in seagrass research since being an undergraduate when she studied the survival rate and percent cover of seagrass transplanted with different species. She is interested in an academic carrier in marine ecology.

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Rohani Ambo-Rappe is a professor in marine ecology at the Faculty of Marine Science and Fisheries. She earned a PhD in marine science from The University of Newcastle, Australia. She was the head of Marine Ecology Laboratory (2008–2014) and served as Secretary of Marine Science Department (2010–2014). Her main research interests are seagrass ecology, ecosystem services, and ecosystem restoration. She is the recipient of national and international research grants and conducted some research collaboration on various topics related to seagrass ecosystem services and restoration.

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Mahatma Lanuru is a lecturer and an associate professor of marine science at Hasanuddin Universiy (Indonesia). He completed his BSc in marine science at Hasanuddin University and continued his Master in marine science at Aarhus University (Denmark). He completed his PhD at University of Kiel (Germany) in 2004. His main research topics are: coastal oceanography, sediment dynamic (erosion/deposition) in the estuarine and coastal areas, and habitat (seagrass) restoration. He has recently conducted research on (i) a transplantation experiment for assessing the feasibility of using seagrass for coastal protection in a small island, and (ii) small island coastal protection using "*Hybrid*" (a combination of seagrass vegetation and submerged submerged wave breaker).

Susan L. Williams
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Susan L. Williams held the rank of Distinguished Professor in the Department of Evolution and Ecology, University of California at Davis and its Bodega Marine Laboratory. She studied the relationship between biodiversity and ecosystem function provided by seaweeds and seagrasses. She worked on ecological restoration for nearly two decades. Susan L. Williams unfortunately passed away prior to the publication of this article.

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