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2 **Restored eelgrass (*Zostera marina* L.) as a refuge for epifaunal biodiversity in mid-Western**
3 **Atlantic coastal bays**

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14 Running head: Eelgrass restoration enhances biodiversity

15 **Abstract:**

16 As nearshore ecosystems are increasingly degraded by human activities, active restoration is a
17 critical strategy in ensuring the continued provision of goods and services by coastal habitats. After
18 being absent for nearly six decades, over 1800 ha of the foundational species eelgrass (*Zostera*
19 *marina* L.) has been successfully reestablished in the coastal bays of the mid-western Atlantic, USA,
20 but nothing is known about the recovery of associated animal communities in this region. Here, we
21 determine the patterns and drivers of functional recovery in epifaunal invertebrates associated
22 with the restored eelgrass habitat from 2001-2013. After less than a decade, the invertebrate
23 community in the restored bed was richer, more even, and exhibited greater variation in functional
24 traits than a nearby reference bed. Analysis of a suite of environmental and physical variables using
25 random forests revealed these differences were primarily due to the increasing area and density of
26 eelgrass directly attributable to ongoing restoration efforts. Based on analysis of functional traits,
27 we propose that the rapid life histories of constituent organisms may have played a key role in their
28 successful recovery. We also speculate that diverse epifaunal communities may have contributed to
29 the restoration success through a predefined mutualism with eelgrass. Given that restored eelgrass
30 now make up 32% of total seagrass cover in the mid-Atlantic coastal bays, this restoration may
31 conserve regional biodiversity by providing new and pristine habitat, particularly given the general
32 decline of existing eelgrass in this region.

33 **Keywords:** seagrass, restoration, functional traits, grazers

34 **Introduction**

35 Coastal habitats are becoming increasingly impacted through anthropogenic forcing
36 (Halpern et al. 2008), leading to loss of important and valuable services such as food production,
37 pollution control, shoreline buffering, and carbon storage (Barbier et al. 2011). At the same time,
38 human impacts are driving the rapid and irreversible loss of marine biological diversity (McCauley
39 et al. 2015). As biodiversity has been generally shown to promote ecosystem functioning in marine
40 systems (Gamfeldt et al. 2015), species extinctions may further erode the ability of nearshore
41 habitats to provide critical goods and services. Thus, there is strong incentive within the
42 conservation movement to protect and manage for high biodiversity in addition to protecting
43 habitat itself, particularly for marine realms (Palumbi et al. 2008; Duffy et al. 2016).

44 More recently, researchers have broadened their definition of biodiversity to incorporate
45 the functional roles of species within an ecosystem, represented by their *functional traits*:
46 measurable characteristics of individual organisms relating to their morphology, physiology,
47 ecology, behavior, and life history (Díaz et al. 2013). Functional diversity, then, captures the
48 breadth of variation in functional traits across all species within an assemblage. The application of
49 functional diversity accounts for the degree of redundancy within an assemblage (Rosenfeld 2002),
50 and thus can be used to refine conservation priorities by identifying areas of particular
51 vulnerability (Micheli and Halpern 2005), high productivity (Duffy et al. 2016), or that harbor
52 unique or functionally varied assemblages (Devictor et al. 2010; Stuart-Smith et al. 2013). By
53 specifying how organisms perform and interact with one another, traits can be also used to
54 mechanistically link pattern and process (Díaz and Cabido 2001), generating more accurate and
55 generalizable predictions for the ecosystem consequences of species losses (Mouillot, Bellwood, et
56 al. 2013).

57 In addition to conserving current coastal habitats and their biological diversity, there have
58 been increasing efforts to actively restore lost or degraded systems, including seagrasses (Orth et
59 al. 2006), marshes (Zedler 2000), mangroves (Ellison 2000), and oyster and coral reefs (Mumby
60 and Steneck 2008; Beck et al. 2011). A recent meta-analysis revealed that aquatic restorations have,
61 on average, recovered 86% of their biodiversity and 80% of their ecosystem services relative to
62 unrestored reference systems (Benayas et al. 2009). These values, however, underscore the general
63 trend that most restored systems have failed to fully recover their pre-disturbance structure and
64 functioning (Lotze et al. 2011; Duarte et al. 2015). Moreover, many assessments of recovery have
65 focused on quantifying the cover or abundance of the restored habitat itself (Lotze et al. 2011;
66 Duarte et al. 2015), and not the abundance or diversity of the organisms that use it (but see
67 Fonseca, Meyer & Hall 1996; Coen *et al.* 2007), even though it is these communities that underpin
68 many of the services provided by coastal ecosystems (Duffy et al. 2014). Finally, only a handful of
69 studies have integrated functional trait information into their assessment of faunal communities
70 associated with restored ecosystems, which may better reflect the recovery of the restored systems
71 by focusing on what constituent organisms are doing, as opposed to replicating some historical –
72 and potentially presently less relevant – community composition (Tullos et al. 2009; Barnes et al.
73 2014; Nordström et al. 2015).

74 One of the most successful examples of coastal restorations has been eelgrass (*Zostera*
75 *marina* L.) in the Delmarva coastal bays (Delaware, Maryland, Virginia) of the mid-western Atlantic,
76 USA (Orth and McGlathery 2012). Eelgrass is a foundational marine angiosperm distributed across
77 the northern hemisphere and provides a number of valuable ecosystem services, including nursery
78 habitat, shoreline protection, and carbon storage (Barbier et al. 2011). Eelgrass habitat supports a
79 variety of epifaunal invertebrates, including amphipods, isopods, decapods, and gastropods, which
80 have a high secondary production (Fredette et al. 1990) but are an important link between primary
81 producers and secondary consumers (Sobocinski and Latour 2015). The presence and diversity of

82 these epifauna has been implicated in the functioning of temperate seagrass ecosystems, with
83 greater abundance and species richness generally leading to increased grazing of fouling epiphytes
84 in numerous experimental mesocosms and field exclusions (Neckles et al. 1993; Duffy et al. 2003;
85 Duffy et al. 2005; Whalen et al. 2013; Reynolds et al. 2014), and more recently, in a synthesis across
86 15 field sites in the northern hemisphere (Duffy et al. 2015). Emerging evidence has also shown
87 that variation in the functional traits of these organisms better predict epifaunal biomass, algal
88 consumption, and transfer to higher trophic levels than species richness alone (Best et al. 2013;
89 Lefcheck and Duffy 2015), suggesting that the functioning of eelgrass systems can, in theory, be
90 more accurately inferred through the functional trait diversity of the grazer community.

91 Here, we present long-term data from two periods spanning 2001-2013 on the recovery of
92 associated epifaunal invertebrate communities alongside the successful restoration of eelgrass
93 habitat in the southern Delmarva coastal bays. Many of these bays had been unvegetated since the
94 early 1930s, after the pandemic decline of eelgrass due to hurricanes and disease (Orth et al. 2010).
95 In the late 1990s, seed-based restoration efforts began to reestablish eelgrass to the region, which
96 at present now supports over 1800 hectares of restored meadows, with more than half occurring in
97 a single area, South Bay (Orth et al. 2013). Despite the rapid and successful reestablishment of this
98 foundational habitat, it remains unclear whether the epifaunal community, which plays a critical
99 role in the maintenance and functioning of these systems, has experienced similar recovery.

100 To address this question, we compared temporal trends in abundance, species, and
101 functional diversity of the epifaunal community in South Bay to a nearby bed in Chincoteague Bay.
102 The Chincoteague bed persisted through the disturbances of the 1930s to the present day, and at
103 the time of the initial restoration, constituted the largest natural bed in the region. It thus served as
104 a useful baseline for assessing restoration success. Drift macroalgae was also collected at each site
105 to understand potential sources of animal recruitment to the newly restored bed. We coupled these
106 survey data with trait, environmental, and water quality data to explore the drivers of various

107 aspects of community structure in both beds through time. We hypothesized that the epifauna in
108 South Bay would initially reflect macroalgal assemblages, representing the assumed recruitment
109 vector, and over time become more like the reference bed as the community matured.

110 **Methods**

111 *Survey Sites*

112 Two coastal lagoons were chosen for comparison: a restored bed in South Bay (37.26 N,
113 75.84 W), and a reference bed in Chincoteague Bay (38.04 N, 75.31 W). Eelgrass had been absent in
114 South Bay since 1933 until seed based restoration efforts began in 1997, leading to recovery of
115 almost 1,500 hectares on what was until only recently unvegetated bottom (Fig. 1a). While eelgrass
116 has since spread to neighboring bays through both additional seed based restoration and passive
117 recruitment, South Bay remains the focus of that initial, successful restoration effort, and has the
118 largest, densest, and most contiguous restored bed by a large margin (Orth et al. 2013). Because of
119 the widespread establishment of eelgrass in South Bay, it was the ideal candidate for assessing the
120 status of animal communities associated with the successful restoration of their habitat. In contrast,
121 eelgrass in Chincoteague Bay recovered naturally after the pandemic decline of the 1930s, and by
122 the late 1990s was dense and extensive. By the early 2000s, when we initiated our sampling
123 program, Chincoteague represented the largest natural eelgrass bed in this region by a factor of 10
124 (Orth et al. 2013), making it the de facto candidate for comparison to the restored site. At the time,
125 Chincoteague Bay also appeared to be on a 15-year upswing in terms of total area¹, implying that
126 faunal communities present there would have had time to reach a climax state, and further
127 solidifying its potential as a representative baseline.

¹ <http://web.vims.edu/bio/sav/SegmentAreaChart.htm>

128 While both South and Chincoteague Bays share generally similar environmental conditions,
129 over the course of the survey, Chincoteague Bay has experienced declining water quality relative to
130 South Bay (Wazniak et al. 2007), and consequently lost a considerable amount of eelgrass by 2013
131 (Fig. 1b). However, this occurred after the initial monitoring period, and thus to maintain
132 consistency through time, we chose to continue sampling in Chincoteague Bay and will continue to
133 refer to it as the reference site. We note that, despite a decrease in aerial extent, remaining eelgrass
134 in Chincoteague Bay remained dense and contiguous (Fig. 1a). More importantly for this work, the
135 two bays are expected to harbor identical fauna based on their geographic proximity (<100 km)
136 and known ranges of target invertebrates (Pollock 1998).

137 *Survey Methods*

138 Faunal sampling occurred in two distinct periods: 2001-2003, when eelgrass was initially
139 colonizing South Bay and covered ~15 ha of bottom; and 2010 -2013, after the restored bed had
140 increased to nearly 1500 ha. Sampling was conducted quarterly from May to November each year.
141 In each bay, random samples were collected using suction sampling (Orth and van Montfrans
142 1987). At low tide, a weighted 0.33-m² metal cylinder was placed over a continuous stand of
143 eelgrass. The suction head was then inserted into the top of the sampling frame and the contents in
144 the cylinder were suctioned into a 0.8-mm mesh bag. Sampling continued for two minutes after
145 which collection bags were sealed, returned to the laboratory, and frozen. In the laboratory, mobile
146 epifauna were enumerated, identified to lowest possible taxon, and preserved in 90% ethyl alcohol.
147 While the number of samples taken on any given date was dictated by the area of eelgrass available
148 for sampling, replication was equivalent for a sampling period.

149 Additionally, we sampled epifauna of drift macroalgae to investigate potential vectors of
150 recruitment. Macroalgal samples were taken by gently enclosing drift algae in the general vicinity of
151 the sampling location in fine mesh bags, and storing and processing the samples identically to the
152 suction samples. The number of algal samples taken during each sampling date varied, with the

153 exact number dependent on the availability of drift macroalgae within a reasonable vicinity of the
154 suction samples, which declined in beds that were denser and more continuous.

155 *Functional Traits*

156 We identified nine functional traits based on their relevance to colonization potential,
157 competitive interactions, and effects on ecosystem functioning (Table S1). Traits included
158 indicators of defense and morphology (exoskeleton material and body plan), trophic ecology
159 (trophic group and specific diet), body size (maximum length), habitat use (mobility and position in
160 the water column), and life history (egg retention and development mode). These traits have been
161 shown to discriminate among epifaunal invertebrates, and to describe and predict benthic
162 community structure and function (Bremner et al. 2003; Bremner et al. 2006; Best et al. 2013;
163 Lefcheck and Duffy 2015). The trait data were collected directly from peer-reviewed literature and
164 verified using expert knowledge of the organisms. The raw trait data and a bibliography of
165 references are found in Supplement 1.

166 *Environmental Covariates*

167 Water quality data from 2001-2003 for South Bay was sampled monthly by the Virginia
168 Coastal Long-Term Ecological Reserve, and from 2010-2013 by the Virginia Estuarine and Coastal
169 Monitoring System program at the Virginia Institute of Marine Science. Physical variables were
170 measured using a YSI 6600 EDS sensor array (YSI Inc., Yellow Springs, Ohio). Additional water
171 samples were taken at eight separate sampling stations to quantify total suspended solids,
172 chlorophyll-*a*, and phosphate concentrations. Further details can be found in (Orth et al. 2012;
173 McGlathery and Christian 2014). Water quality data from 2001-2013 for Chincoteague Bay was
174 collected by the National Park Service at Assateague Island National Seashore (NPS) and the
175 Maryland Department of Natural Resources (DNR) Water Quality Monitoring Programs. Both
176 programs recorded on-site water quality parameters, and collected samples to send to laboratories
177 for nutrient and chlorophyll-*a* analyses. Further details can be found in (Wazniak et al. 2007).

178 Eelgrass bed extent and density in both bays were derived from aerial photography
179 acquired annually from 2001 through 2013, except for 2005, when weather conditions prohibited
180 photography. Black and white photography was acquired at a scale of 1:24,000 along two flight
181 lines covering all shorelines and adjacent shoal areas of the two bays. Aerial photography was
182 scanned from negatives, and *Z. marina* bed boundaries were then directly photo-interpreted on-
183 screen while maintaining a fixed scale using ESRI ArcMap GIS software (ESRI, Redlands CA). *Z.*
184 *marina* beds were categorized as very sparse (1-10% cover), sparse (11-40% cover), moderate (41-
185 70% cover), or dense (70-100% cover) based on a visual estimate of the percent cover. Ground
186 surveys were conducted in the bays each year to corroborate the occurrence of *Z. marina* identified
187 in the photography outside the boundaries of the seeded plots. Further details can be found in (Orth
188 et al. 2010).

189 *Statistical Analysis*

190 To adjust for varying sampling effort through time, we averaged all observations for a
191 particular quarterly sampling period so that each period constituted a single replicate (e.g.,
192 Dornelas et al. 2014). This choice reduces the power of our analysis, but provides three advantages:
193 it circumvents any potential for pseudoreplication, permits fitting of various correlation structures
194 to address temporal autocorrelation, and allows the number of samples taken to be included as a
195 covariate in subsequent analyses. It is well known that sampling effort increases estimates of both
196 abundance and richness (Azovsky 2011), so including sample size as a covariate in any modeling
197 exercise should yield less biased estimates of the predictors of interest.

198 For each replicate, we calculated a number of community metrics. First, we averaged the
199 number of individuals observed in each replicate to yield a measure of mean total abundance. Next,
200 we calculated species richness (S) as the mean number of species observed, and Simpson diversity
201 (D), which further incorporates information on species' (mean) relative abundances. For Simpson

202 diversity, we converted the resulting probability values to ‘effective numbers’ of species using the
 203 transformation from (Jost 2006):

$$D_{eff} = \frac{1}{(1 - D)} \quad (1)$$

204 which obey the doubling property, and scales the values comparably with species richness. We used
 205 these two indices to construct an index of relative evenness (J), which is calculated as:

$$J = \frac{\ln(D)}{\ln(S)} \quad (2)$$

206 Unlike other indices of evenness, this index of evenness has been shown to independent of both
 207 richness and Simpson diversity (Jost 2010), and is bound (0, 1).

208 For functional diversity (FD) we used the index of Rao’s quadratic entropy (Rao 1982). This
 209 index has been shown to be independent of species richness (Botta-Dukát 2005), and is calculated
 210 using the following equation:

$$Q = \sum_{i=1}^{s-1} \sum_{j=i+1}^s d_{ij} p_i p_j \quad (3)$$

211 where d_{ij} is the difference between species i and j based on their functional traits, p_i is the relative
 212 abundance of species i , and p_j is the relative abundance of species j . The differences d_{ij} are derived
 213 from any combination of functional traits using Gower’s dissimilarity measure (Gower 1971), which
 214 allows both continuous and categorical trait data to be collapsed into a single continuous distance
 215 measure. Because Rao’s Q can be maximized when fewer than all functional types are present when
 216 Gower’s distances are not ultrametric (Pavoine et al. 2005), we generated ultrametric distances
 217 using the procedure described in (Mouchet et al. 2008; Mérigot et al. 2010). In the event where
 218 species are either the same or different, d_{ij} collapses to 0 or 1 and $Q = D$, or Simpson diversity.
 219 Thus, Rao’s Q can also be transformed using Equation (1) to yield units that are on the same scale as
 220 Simpson diversity. We calculated two separate indices of FD: one weighted by relative abundances,

221 which we interpret as the functional analogue to Simpson diversity, and one based on presence-
222 absence, or the functional analogue to species richness.

223 Finally, to further account for variable effort, we generated rarefied estimates of species
224 richness and Simpson Diversity using fixed-coverage subsampling (Chao and Jost 2012). This
225 method generates a value of sample coverage (i.e., how complete the sample is) based on the
226 number of observed singletons (species for which only 1 individual was observed), and estimates of
227 diversity are then rarefied down to a fixed level of coverage, as opposed to a number of individuals
228 or samples. This method results in less data loss than traditional rarefaction, and more efficiently
229 ranks communities based on their true diversities (Chao and Jost 2012). Unfortunately, this method
230 has not yet been extended to indices of functional diversity. Rarefied estimates were calculated
231 using the *iNEXT* package in R (Hsieh et al. 2014).

232 Differences among the community metrics for each bay and sampling period were assessed
233 using general linear mixed effects models with an autoregressive 1 (AR1) correlation structure
234 corresponding to each sampling period. We additionally modeled the random variance associated
235 with being in a particular sampling period. As mentioned previously, the number of samples
236 collected on each date was included as a covariate to account for influence of variable effort on the
237 community response. Both the response and sample size were \log_{10} -transformed, as the species-
238 sampling effort relationship is known to follow a power law (Azovsky 2011). Assumptions of
239 normality of errors and homogeneity of variance were assessed visually. Pseudo- R^2 values were
240 calculated using the variance of both the fixed and random effects (conditional R^2 , *sensu* Nakagawa
241 & Schielzeth 2012). Models were constructing using the *nlme* package in R (Pinheiro et al. 2015),
242 and evaluated using the *piecewiseSEM* package (Lefcheck 2016).

243 The role of environmental covariates in driving the observed patterns was then estimated
244 using random forests (Breiman 2001). We built an ensemble of 50 trees, after which we observed
245 no appreciable decrease in mean squared error, with 'out-of-bag' (OOB) permutation to estimate

246 importance partitioned based on Pearson correlation threshold ≥ 0.5 . Each community metric
247 (abundance, richness, etc.) was regressed against the following variables that had near complete
248 coverage across all sampling locations and periods: year, bed location, area, and density,
249 temperature, salinity, dissolved oxygen, pH, and water column chl-*a* and phosphates (as a proxy for
250 suspended organic material). We then evaluated the importance of each predictor by quantifying
251 the mean percent decrease in accuracy, derived from the increase in mean error across all trees in
252 the ensemble when a given variable is randomly permuted and then challenged with the OOB data.
253 Model parameters were optimized using the *caret* package (Kuhn 2015), and RFs were constructed
254 using the *randomForest* package in R (Liaw and Wiener 2002). For the top predictors, we plotted
255 bivariate correlations and tested whether the observed correlation was significantly different from
256 zero by comparing values to a *t*-distribution with $n - 2$ degrees of freedom.

257 We used non-metric multidimensional scaling (NMDS) to visualize differences in
258 multivariate community structure across bays, algal vs. eelgrass samples, and through time.
259 Because algal samples were collected differently than eelgrass samples, we used a sample-by-
260 species incidence matrix to downplay the influence of the amount of habitat or area sampled. We
261 also ran a separate NMDS for each habitat type using relative abundances, applying a Wisconsin
262 square-root transformation to reduce the impact of highly abundant species. To statistically test for
263 differences among species composition through time, we conducted PERMANOVA, which
264 partitioned variance in the community dissimilarity matrix as a function of sampling period, and
265 used random permutations of the data to assess significance (McArdle and Anderson 2001).
266 Separate PERMANOVAs were conducted for each bay. We performed all multivariate analyses using
267 the *vegan* package (Oksanen et al. 2013).

268 All statistical analyses were conducted in R version 3.1.2 (R Development Core Team 2015),
269 and we held a study-wide $\alpha = 0.05$ for assessing statistical significance. All data and R scripts used
270 to conduct the analyses are provided in Supplement 1.

271 **Results**

272 In contrast to our expectations that the restored bed would appear more like the reference
273 bed through time, the two were not significantly different in terms of most community metrics after
274 only one year (Fig. 2, $P > 0.05$ based on output from general linear mixed effects models). The two
275 exceptions were average abundance, which was significantly lower in South Bay during the period
276 from 2001-2003 (Fig. 2a, $P = 0.017$), and functional diversity based on presence-absence, which
277 was, on average, significantly higher (Fig. 2f, $P = 0.034$). The number of samples taken did not
278 significantly influence any response during this time ($P > 0.05$ in all cases). Conditional R^2 values
279 ranged from 0.21–0.62, implying relatively high accuracy of these predictions, particularly for
280 ecological data.

281 By the early 2010s, most community metrics were actually significantly higher in the
282 restored bed, particularly functional diversity (Fig. 2b, $P = 0.031$; Fig. 2c, $P = 0.032$; Fig. 2e-f, $P <$
283 0.001). Average abundance was still significantly lower in South Bay during the later period ($P =$
284 0.045), although we note the expected difference between the two was approximately 50% less
285 than in the earlier period based on coefficients from the mixed models ($\beta = 0.54$ *cf.* $\beta = 1.10$).
286 Evenness was the only index that was not significantly different between the two bays (Fig. 2d, $P =$
287 0.132). Instead, this was the only variable that was more strongly predicted by sample size ($P =$
288 0.007). Conditional R^2 values ranged from 0.23–0.71, reinforcing once again that these models
289 explained a substantial proportion of variance in the responses.

290 Random forests consistently identified bed location (restored vs. unrestored), total area and
291 mean eelgrass density to be the top three most important predictors across all community metrics
292 (Fig. S1). Bivariate plots revealed strong and highly significant positive correlations between area
293 and density for almost all metrics of diversity in South Bay (Fig. 3), particularly estimated richness
294 and Simpson diversity (Fig. 3b, c) and functional diversity weighted by relative abundance (Fig. 3f).

295 Chincoteague Bay showed generally weaker or sometimes opposite trends in these bivariate
296 correlations. However, it is important to recall that random forests account for collinearity and
297 interactions among variables, and thus the ranking reflects the importance independent of other
298 confounding factors, while the bivariate plots in Figure 3 do not.

299 Exploration of individual trait values revealed that assemblages in the South Bay bed
300 generally exhibited greater variation in traits related to habitat use, life history, and morphology,
301 particularly during the later stages of restoration (Fig. S2). Specifically, South Bay had
302 proportionally more benthic-dwelling crawlers, with calcium carbonate exoskeletons, and external
303 release of eggs with subsequent planktonic dispersal (Figs. S3-7). Thus, it appears that gastropods
304 are responsible for a large proportion of the difference in functional diversity between the restored
305 and reference beds. Even within this taxonomic group, however, richness, Simpson, and functional
306 diversity weighted by relative abundance were all higher in South Bay during the late period (Fig.
307 S8).

308 Analysis of multivariate community data using non-metric multidimensional scaling and
309 PERMANOVA revealed that the composition of the restored bed changed significantly from the
310 early period of restoration to the late period (Fig. 4), particularly when factoring in relative
311 abundances and re-analyzing the community data separately by habitat type ($P < 0.001$ based on
312 9,999 random permutations of the data, Fig. S9b). Shifts in community composition were
313 principally driven by declines in the relative abundances of the amphipod *Batea catharinensis*, the
314 snail *Astyris lunata*, and the shrimp *Hippolyte pleuracanthus*, and by the appearance of the snail
315 *Costoanachis avara*. In contrast, there were no significant changes in community structure across
316 years in Chincoteague Bay based on relative abundances ($P > 0.05$, Fig. 4, Fig. S9b). Further, the
317 changes in community structure through time did not appear to be a consequence of recruitment
318 via drift macroalgae, with the macroalgal communities in each bay being significantly distinct from
319 the corresponding grass beds ($P < 0.001$, Fig. 4, Fig. S9a).

320 While the full NMDS had a borderline acceptable value of stress, implying somewhat poor
321 reproducibility of the multivariate data in two dimensions (0.26, Fig. 4), identical patterns emerged
322 after repeated runs using different start values, and separate analyses by habitat type using relative
323 abundances returned more acceptable values of stress (0.17 for eelgrass, Fig. S9b). Thus, the trends
324 in Figure 4 appear to be robust to further explorations of these data, despite the higher stress value,
325 and reinforce conclusions from independent analyses using PERMANOVA.

326 Of the 42 species captured over the entire survey, five were found exclusively in South Bay,
327 including three gastropod species in the genus *Costoanachis*, as well as the grazing snail
328 *Marshallora nigrocincta*, and the detritivorous amphipod *Photis macrocoxa* (although this species
329 was found only on drift macroalgae). All five of these species occupied unique parts of functional
330 trait space, based on principal coordinates analysis of their trait values (Fig. S10). Only two species
331 – the grazing isopod *Paracerceis caudata* and the detritivorous amphipod *Lysianopsis alba* – were
332 found exclusively in Chincoteague Bay, and they were nearly functionally equivalent with other
333 species (Fig. S10).

334 Discussion

335 In this study, we found that the diversity of epifaunal invertebrates and their functional
336 traits in a newly restored eelgrass bed matched, and then exceeded, values exhibited by a nearby
337 reference bed in less than a decade (Fig. 1). Further, the rapid recovery of the epifaunal community
338 was shown to be a direct consequence of restoration actions that encouraged the growth and
339 expansion of the restored bed, represented by bed area and density (Fig. 3). These findings may be
340 of particular consequence as eelgrass cover has generally declined in the region over the past two
341 decades (Orth et al. 2013), and is likely to continue this downward trajectory without further
342 restorative measures. The area of the reference bed, for example, declined 49% over the 12 years of
343 the survey (Fig. 1a), as a consequence of decreasing water quality and thermal stress known to

344 drive eelgrass decline in the nearby Chesapeake Bay (Wazniak et al. 2007; Moore et al. 2012). In
345 contrast, the area of the restored bed increased by 910% over the same time period (Fig. 1b), owing
346 to better water quality, persistent restoration, and natural recruitment from the restored beds.
347 Thus, assuming these trends continue, restored beds in an environment not challenged by poor
348 water quality may play an increasingly vital role in providing habitat for a variety of taxa and
349 functional forms present in the region. Indeed, restored beds now make up roughly one-third of
350 total seagrass cover in the Delmarva coastal bays (Orth et al. 2013), They may one day even set
351 targets for both restoration efforts in South Bay and elsewhere, and, in an ironic reversal, natural
352 sites experiencing eelgrass loss due to declining water quality, such as Chincoteague Bay.

353 If many aquatic restorations fail to achieve pre-disturbance levels of diversity (Benayas et
354 al. 2009), then why has this particular effort been so successful? Low human impacts in this region
355 are undoubtedly a major factor. Long-term monitoring by the Virginia Coastal LTER has shown that
356 nutrient loading and water column chlorophyll-*a* have been low and relatively stable across all of
357 Virginia's coastal bays over the past two decades (Orth and McGlathery 2012) but, as noted earlier,
358 not in Maryland's Chincoteague Bay (Wazniak et al. 2007). South Bay also experiences regular
359 flushing with cooler ocean water, alleviating temperature stress that is a major driver of eelgrass
360 die-backs in nearby regions, such as the Chesapeake Bay (Moore et al. 2012). Moreover, as the
361 restored bed has increased in size and density, it has more effectively captured particulates, leading
362 to increased water clarity and greater light availability for photosynthesis (Moore et al. 2012; Orth
363 et al. 2012). This self-facilitation has been identified as a key predictor of the persistence of
364 restored seagrass ecosystems (van Katwijk et al. 2009).

365 Altogether, the factors that promote the growth and expansion of the restored bed should,
366 in theory, facilitate the recruitment and survival of epifaunal invertebrates, principally by
367 increasing the availability of habitat and substrate for algal resources. While the positive
368 relationship between habitat and area sampled and species richness has been established generally,

369 there are few examples from seagrass systems (Boström, Jackson & Simenstad 2006). Our study is
370 also unique in the sense that increasing area does not simply represent a shift in geographic focus,
371 but a product of ongoing efforts to actively increase the total habitat in the same location,
372 supplemented by the natural spread of eelgrass from the initial effort to restore this habitat. Indeed,
373 it is the recurring annual restoration efforts combined with natural recruitment from these
374 restored beds over the past two decades that has led to the impressive recovery of eelgrass in the
375 region, and undoubtedly this reliable influx of habitat-forming seeds has played a key role in
376 promoting the diverse epifaunal assemblage observed in our study, and may distinguish this
377 success from other restoration attempts.

378 There is also potential for an interesting and hitherto unrecognized positive feedback
379 involving epifauna and eelgrass contributing to restoration success. Numerous mesocosm and
380 caging studies have demonstrated that the presence and diversity of these grazers has been shown
381 to promote the growth and productivity of eelgrass through the removal of fouling epiphytes
382 (Neckles et al. 1993; Duffy et al. 2003; Duffy et al. 2005; Douglass et al. 2007; Whalen et al. 2013;
383 Reynolds et al. 2014; Duffy et al. 2015). This action releases eelgrass blades from competition for
384 light and nutrients, which in turn increases productivity and ultimately the amount of habitat. We
385 show here that habitat directly enhances diversity (Fig. 4), leading to more habitat, more animals,
386 and so on. While this link is tenuous in the absence of robust data on epiphyte fouling, it is a
387 foundational concept in temperate seagrass ecology (van Montfrans et al. 1984; Duffy et al. 2014),
388 and in light of considerable empirical verification in other systems, it is likely to play a role in the
389 persistence and rapid expansion of the bed in South Bay. The degree to which animals and their
390 diversity promote eelgrass versus the annual sowing of seeds and natural expansion is probably
391 small, but parsing these effects is certainly deserving of further attention.

392 The reproductive biology and dispersal abilities of the focal organisms may have also played
393 a pivotal role in the rapid recovery of the epifaunal community in the restored bed. Recent reviews

394 have suggested that ‘successful restorations’ – those that have achieved similar levels of
395 biodiversity as before a disturbance – have concerned communities of fast-reproducing organisms
396 with high dispersal ability (Jones and Schmitz 2009; Duarte et al. 2015). While there did not appear
397 to be a change in the proportion of individuals belonging to high vs. low dispersal species
398 throughout the course of restoration – those that brooded or released their eggs, and those with
399 planktonic vs. non-planktonic larval forms (Figs. S6-7) – most of the organisms in this system have
400 generation times on the scale of weeks to months. The amphipod *Gammarus mucronatus*, for
401 instance, can reach reproductive maturity in as few as three weeks during summer months
402 (Fredette and Diaz 1986). The quick generation and turnover of populations certainly contributed
403 to the ability of these small invertebrates to reach and exploit this new habitat.

404 A complementary hypothesis is that, as the bed expanded, it also recruited mesopredators
405 of epifauna, including various fishes and crabs, which also utilize the eelgrass as habitat. Predator
406 trawls conducted in South Bay the early 2010s revealed a diverse and abundant predator
407 community (Schmitt et al. 2016). A recent meta-analysis produced strong evidence supporting the
408 long-standing hypothesis that predation enhances prey diversity by relieving competition among
409 prey species (Katano et al. 2015), a trend which has been seen in mesocosm experiments using
410 several of the species observed in our surveys (Duffy et al. 2005; Douglass et al. 2008). Consistent
411 with an active and increasingly abundant predator community, epifaunal abundance actually had
412 an inverse relationship with bed area and density in South Bay (Fig. 3a). An alternative explanation
413 is that epifauna are resource-limited, as suggested by their remarkably invariant mean abundances
414 observed in the later stages of restored bed (Fig. 1a). Thus, increasing the density of habitat but not
415 resources could have diluted the average abundance per unit sampling area.

416 One of the more striking differences between the restored and reference beds was the
417 higher functional diversity in South Bay compared to Chincoteague Bay (Fig. 1e-f). Habitat
418 complexity and resource availability – proxied by mean density and total phosphates in our random

419 forest analysis – may have played a role here as well (Fig. 3e-f, Fig. S1). Increasing both should
420 theoretically open niche space and facilitate coexistence, leading to a wider variety of observed
421 functional morphologies, behaviors, and life histories. Classical successional theory would predict
422 that this would be especially true during the later stages of restoration, as biotic as opposed to
423 abiotic filters play an increasingly larger role and functionally similar species are weeded out as
424 consequence of competitive interactions (Connell and Slatyer 1977). Given these predictions, it is
425 surprising that we observed significantly higher functional diversity in the restored bed compared
426 to the reference bed even in the early stages of restoration. Once again, the relatively fast
427 recruitment and generation times of the organisms may provide explanation, allowing such
428 interactions to play out on much shorter time scales than might be expected in other systems in
429 which this phenomenon has been investigated, such as terrestrial plants (Purschke et al. 2013).

430 A recent publication also suggested that it is not competitive interactions, but continued
431 colonization, that drives the functional trait structure of successional communities (Li et al. 2015).
432 We observed significant differences in community composition through time, particularly in the
433 restored bed (Fig. 4), which was a consequence of the arrival of new species or shifts in dominance.
434 Along similar lines, the demography of these epifaunal invertebrates is notoriously unpredictable.
435 In nearby systems in the Chesapeake Bay, which have been well studied for decades, species appear
436 and then disappear regularly, generally in response to loss of habitat (Douglass et al. 2010). Similar
437 stochastic processes may also be at play here, with high trait diversity in the early years simply an
438 outcome of chance processes that favored recruitment of functionally varied individuals to the
439 sudden appearance of uncolonized habitat. Interestingly, our analysis showed little role of rafting
440 macroalgae in providing a recruitment vector for new species (Fig. 4). Where these animals are
441 coming from, and how they are arriving at the bed, remains a frontier in seagrass ecology.

442 Finally, we must acknowledge the possibility that we are still observing some transitional
443 state, and that the restored bed is still progressing towards the stable state exhibited by the

444 reference bed (Fig. 4). Several lines of evidence suggest this is not the case. First, inter- and intra-
445 annual variability was similar between both bays (Fig. 1), suggesting that the reference bed had not
446 achieved a more stable, and potentially more mature, state than the restored bed. In fact, the errors
447 around most means of community properties in the restored bed are actually lower than in the
448 reference bed (Fig. 1). Second, we observed significant compositional differences between the beds,
449 suggesting potentially different avenues for colonization (Fig. 4). Finally, given the contrasting
450 trajectories of the two beds (Fig. 1), it may be unreasonable to suspect these two communities to
451 ever converge.

452 Aggregating at broad temporal scales emphasizes overall trajectories of these beds, but
453 ignores some of the finer scale variation. One particularly notable instance occurred in June 2012,
454 with the recruitment of juvenile pinfish (*Lagodon rhomboides*) to these coastal bays. During early
455 life history stages, pinfish are known to be voracious predators of epifaunal invertebrates
456 (Luczkovich and Stellwag 1993), and were indisputably responsible for the steep declines in
457 epifaunal abundance and diversity during this month (Fig. S11). Generally, pinfish do not range this
458 far north, but with increasing temperatures, we may be witness to a northward range expansion.
459 Such a shift may have drastic consequence for the eelgrass: first, by removing the critical top-down
460 control provided by epifaunal grazers, and second, by directly consuming eelgrass, particularly
461 later during their ontogeny (Luczkovich and Stellwag 1993). Thus, while local conditions over the
462 last decade have favored the growth and expansion of eelgrass in Virginia's coastal bays, climate
463 change may introduce a new variable in the form of pinfish with uncertain consequences for the
464 maintenance of eelgrass diversity and function in South Bay.

465 Within the larger context of restoration ecology, our study stands out in that it documents
466 the transition from a near complete lack of vegetation to dense, contiguous beds (Fig. 1, Orth &
467 McGlathery 2012). This state-shift stands in contrast to many other restoration projects, which
468 have focused on recovery of degraded, but not totally absent, systems. The drastic transition from

469 an unvegetated to a vegetated state may explain some of our results by widening the scope for
470 detectable effects. We note, however, that the greatest differences occurred during the later stages
471 of restoration, when the restored and reference beds were comparable in terms of their total
472 coverage (Fig. 1). Further, even in degraded eelgrass beds, remediation of environmental stressors
473 has been show to enhance the functional trait diversity of epifaunal invertebrates (Dolbeth et al.
474 2013). As with our results (Fig. 1e), functional recovery was partly a consequence of the
475 redistribution of biomass among different functional types (Dolbeth et al. 2013). Similarly rapid
476 recovery of functional diversity has been observed in other invertebrate communities, such as
477 beetles in restored wetlands (Watts and Mason 2015). These studies, along with ours, suggest that
478 functional traits can be a powerful tool for assessing the response and subsequent recovery of
479 communities to disturbance (Mouillot, Graham, et al. 2013).

480 It is worth noting the limitations of this study. First, we are comparing two bays, even
481 though these bays combined account for 88% of the submersed aquatic vegetation in the Delmarva
482 coastal bays. While our results may not be representative of eelgrass systems in general, we do
483 demonstrate that restored ecosystems on a comparatively large scale at least have the potential to
484 greatly exceed the diversity of reference or pre-disturbance systems, which is a rare outcome in
485 restoration ecology (Benayas et al. 2009). Second, we had variable sampling effort through time,
486 largely as a consequence of available habitat to sample, which could have biased our summary
487 statistics. However, incorporation of sample size as a covariate in our analyses revealed that it has
488 no significant effect in the vast majority of cases (with the sole exception of evenness in the latter
489 period, Fig. 1d). Finally, we did not have robust and consistent estimates of the local density of the
490 habitat to use in our analysis. Future monitoring efforts should focus on a method that is not only
491 standard to the area of bottom sampled, but also yields some value of habitat availability (biomass,
492 etc.).

493 In this study, we show that epifaunal community diversity in a restored eelgrass bed was
494 significantly higher than an unrestored bed in the region, particularly when considering the
495 breadth of organismal functional traits. Given the wealth of evidence linking both epifaunal species
496 and trait diversity to enhanced ecosystem functioning (Best et al. 2013; Duffy et al. 2015; Lefcheck
497 and Duffy 2015), it is reasonable to infer that the restored bed may also experience higher levels
498 and greater stability in ecosystem functioning than unrestored beds. Indeed, sediment organic
499 content and ammonium exchange have been shown to be higher during the later stages of
500 restoration (McGlathery et al. 2012). While these functions were attributed to the recovery of the
501 eelgrass itself, previous mesocosm experiments have shown that epifaunal richness also impacts
502 these properties as well, irrespective of eelgrass biomass (Duffy et al. 2003; Spivak et al. 2007).
503 Future work, however, will have to directly quantify processes related to these grazers, such as
504 secondary production or biogeochemical processes, to demonstrate their independent
505 contributions to the eelgrass ecosystem function. In the interim, the restored systems in Virginia's
506 coastal bays may serve an important role in conserving regional biological diversity in the face of
507 large-scale declines in existing beds.

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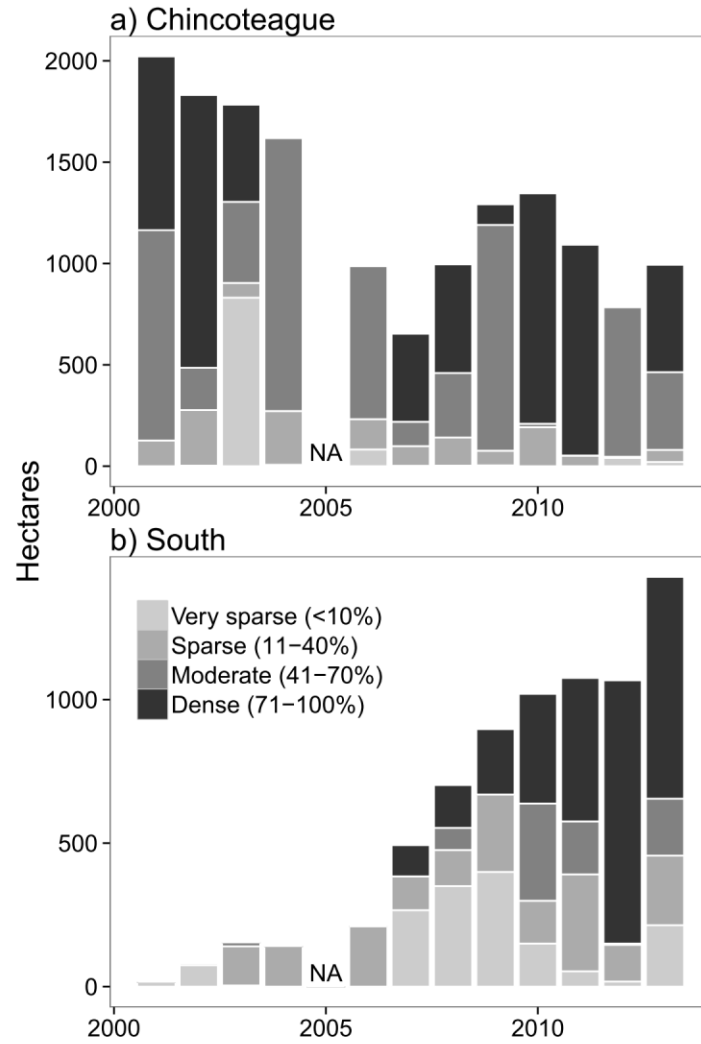
777 **Figure Captions**

778 **Figure 1:** Total area (in hectares) of eelgrass beds in **(a)** Chincoteague Bay and **(b)** South Bay
779 through time. Bars are divided into estimated density bins (% cover) based on comparison of aerial
780 footage to a crown density scale. Note: aerial photography could not be conducted in 2005 due to
781 poor weather conditions.

782 **Figure 2:** Time series plotting the annual mean \pm 1 SE for various faunal community properties.
783 Light grey circles represent the mature bed in Chincoteague Bay. Black triangles represent the
784 restored bed in South Bay. FD = functional diversity, calculated as Rao's quadratic entropy from all
785 nine functional traits.

786 **Figure 3:** Plots of total bed area (in hectares, left column) and mean density (as the average density
787 bin based on comparison of aerial footage against a crown density scale, ranging from 0 for no
788 cover to 1 for full cover) for South Bay. Points represent each year and month of the survey. The
789 black line represents a simple linear regression between the two variables. The Pearson correlation
790 (r) from this regression is given in the bottom of each panel along with the following indicator of
791 statistical significance: * $P = 0.05$, ** $P = 0.01$, *** $P = 0.001$.

792 **Figure 4:** Non-metric multidimensional scaling conducted on relative abundance data for both
793 eelgrass (green) and drift macroalgal (brown) communities. Small open points represent each year
794 and month of the survey. Large points represent the centroid for each year, graded from early years
795 (dark grey) to later years (light grey). Arrows represent the trajectories from one year to the next.
796 Stress – a measure of concordance between the multivariate data and this two-dimensional
797 representation – is given in the lower right.

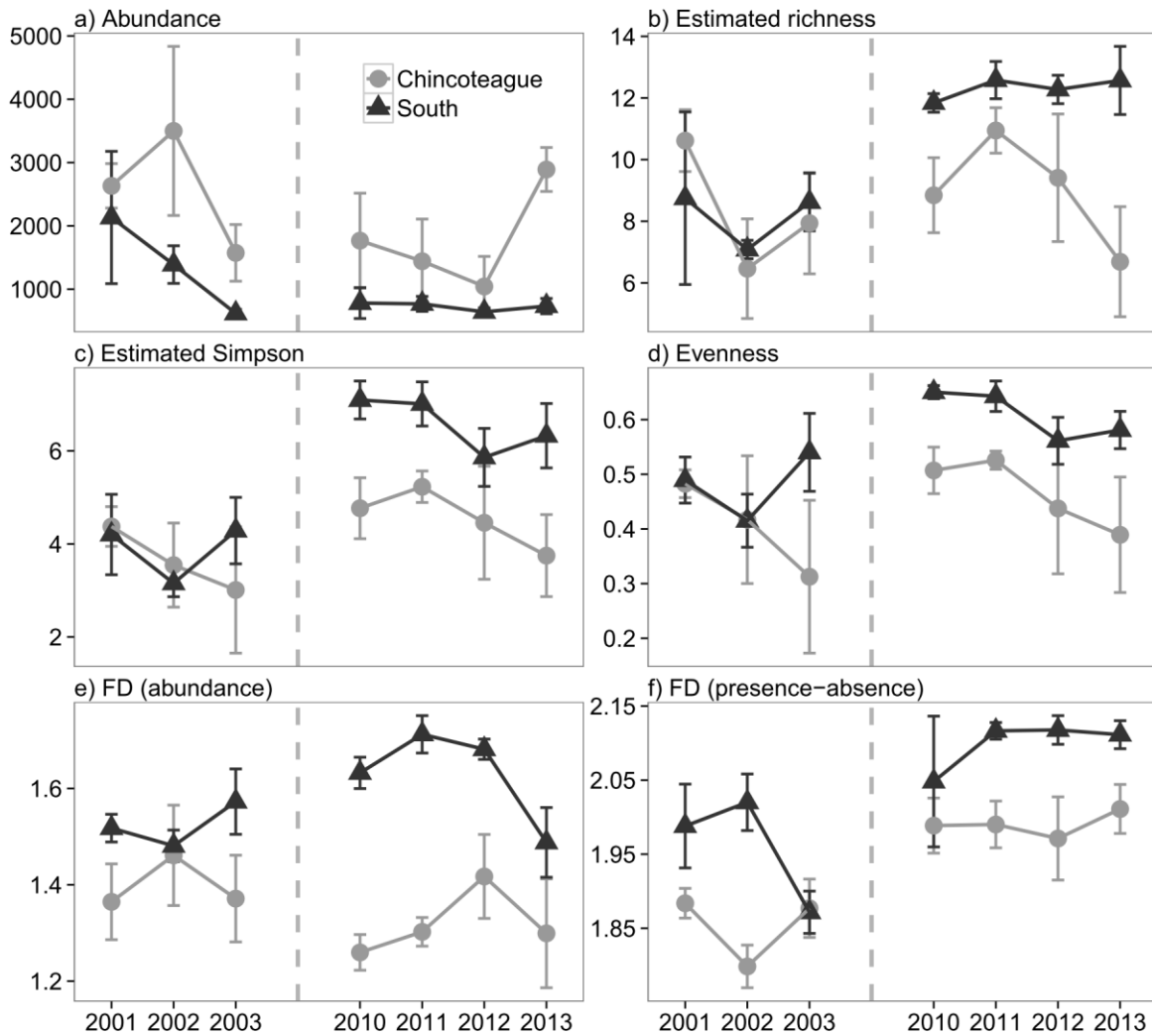


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Figure 1

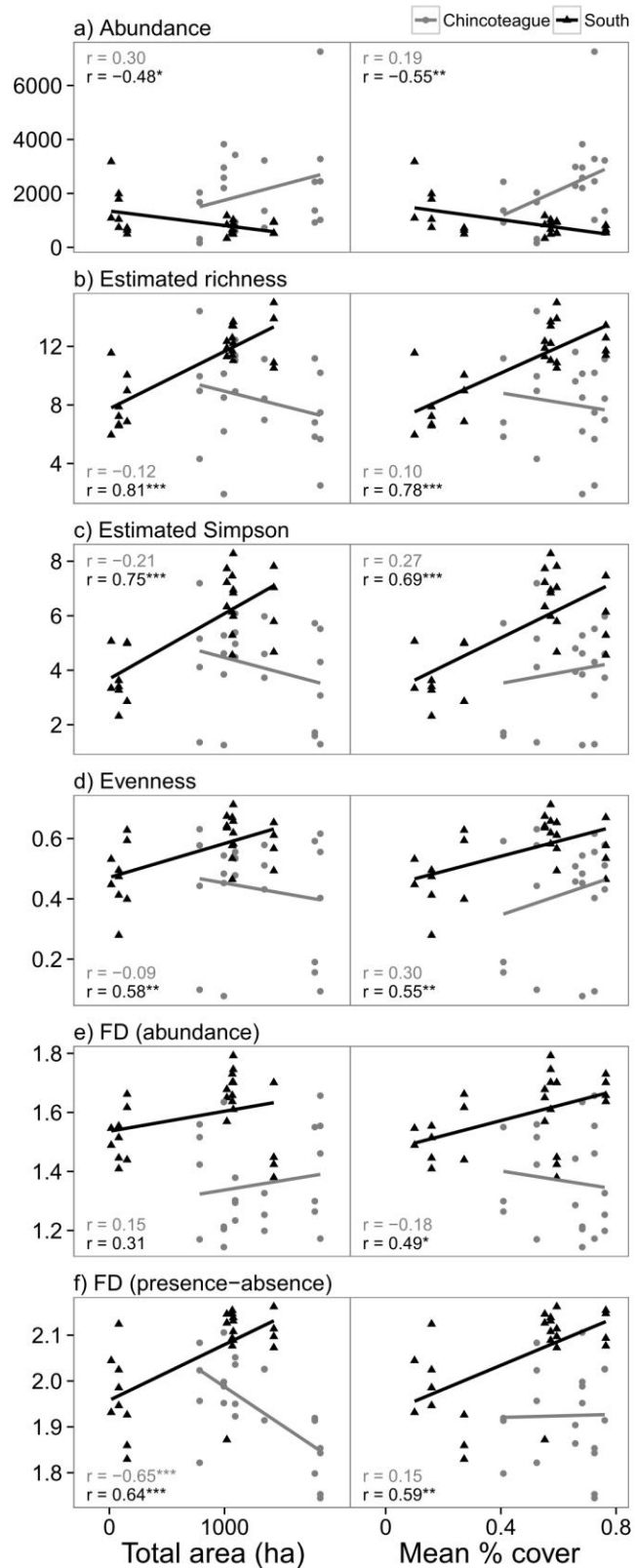
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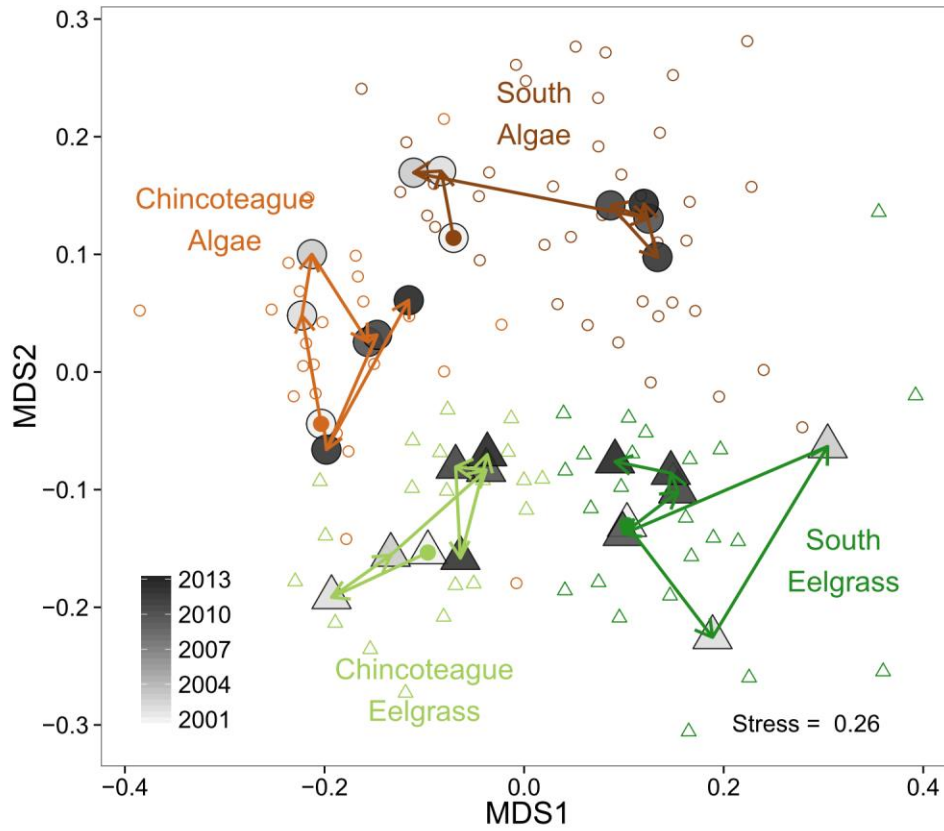
Figure 2



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Figure 3



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Figure 4