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Actively restored ecosystems as a refuge for biological diversity: A case study from eelgrass (*Zostera marina* L.)

Jonathan S. Lefcheck[1†], Scott R. Marion[2], Robert J. Orth[1]

[1]Virginia Institute of Marine Science, The College of William & Mary, Gloucester Point, VA

[2]Oregon Department of Fish & Wildlife, Marine Resources Program, Newport, OR

[†]Corresponding author. Email: jslefche@vims.edu. Phone: +1 804 684 7150. Mailing address: PO Box 1346, Rt 1208 Greate Rd, Gloucester Point, VA 23062, USA

Running head: Eelgrass restoration and biodiversity

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Abstract:

As nearshore ecosystems are increasingly degraded by human activities, active restoration is a critical element in ensuring the continued provision of goods and services by coastal habitats. Since 1997, over 1800 ha of the foundational species eelgrass (*Zostera marina* L.) has been reestablished in the coastal bays of the mid-western Atlantic. Here, we follow the functional recovery of the epifaunal invertebrate community associated with a restored eelgrass habitat from 2001-2013. Epifauna provide critical services by removing fouling epiphytes from eelgrass blades and transferring energy to higher trophic levels. After less than a decade, the invertebrate community in the restored bed was richer, more even, and exhibited greater variation in functional traits than a nearby natural bed. Analysis of environmental and physical data using random forests revealed the primary drivers of these differences was the increasing area and density of the restored bed directly attributable to both ongoing restoration efforts, and expansion from the initial planting efforts. Given that restored eelgrass now make up 32% of total seagrass cover in the mid-Atlantic, this restoration may foster regional biodiversity by providing new and pristine habitat, particularly given the general decline of natural eelgrass in this region and globally.

Keywords: biodiversity, seagrass, restoration, functional traits, grazers

Introduction

Coastal habitats are becoming increasingly impacted through human activities (Halpern et al. 2008), leading to loss of important and valuable services such as food production, pollution control, shoreline buffering, and carbon storage (Barbier et al. 2011). At the same time, anthropogenic impacts are driving the rapid and irreversible loss of marine biological diversity (McCauley et al. 2015). As high biodiversity has been generally shown to promote ecosystem functioning (Cardinale et al. 2012) – including in marine systems (Gamfeldt et al. 2015) – species extinctions may further erode the ability of nearshore habitats to provide goods and services. Thus, there is strong incentive within the conservation movement to protect and manage for high biodiversity in marine realms (Palumbi et al. 2008), in addition to protecting habitat itself.

More recently, researchers have broadened their definition of biodiversity to include species' functional identities, represented by their *functional traits*: measurable characteristics of individual organisms relating to their morphology, physiology, ecology, behavior, and life history (Díaz et al. 2013). Functional diversity, then, captures the breadth of variation in functional traits within an assemblage. Traits can quantify the degree of redundancy with an assemblage (Rosenfeld 2002), and thus be used to refine conservation priorities by identifying areas of particular vulnerability (Micheli and Halpern 2005), or that harbor unique or functionally varied assemblages (Devictor et al. 2010, Stuart-Smith et al. 2013). By specifying how organisms perform and interact with one another, traits can be also be used to mechanistically link patterns and processes (Díaz and Cabido 2001), generating more accurate and generalizable predictions for the ecosystem consequences of species losses (Mouillot et al. 2013a).

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

One of the more successful examples of coastal restorations has been eelgrass (*Zostera marina* L.) in the Delmarva coastal bays of the mid-western Atlantic (Orth and McGlathery 2012). Eelgrass is a foundational marine angiosperm distributed across the northern hemisphere and provides a number of valuable ecosystem services, including nursery habitat, shoreline protection, and carbon storage (Barbier et al. 2011). Eelgrass habitat supports a variety of epifaunal invertebrates, including amphipods, isopods, decapods, and gastropods, which are an important link between primary producers and secondary consumers (Sobocinski and Latour 2015). The diversity of these epifauna has been implicated in the functioning of temperate seagrass ecosystems, with greater species richness generally leading to increased grazing of fouling epiphytes in experimental mesocosms and field exclusions, and more recently, across 15 field sites in the northern hemisphere (Duffy et al. 2015). Emerging evidence has also shown that variation in the functional traits of these organisms better predicted epifaunal biomass, algal consumption, and transfer to higher trophic levels than species richness alone (Best et al. 2013, Lefcheck and Duffy 2015), suggesting that the functioning of eelgrass systems can, in principal, be accurately inferred through functional trait diversity.

Here, we present long-term data from 2001-2003 and again from 2010-2013 on the recovery of associated epifaunal invertebrate communities alongside the successful restoration of eelgrass habitat in the Delmarva coastal bays. Many of these bays had been unvegetated since the early 1930s, after the pandemic decline of eelgrass due to hurricanes and disease (Orth et al. 2010). In the late 1990s, seed-based restoration efforts began to reestablish eelgrass to the region, which at present now supports over 1800 hectares, with more than half occurring in a single area, South Bay (Orth et al. 2013). Despite the rapid reestablishment of this foundational habitat, it remains unclear whether the epifaunal community, which plays a critical role in the maintenance and functioning of these systems, has experienced similar recovery. To address this question, we compared temporal trends in the epifaunal community in South Bay to a nearby persistent bed in Chincoteague Bay, which served as a baseline or reference bed for assessing restoration success. Drift macroalgae was also collected at each site to understand potential sources of recruitment to the restored bed. We coupled these survey data with information on nine functional traits representing differences in morphology, diet, habitat use, and life history (Table A1). We hypothesized that the epifauna in South Bay would initially reflect macroalgal assemblages, representing the primary recruitment vector, and over time to become more like the reference bed as the communities matured.

Methods

Survey Sites

Two coastal lagoons were chosen for the final analysis: South Bay (37.26 N, -75.84 W) and Chincoteague Bay (38.04 N, -75.31 W). Eelgrass had been absent in South Bay since 1933, until seed-based restoration efforts began in 1997. As of 2013, South Bay contained nearly 1500 ha of dense, continuous eelgrass. In contrast, eelgrass recovered naturally after the pandemic decline in Chincoteague Bay, and by the late 1990s constituted a significant area of our study region. By the early 2000s, Chincoteague represented the largest natural eelgrass bed remaining in this region by at least a factor of 10 (Orth et al. 2013), making it the default candidate for comparison. The two are generally expected to share fauna based on their proximity and known ranges of target invertebrates (Pollock 1998).

Survey Methods

Faunal sampling occurred in two distinct periods: (1) 2001-2003 when eelgrass was initially colonizing South Bay and beds were sparse and patchy, covering only 15 ha of bottom; and (2) 2010 -2013 after the restored bed had increased to nearly 1500 ha. Sampling was conducted quarterly from May to November each year. In each bay, 2-22 random samples (contingent on the area sampled) were collected using suction sampling (Orth and van Montfrans 1987). At low tide, a weighted 0.33-m^2 metal cylinder was placed over a continuous stand of eelgrass. The suction head was then inserted into the top of the sampling frame and the contents in the cylinder were suctioned into a 0.8-mm mesh bag. Sampling continued for two minutes after which collection bags were sealed, returned to the laboratory, and frozen. In the laboratory, mobile epifauna were enumerated, identified to lowest possible taxon, and preserved in 90% ethyl alcohol. Additionally, we sampled epifauna of drift macroalgae to investigate potential vectors of recruitment. Macroalgal samples were taken by gently enclosing drift algae in the general vicinity of the sampling location in fine mesh bags, and storing and processing the samples identically to the suction samples. The number of algal samples taken during each sampling date ranged from 5-38, with the exactly number dependent on the availability of drift macroalgae, which declined in beds that were denser and more continuous.

Functional Traits

We identified nine functional traits based on their potential ability to explain both colonization potential, as well as competitive interactions among resident epifauna and effects on ecosystem functioning. Traits included indicators of defense and morphology (exoskeleton material and body plan), trophic ecology (trophic group and specific diet), body size (maximum length), habitat use (mobility and position in the water column), and life history (egg retention and development mode). These traits have shown to discriminate among epifaunal invertebrates, and to describe and predict benthic community structure and function (Bremner et al. 2003, 2006, Best et al. 2013, Lefcheck and Duffy 2015). The trait data were collected directly from peer-reviewed literature and verified using expert knowledge of the organisms. A detailed description of these traits, including their units and functional interpretations, is given in Table A1. The trait data themselves and a bibliography of references from which they were extracted is found in Supplement 1.

Environmental Covariates

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

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

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Statistical Analysis

To adjust for vary effort through time, we averaged all observations for a particular quarterly sampling period so that each period constituted a single replicate (e.g., Dornelas et al. 2014). Then, for each replicate, we calculated a number of community metrics. First, we summed the total number of mean individuals observed in each averaged replicate to yield a measure of mean total abundance. Next, we calculated species richness (*S*), as the mean number of species observed, and Simpson diversity (*D*), which further incorporates information on species' (mean) relative abundances. For Simpson diversity, we converted the resulting probability values to 'effective number' of species using the transformation from (Jost 2006):

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

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

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

Unlike other indices of evenness, this index of evenness has been shown to independent of both richness and Simpson diversity (Jost 2010).

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

$$Q = \sum_{i=1}^{S-1} \sum_{j=i+1}^{S} d_{ij} p_i p_j \tag{3}$$

where d_{ij} is the difference between species *i* and *j* based on their functional traits, p_i is the relative abundance of species *i*, and p_j is the relative abundance of species *j*. The differences d_{ij}

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are derived from any combination of functional traits using Gower's dissimilarity measure (Gower 1971), which allows both continuous and categorical trait data to be collapsed into a single continuous distance measure. Because Rao's *Q* can be maximized when fewer than all functional types are present when Gower's distances are not ultrametric (Pavoine et al. 2005), we generated ultrametric distances using the procedure described in (Mouchet et al. 2008, Mérigot et al. 2010). In the event where species are either the same or different, d_{ij} collapses to 0 or 1 and *Q* = *D*, or Simpson diversity. Thus, Rao's *Q* can also be transformed using Equation (1) to yield units that are on the same scale as Simpson diversity. We calculated two separate indices of FD: one weighted by relative abundances, which we interpret as the functional analogue to Simpson diversity, and one based on presence-absence, or the functional analogue to species richness.

Finally, to further account for variable effort, we generated rarefied estimates of species richness and Simpson Diversity using fixed-coverage subsampling (Chao and Jost 2012). This method generates a value of sample coverage (i.e., how complete the sample is) based on the number of observed singletons (species for which only 1 individual was observed), and estimates of diversity are then rarefied down to a fixed level of coverage, as opposed to a number of individuals or samples. This method results in less data loss than traditional rarefaction, and more efficiently ranks communities based on their true diversities (Chao and Jost 2012). Rarefied estimates were calculated using the *iNEXT* package in R (Hsieh et al. 2014).

Statistical Analysis

Differences among the community metrics for each bay and sampling period were assessed using general linear mixed effects models with an autoregressive 1 (AR1) correlation structure corresponding to each sampling period. Assumptions of normality of errors and homogeneity of variance were assessed visually. Models were constructing using the *nlme* package in R (Pinheiro et al. 2013). The role of environmental covariates in driving the observed patterns was then estimated using random forests (RF, (Breiman 2001). We built an ensemble of 50 trees, after which we observed no appreciable decrease in mean squared error, with ‘out-of-bag’ (OOB) permutation to estimate importance partitioned based on Pearson correlation threshold ≥ 0.5. Each community metric (abundance, richness, etc.) was regressed against the following variables that had near complete coverage across all sampling locations and periods: year, bed location, area, and density, temperature, salinity, dissolved oxygen, pH, and water column chl-*a* and phosphates (as a proxy for suspended organic material). We then evaluated the importance of each predictor by quantifying the mean percent decrease in accuracy, derived from the increase in mean error across all trees in the ensemble when a given variable is randomly permuted and then challenged with the OOB data. Model parameters were optimized using the *caret* package (Kuhn 2015), and RFs were constructed using the *randomForest* package in R (Liaw and Wiener 2002). For the top predictors, we plotted bivariate correlations and tested whether the observed correlation was significantly different from zero by comparing values to a *t*-distribution with $n - 2$ degrees of freedom.

We used non-metric multidimensional scaling (NMDS) to visualize differences in multivariate community structure across bays, algal vs. eelgrass samples, and through time in two dimensions. We used Wisconsin transformation on the species-by-site matrix, then characterized community dissimilarity using Bray-Curtis distances. The distance matrix was further square-root transformed to reduce the influence of highly abundant species. To statistically test for differences among species composition through time, we conducted PERMANOVA, which partitioned variance in the community dissimilarity matrix as a function of sampling period, and uses random permutations of the data to assess significance (McArdle and Anderson 2001). We conducted the NMDS and PERMANOVA using the *vegan* package (Oksanen et al. 2013).

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

Results

In contrast to our expectations that the restored bed would appear more like the reference bed through time, the two were not significantly different in terms of most community metrics even after only one year (Fig. 1, $P > 0.05$ based on output from general linear mixed effects models). The two exceptions were average abundance, which was significantly lower in South Bay during the period from 2001-2003 (Fig. 1a, $P = 0.027$), and functional diversity based on presence-absence, which was, on average, significantly higher (Fig. 1f, $P < 0.001$). By the early 2010s, all but one community metric were actually higher in the restored bed (Fig. 1b-f, $P < 0.001$). Functional diversity weighted by relative abundances in particular was 15-32% higher in South Bay than in Chincoteague Bay from 2010-2013 (Fig. 1e). Average abundance was still significantly lower in South Bay during the later period ($P < 0.001$), although we note the expected difference between the two was approximately 25% less than in the earlier period (based on parameter estimates from mixed models).

To understand the factors driving the rapid recovery and ultimate transcendence of the restored bed, we fit random forests for each community metric to a suite of environmental and physical covariates. Random forests consistently identified bed location, total area and mean density to be the top three most important predictors across all community metrics (Fig. A1).

Bivariate plots revealed strong and highly significant positive correlations between area and density for almost all metrics of diversity in South Bay (Fig. 2), particularly estimated richness and Simpson diversity (Fig. 2b, c) and functional diversity weighted by relative abundance (Fig. 2f). It is worth noting that Chincoteague Bay showed generally weaker or even opposite trends in these bivariate correlations, which may at first appear to be at odds with the output from the random forest analysis. However, it is important to recall that random forests account for collinearity and interactions among variables, and thus the ranking reflects the importance independent of other confounding factors, while the bivariate plots do not.

Exploration of individual trait values revealed that assemblages in the South Bay bed generally exhibited greater variation in traits related to habitat use, life history, and morphology, particularly during the later stages of restoration (Fig. A3). Specifically, South Bay had proportionally more benthic-dwelling crawlers, with calcium carbonate exoskeletons, and external release of eggs with subsequent planktonic dispersal (Figs. S4-8). Thus, it appears that gastropods are responsible for a majority of the difference in functional diversity between the restored and reference beds. Even within this taxonomic group, however, richness, Simpson, and functional diversity weighted by relative abundance were all higher in South Bay during the late period (Fig. A9).

Analysis of multivariate community data using non-metric multidimensional scaling and PERMANOVA revealed that the composition of the restored bed changed significantly from the early period of restoration to the late period ($P < 0.001$ based on 9,999 random permutations of the data, Fig. 3). Shifts in community composition were principally driven by declines in the relative abundances of the grazing amphipod *Batea catharinensis*, the grazing snail *Astyris lunata*, and the shrimp *Hippolyte pleuracanthus*, and by the appearance of the snail *Costoanachis* *avara*. In contrast, there were no significant changes in community structure across years in Chincoteague Bay ($P > 0.05$, Fig. 3). Further, the changes in community structure through time did not appear to be a consequence of recruitment via drift macroalgae, with the macroalgal communities in each bay being significantly distinct from the corresponding grass beds ($P < 0.001$, Fig. 3). In fact, the same species that were responsible for changes in eelgrass community structure in South Bay through time were generally less abundant on drift macroalgae than in the eelgrass itself (Fig. A2).

Of the 42 species captured over the entire survey, five were found exclusively in South Bay, including three gastropod species in the genus *Costoanachis*, as well as the grazing snail *Marshallora nigrocincta*, and the detritivorous amphipod *Photis macrocoxa* (although this species was found only on drift macroalgae). All five of these species occupied unique parts of functional trait space, based on principal coordinates analysis of their trait values (Fig. A10). Only two species – the grazing isopod *Paracerceis caudata* and the detritivorous amphipod *Lysianopsis alba* – were found exclusively in Chincoteague Bay, and they were nearly functionally equivalent with other species (Fig. A10).

Discussion

In this study, we found that the diversity of epifaunal invertebrates and their functional traits in a restored eelgrass bed matched and then exceeded values exhibited by a nearby reference bed in less than a decade (Fig. 1). These invertebrates, and particularly their diversity, are known to play a critical role in the maintenance, structure, and functioning of eelgrass ecosystems (Duffy et al. 2014). Further, the rapid recovery of the epifaunal community was shown to be a direct consequence of restoration actions that encouraged the growth and expansion of the restored bed (Fig. 2). These findings may be of particular consequence as eelgrass cover has generally declined in the region (Orth et al. 2013) and worldwide (Waycott et al. 2009), and may continue this downward trajectory without further intervention. The area of the reference bed, for example, declined 49% over the 12 years of the survey (Fig. 4a), presumably as a consequence of decreasing water quality and thermal stress known to drive eelgrass decline in the nearby Chesapeake Bay (Wazniak et al. 2007, Moore et al. 2012). In contrast, the area of the restored bed increased by 910% over the same time period (Fig. 4b). Thus, if these trends continue, then restored beds in an environment not challenged by poor water quality may play an increasingly vital role in providing habitat for a variety of taxa and functional forms present in the region. Indeed, restored beds now make up roughly one-third of total seagrass cover in the Delmarva coastal bays (Orth et al. 2013).

If many aquatic restorations fail to achieve pre-disturbance levels of diversity (Benayas et al. 2009), including in other seagrasses (Paling et al. 2009), then why has this particular effort been so successful? Low human impacts in this region are undoubtedly a major factor. Long-term monitoring by the Virginia Coastal LTER has shown that nutrient loading and water column chlorophyll-*a* have been low and relatively stable across all of Virginia's coastal bays over the past two decades (Orth and McGlathery 2012). The bays also experience regular flushing with cooler ocean water, alleviating temperature stress that is a major driver of eelgrass die-backs in nearby regions, such as the Chesapeake Bay (Moore et al. 2012). Moreover, as the restored bed has increased in size and density, it has more effectively captured particulates, leading to increased water clarity and greater light availability for photosynthesis (Moore et al. 2012, Orth et al. 2012). This self-facilitation has been identified as a key predictor of the persistence of restored seagrass ecosystems (van Katwijk et al. 2009).

Altogether, the factors that promote the growth and expansion of the restored bed should, in theory, facilitate the recruitment and survival of epifaunal invertebrates, principally by increasing the availability of habitat and substrate for algal resources. While the positive relationship between area sampled and species richness has established generally, there are few examples from seagrass systems (Boström et al. 2006). Our study is also unique in the sense that increasing area does not simply represent a shift in geographic focus, but a product of ongoing efforts to actively increase the total habitat in the same location, and the natural spread of eelgrass from the initial effort to restore this habitat. Moreover, the presence and diversity of these grazers has been shown to promote their eelgrass habitat both in experiments and observational studies, generating a positive feedback where habitat begets diversity, and so on. Thus, the abundant and functionally diverse grazer community in the restored bed may play an important role in the self-facilitation mentioned above.

The reproductive biology and dispersal abilities of the focal organisms may have also played a large role in the rapid recovery of the epifaunal community in the restored bed. Recent reviews have suggested that 'successful restorations' – those that have achieved similar levels of biodiversity as before a disturbance – have concerned communities of fast-reproducing organisms with high dispersal ability (Jones and Schmitz 2009, Duarte et al. 2015). While there did not appear to be a change in the proportion of individuals belonging to high vs. low dispersal species throughout the course of restoration – those that brooded or released their eggs, and those with planktonic vs. non-planktonic larval forms (Figs. S7-8) – most of the organisms in this system have generation times on the scale of weeks to months. The amphipod *Gammarus mucronatus*, for instance, can reach reproductive maturity in as few as three weeks during hotter months (Fredette and Diaz 1986). The quick generation and turnover of populations certainly contributed to the ability of these small invertebrates to reach and exploit this new habitat.

A complementary hypothesis is that, as the bed expanded, it also recruited mesopredators of epifauna, including various fishes and crabs, which also utilize the eelgrass as habitat. Predator trawls conducted in South Bay the early 2010s revealed a diverse and abundant predator community (Schmitt et al., *submitted*). A recent meta-analysis produced strong evidence supporting the long-standing hypothesis that predation enhances prey diversity by relieving competition among prey species (Katano et al. 2015), a trend which has been seen in mesocosm experiments using several of the species observed in our surveys (Duffy et al. 2005, Douglass et al. 2008). Consistent with an active and increasingly abundant predator community, epifaunal abundance actually had an inverse relationship with bed area and density in South Bay (Fig. 2a). An alternative explanation is that epifauna are resource-limited, as suggested by their remarkably invariant mean abundances observed in the later stages of restored bed (Fig. 1a). Thus, increasing the density of habitat but not resources could have diluted the average abundance per unit sampling area.

One of the more striking differences between the restored and reference beds was the higher functional diversity in South Bay compared to Chincoteague Bay (Fig. 1e-f). Habitat complexity and resource availability, proxied by mean density and total phosphates in our random forest analysis, likely played a large role here as well (Fig. 2e-f, Fig. A1). Increasing both should theoretically open niche space and facilitate coexistence, leading to a wider variety of observed functional morphologies, behaviors, and life histories. Classical successional theory would predict that this would be especially true during the later stages of restoration, as biotic as opposed to abiotic filters play an increasingly larger role and functionally similar species are weeded out as consequence of competitive interactions (Connell and Slatyer 1977). Given these predictions, it is surprising that we observed significantly higher functional diversity in the restored bed compared to the reference bed in the early stages of restoration. Once again, the relatively fast recruitment and generation times of the organisms may play a role, allowing such interactions to play out on much shorter time scales than might be expected in other systems, such as terrestrial plants (Purschke et al. 2013).

A recent publication also suggested that it is not competitive interactions, but continued colonization, that drives the functional trait structure of successional communities (Li et al. 2015). We observed significant differences in community composition through time, particularly in the restored bed (Fig. 3), which was a consequence of the arrival of new species or shifts in dominance. Along similar lines, the demography of these epifaunal invertebrates is notoriously unpredictable. In nearby systems in the Chesapeake Bay, which have been well studied for decades, species appear and then disappear regularly, generally in response to loss of habitat (Douglass et al. 2010). Similar stochastic processes may also be at play here, with high trait diversity in the early years simply an outcome of chance processes that favored recruitment of functionally varied individuals to the sudden appearance of uncolonized habitat.

Finally, we must acknowledge the possibility that we are still observing some transitional state, and that the restored bed is still progressing towards the stable state exhibited by the reference bed (Fig. 3). Several lines of evidence suggest this is not the case. First, inter- and intra-annual variability was similar between both bays (Fig. 1), suggesting that the reference bed was not more ‘stable’ than the restored bed. In fact, the error around most of the means in the restored bed is actually lower than in the reference bed. Second, we observed significant compositional differences between the beds, suggesting potentially different avenues for colonization (Fig. 3). Finally, given the contrasting trajectories of the two beds (Fig. 4), it may be unreasonable to suspect these two communities to ever converge.

Aggregating at broad temporal scales emphasizes overall trajectories of these beds, but ignores some of the finer scale variation. One particularly notable instance occurred in June 2012, with the recrtuiment of juvenile pinfish (*Lagodon rhomboides*) to these coastal bays. During early life history stages, pinfish are known to be voracious predators of epifaunal invertebrates (Luczkovich and Stellwag 1993), and were indisputably responsible for the steep declines in epifaunal abundance and diversity during this month (Fig. A11). Generally, pinfish do not range this far north, but with increasing temperatures, we may be witness to a northward range expansion. Such a shift may have drastic consequence for the eelgrass: first, by removing the critical top-down control provided by epifaunal grazers, and second, by directly consuming eelgrass, particularly later during their ontogeny (Luczkovich and Stellwag 1993). Thus, while local conditions over the last decade have favored the growth and expansion of eelgrass in Virginia's coastal bays, climate change may introduce a new variable in the form of pinfish with uncertain consequences for the maintenance of eelgrass diversity and function in South Bay.

Within the larger context of restoration ecology, our study stands out in that it documents the transition from a near complete lack of vegetation to dense, contiguous beds (Fig. 4, Orth & McGlathery 2012). This state-shift stands in contrast to many other restoration projects, which have focused on recovery of degraded, but not totally destroyed, systems. The drastic transition from a near unvegetated to a vegetated system may explain some of our results by widening the scope for detectable effects. We note, however, that the greatest differences occurred during the later stages of restoration, when the restored and reference beds were comparable in terms of their total coverage (Fig. 4). Further, even in degraded eelgrass beds, remediation of environmental stressors has been show to enhance the functional trait diversity of epifaunal invertebrates (Dolbeth et al. 2013). As with our results (Fig. 1e), functional recovery was partly a consequence of the redistribution of biomass among different functional types (Dolbeth et al. 2013). Similarly rapid recovery of functional diversity has been observed in other invertebrate communities, such as beetles in restored wetlands (Watts and Mason 2015). These studies, along with ours, suggest that functional traits can be a powerful tool for assessing the response and subsequent recovery of communities to disturbance (Mouillot et al. 2013b).

It is worth noting a few limitations of this study. First, we are comparing two bays, even though these bays combined account for 88% of the submersed aquatic vegetation in the Delmarva coastal bays. While our results may not be representative of eelgrass systems in general, or even restored systems, we do demonstrate that restored ecosystems at least have the potential to greatly exceed the diversity of reference systems, which is a relatively rare outcome in restoration ecology (Benayas et al. 2009). Second, we had variable sampling effort through time, largely as a consequence of available habitat to sample. To further explore the potential for bias, we additionally weighted our regression analyses by the inverse of sample size ($1 / N$) to explore the relative influence of poorly sampled periods (see Supplement 1). This exercise yielded nearly identical results, with the one exception that functional diversity weighted by relative abundance (Fig. 1e) was now significantly higher in the restored bed than the reference bed ($P = 0.017$), where it was previously non-significant in the unweighted regression. Finally, we did not have robust and consistent estimates of the point density of the habitat to use in our analysis. Future monitoring efforts should focus on a method that is not only standard to the area of bottom sampled, but also yields some value of habitat availability (biomass, etc.).

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

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Figure Captions

Figure 1: Times series plotting the annual mean ± 1 SE for various community properties. Light grey circles represent the mature bed in Chincoteague Bay. Black triangles represent the restored bed in South Bay. FD = functional diversity, calculated as Rao's quadratic entropy from all nine functional traits.

Figure 2: Plots of total bed area (in hectares, left column) and mean density (as the average density bin based on comparison of aerial footage against a crown density scale, ranging from 0 for no cover to 1 for full cover) for South Bay. Points represent each year and month of the survey. The black line represents a simple linear regression between the two variables. The Pearson correlation (*r*) from this regression is given in the bottom of each panel along with the following indicator of statistical significance: * $P = 0.05$, ** $P = 0.01$, *** $P = 0.001$.

Figure 3: Non-metric multidimensional scaling conducted on relative abundance data for both eelgrass (green) and drift macroalgal (brown) communities. Small open points represent each year and month of the survey. Large points represent the centroid for each year, graded from early years (dark grey) to later years (light grey). Arrows represent the trajectories from one year to the next. Stress – a measure of concordance between the multivariate data and the two-dimensional representation – is given in the lower right.

Figure 4: Total area (in hectares) of eelgrass beds in **(a)** Chincoteague Bay and **(b)** South Bay through time. Bars are divided into estimated density bins (% cover) based on comparison of aerial footage to a crown density scale. Note: aerial photography could not be conducted in 2005 due to poor weather conditions.

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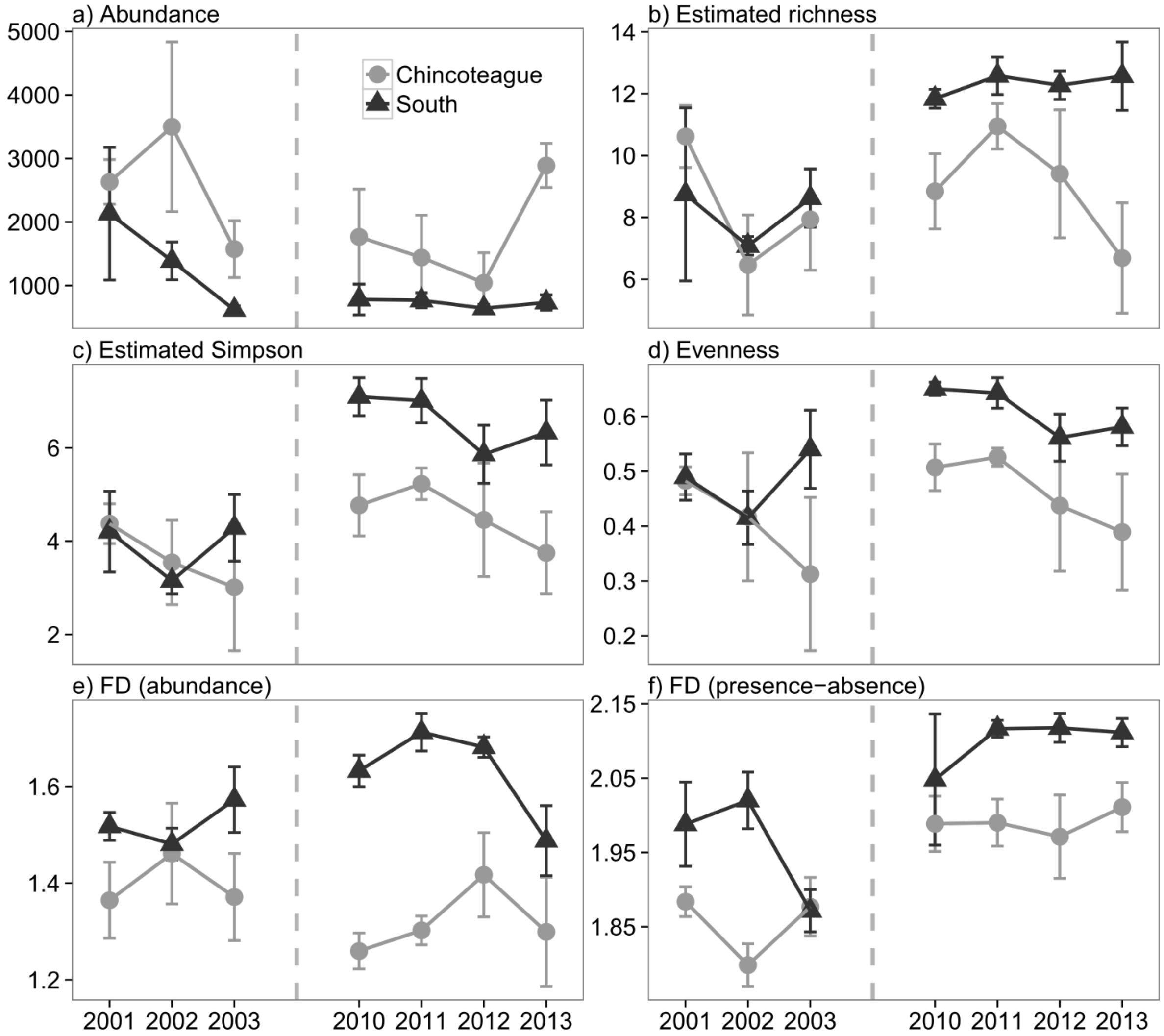

Figure 1

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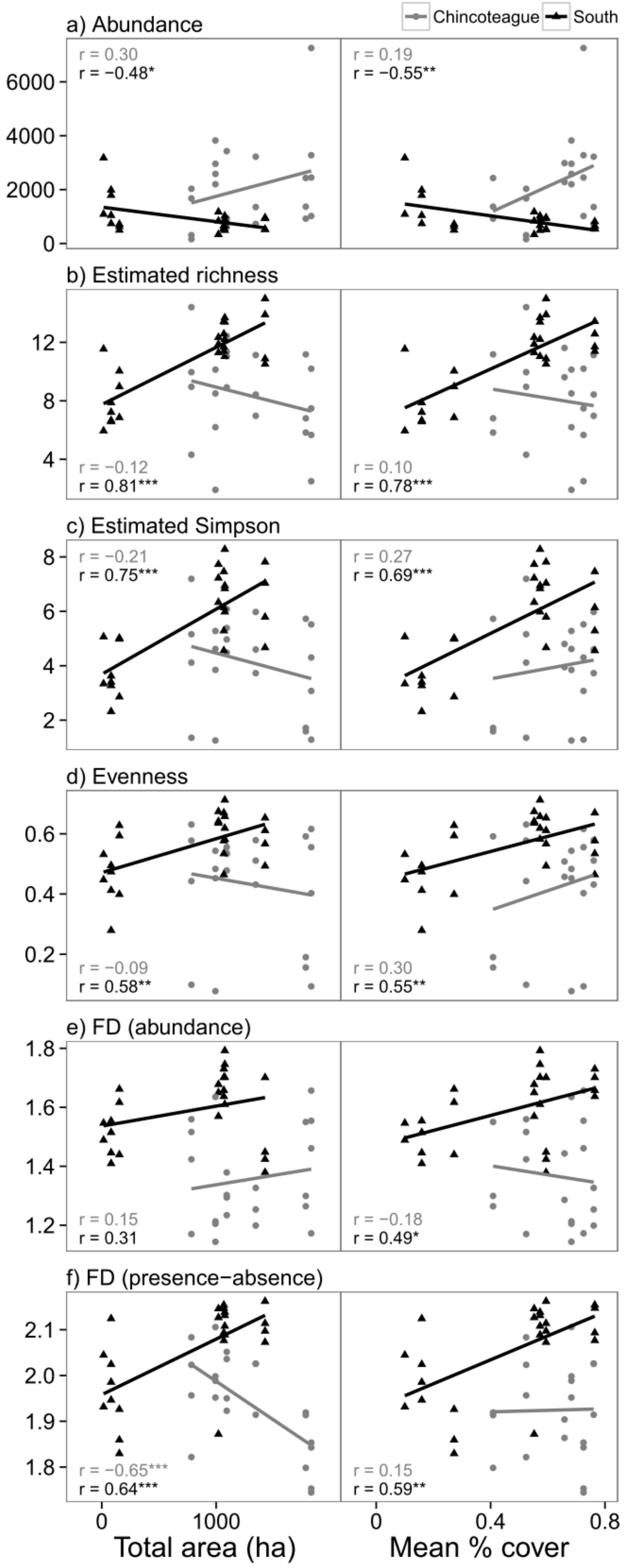
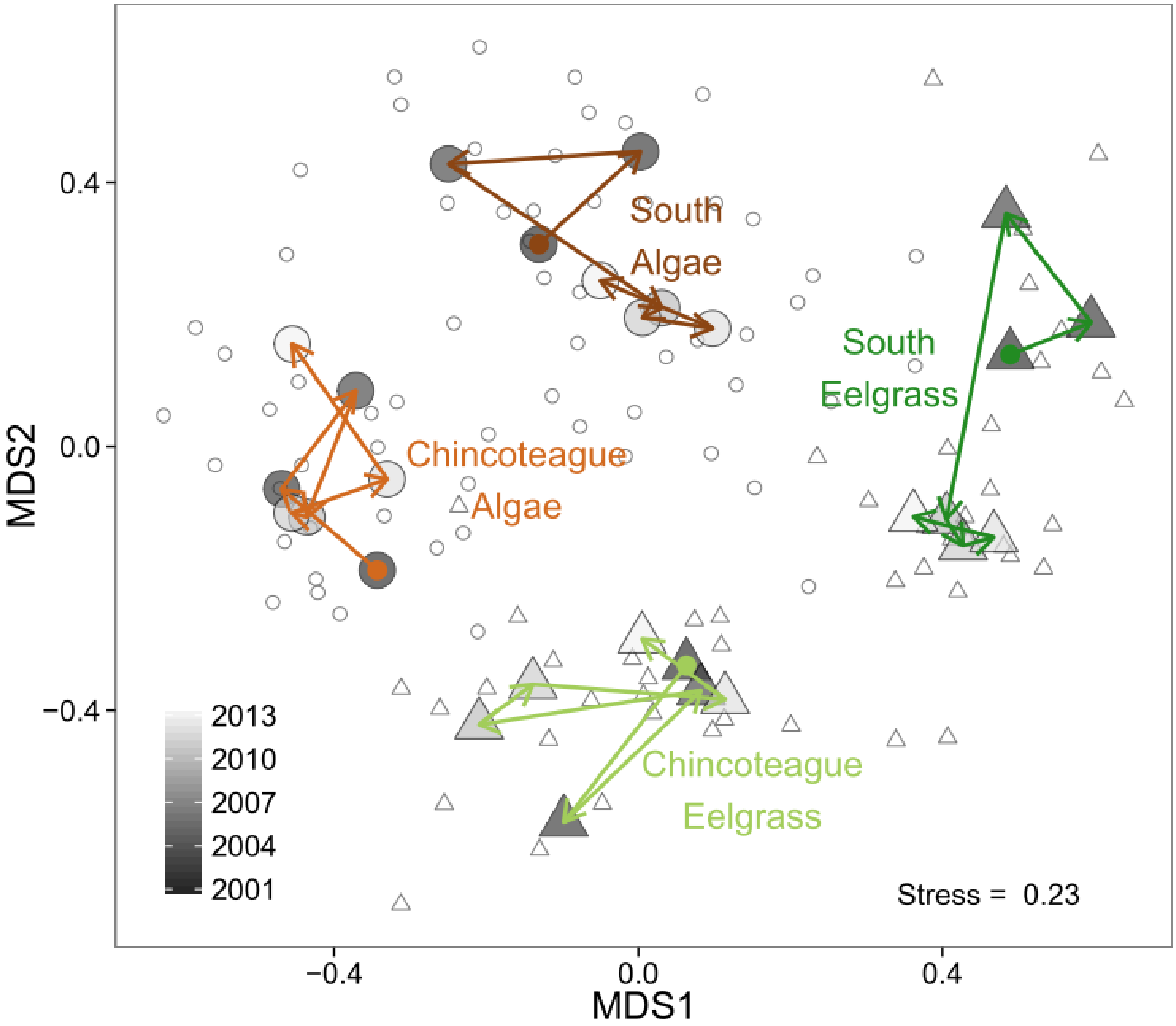

Chincoteague
South
a) Abundance
r = 0.30
r = −0.48*
r = 0.19
r = −0.55**
6000
4000
2000
0
b) Estimated richness
12
8
4
r = −0.12
r = 0.81***
r = 0.10
r = 0.78***
c) Estimated Simpson
8
6
4
2
r = −0.21
r = 0.75***
r = 0.27
r = 0.69***
d) Evenness
0.6
0.4
0.2
r = −0.09
r = 0.58**
r = 0.30
r = 0.55**
e) FD (abundance)
1.8
1.6
1.4
1.2
r = 0.15
r = 0.31
r = −0.18
r = 0.49*
f) FD (presence−absence)
2.1
2.0
1.9
1.8
r = −0.65***
r = 0.64***
r = 0.15
r = 0.59**
0
1000
0
0.4
0.8
Total area (ha)
Mean % cover

Figure 2



709

710 **Figure 3**

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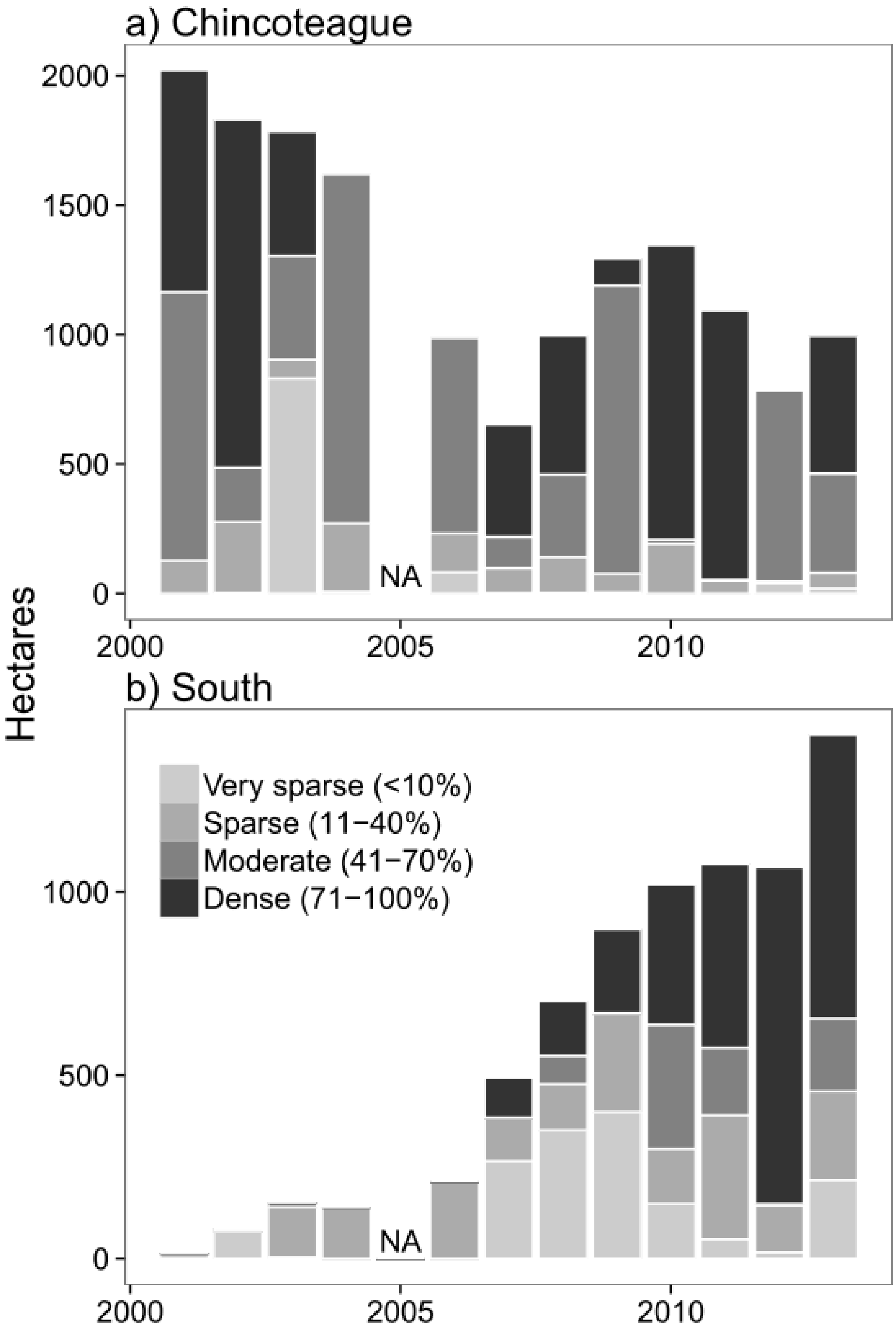
a) Chincoteague
2000
1500
1000
500
0
NA
2000
2005
2010
Hectares
b) South
Very sparse (<10%)
Sparse (11−40%)
Moderate (41−70%)
Dense (71−100%)
1000
500
0
NA
2000
2005
2010

Figure 4