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Recovering ecosystem functions in a restored salt marsh by leveraging positive effects of biodiversity

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Abstract. Natural and managed ecosystems provide a variety of ecological, economic, and cultural benefits; yet most have been altered by human activity such that they exhibit deficits in both biodiversity and functionality. Identifying factors accelerating the recovery of key species and associated functions in degraded systems is therefore a global priority. We tested the hypotheses that explicitly incorporating biodiversity into restoration design will lead to greater ecosystem function and that positive effects of diversity will strengthen over time due to an increase in the importance of complementarity relative to selection effects. We did this by manipulating salt marsh plant species richness across a tidal elevation gradient as part of a coastal wetland restoration project in southern California. Overall, diversity enhanced biomass accumulation in experimental plots, with the magnitude of the effect strengthening from one to three years post-restoration due to a combination of decreasing performance in monocultures and increasing performance in multispecies mixtures over time. Positive diversity effects were initially due exclusively to selection, as mixtures were dominated by species also exhibiting high performance in monoculture, although the identity of the highest performing species varied across tidal elevations and over time. By the end of the study, complementarity, indicative of niche partitioning and/or positive interactions among species, contributed to productivity at least as much as selection effects. Our study provides real-world support for a recent theoretical model predicting strong positive biodiversity effects when functionally different species coexist in a heterogeneous landscape. Incorporating biodiversity into restoration designs can result in net gains in ecosystem function especially in low diversity systems, yet shorter experiments lacking broad environmental and species trait variability may both underestimate the strength of and misidentify the mechanisms underlying positive diversity effects.

Key words: BEF; biodiversity–ecosystem function; coastal wetland; complementarity; ecological restoration; environmental variability; primary productivity; selection effects; trait variability.

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Introduction

Natural and managed ecosystems provide a variety of ecological, economic, and cultural benefits to humans that include food, water, fuel, disease control, and recreation (Costanza et al. 1997, 2014). Many ecosystem functions and services are positively related to local biodiversity

Box 1 Glossary of terms

> *Biodiversity:* the variety of genes, species, or functional traits in an ecosystem.
> *Complementarity:* niche partitioning and/or positive interactions among species that result in multiple species performing better in mixtures than they do in monoculture.
> *Ecosystem functions:* aggregate biological processes that control the fluxes of energy, nutrients, and organic matter through an environment.
> *Ecosystem services:* biological processes considered to have value to humanity.
> *Functional traits:* morphological, physiological, or phenological attributes of an individual that affect fitness via survival, growth, or reproduction.
> *Restoration science–practice gap:* when ecological knowledge based on scientific research is not incorporated into the design, implementation, and study of restorations.
> *Selection effects:* dominance of mixtures by species exhibiting either high or low performance in monoculture; can be positive or negative.

(Box 1 provides a glossary of terms; Cardinale et al. 2012, Hooper et al. 2012, Tilman et al. 2014, Duffy et al. 2017). Relative to their pre-disturbance states, most ecosystems exhibit reduced biodiversity due to human alterations and diversity continues to be lost at an unprecedented rate (Kareiva et al. 2007, Butchart et al. 2010, Moreno-Mateos et al. 2017). As a consequence, disturbed ecosystems also typically exhibit deficits of function that may persist for years to decades depending upon the ecosystem and type of disturbance (Isbell et al. 2015, Moreno-Mateos et al. 2017). Identifying factors that will accelerate the return of key species and associated processes in ecosystems that have been damaged or destroyed by human activities is therefore a critical research priority (Tilman et al. 2014).

In recent decades, ecological restoration has become an essential tool for improving degraded ecosystems and returning these key species

(Perring et al. 2015, Suding et al. 2015, Freedman et al. 2016). A major challenge for practitioners is to reestablish communities that support ecosystem functions and services at levels comparable to those under pre-disturbance or reference conditions (Hallett et al. 2013). Unfortunately, current restoration practice often fails to accomplish this goal (e.g., Benayas et al. 2009, Moreno-Mateos et al. 2012). Given well-established positive relationships between biodiversity and multiple ecosystem functions, explicitly incorporating genetic, species, or trait diversity into habitat restoration efforts might be expected to result in increased ecosystem performance over time (Funk et al. 2008, Benayas et al. 2009, Kettenring et al. 2014). Nevertheless, a recent review of published literature on habitat restoration found that only 13% of studies with a biodiversity component focused on manipulating diversity in the restoration design (Hughes et al. 2018); most, instead, monitored biodiversity as a response to the intervention. Hughes et al. (2018) suggest that this restoration science–practice gap is an important barrier to increasing the scope and effectiveness of habitat recovery efforts. One possible explanation for the gap is that our understanding of the mechanisms underlying observed biodiversity–ecosystem function (BEF) relationships is still incomplete, particularly with respect to the environmental and biological conditions most likely to promote positive effects of diversity on local ecological processes (Hillebrand and Matthiessen 2009, Grace et al. 2016).

Ecosystem responses to variation in biodiversity can be partitioned mathematically into contributions from two different mechanisms: selection effects and complementarity (Loreau and Hector 2001). Selection effects are a function of fitness differences associated with species identity—they are positive when the dominant species in a mixture are among those that also perform best in monoculture and negative when the dominant species in a mixture perform poorly in monoculture (e.g., with respect to productivity, a competitively superior species may nonetheless be slow-growing). In contrast, complementarity results from niche partitioning and/or facilitation, such that multiple species perform better in mixture than in monoculture. Complementarity essentially quantifies overyielding (an increase in biomass or yield in mixture) above

the expectation based on species performance in monocultures (Loreau et al. 2012). Less commonly, underyielding (when mixtures produce less than expected) is possible. Selection effects and complementarity are linked to competitive exclusion (via fitness differences) and species coexistence (via niche partitioning or facilitation), respectively (Carroll et al. 2011, Loreau et al. 2012). Under experimental conditions, selection effects often dominate initially, yet complementarity is expected to become more important as communities develop (Cardinale et al. 2007, Stachowicz et al. 2008a). Environmental variation increases with increasing measurement duration (Denny et al. 2004), perhaps allowing for greater expression of species-specific differences over time. Longer experiments may also be more likely to capture population-level processes such as recruitment and facilitation, in addition to differences in individual-level performance (Stachowicz et al. 2008a).

Morphological, physiological, and phenological attributes of individuals—so-called functional traits (Violle et al. 2007)—have been linked to both fitness and niche differences among species, suggesting that they may also explain BEF relationships (Kraft et al. 2015, Cadotte et al. 2017). Current theory predicts that the relative contribution of selection effects vs. complementarity to net positive effects of diversity on ecosystem function depends upon the presence and magnitude of environmental heterogeneity (Hodapp et al. 2016). Selection effects should be strongest under homogeneous environmental conditions, as species-specific trait differences will lead to large variation in performance, although the identity of the dominant species may differ as conditions change. Complementarity, on the other hand, should be strongest when functionally different species coexist in a heterogeneous landscape, as under such conditions high trait diversity will facilitate niche partitioning (Hodapp et al. 2016). To date, experimental tests of these ideas remain scarce (but see Cadotte et al. 2017, Mandal et al. 2018).

Wetlands are among the most productive and economically valuable ecosystems in the world (Costanza et al. 1997, 2014), providing a variety of key ecosystem functions that include food web support, nutrient cycling, sediment stabilization, and nursery habitat for many ecologically and economically important species (Minello et al. 2003, Mitsch and Gosselink 2007). They are also among the ecosystems most vulnerable to human activity. For example, in southern California, some 70% of vegetated coastal wetland area has been destroyed over the past 150 yr and much of the remainder damaged by development, fragmentation, and urban runoff (SCWRP 2018). Unfortunately, as in other ecosystems, ecological restorations in wetlands rarely incorporate diversity manipulations and have not been entirely successful at recovering targeted ecosystem functions and services (Moreno-Mateos et al. 2012, Hughes et al. 2018). Although revegetation efforts using mixtures of plant species can be at least as effective as single-species plantings with respect to multiple indicators of ecosystem function (Callaway et al. 2003, Blair et al. 2013), most wetland restoration plans still incorporate monocultures of competitive dominants under the belief that this approach will lead to faster increases in plant cover—a typical management goal (Sullivan 2001).

Here we test the hypotheses that (1) explicitly incorporating biodiversity into restoration design will enhance ecosystem functioning relative to single-species plantings; (2) positive effects of biodiversity will strengthen over time; and (3) the importance of complementarity relative to selection effects will also increase, as predicted when high environmental variation co-occurs with high trait variability (Hodapp et al. 2016). We did this by manipulating salt marsh plant species richness across a tidal elevation gradient as part of a coastal wetland restoration project in southern California. We quantified plant percent cover—a proxy for biomass production—as a measure of ecosystem functioning after one and three years, allowing us to measure changes in both the magnitude of net diversity effects and the relative contribution of selection vs. complementary over space and time. Finally, we evaluated our observed results in the context of theoretical expectations based upon the degree of observed variation in environmental conditions and plant functional traits in our experimental system.

METHODS

All work was done on an initially unvegetated intertidal mudflat in Colorado Lagoon, Long

Beach, California, USA (33°46′19.2″ N, 118°8′12.5″ W). The lagoon is connected to open water via an underground culvert that prior to restoration severely restricted circulation such that tidal range in the lagoon was muted by as much as 1.2 m relative to the nearby ocean. Natural water flow to and from the lagoon was substantially increased in fall 2012 via extensive sediment removal and shoreline contouring; initial sampling and planting were done in February 2013.

Experimental design and planting

To test the effect of plant species diversity on post-restoration recovery of ecosystem functions, we established a series of plots with either 1, 3, or 6 plant species: *Batis maritima* (saltwort), *Distichlis littoralis* (shoregrass, formerly *Monanthochloe littoralis)*, *Distichlis spicata* (salt grass), *Frankenia salina* (alkali heath), *Jaumea carnosa* (salty Susan), and *Salicornia pacifica* (pickleweed). These species commonly co-occur in southern California salt marshes, represent nearly the full suite of dominant taxa found at the site pre-restoration, exhibit a range of species-specific morphological and physiological trait values, and are often used in restoration projects (Sullivan and Zedler 1999, Callaway et al. 2003, Blair et al. 2013). We established 10 blocks horizontally along the shore at five tidal elevations (0.91, 1.04, 1.18, 1.29, and 1.40 m above mean lower low water [MLLW]; $n = 2$ blocks per elevation) measured with a surveyor's auto level relative to an adjacent benchmark. Each block included a single row of 27 experimental plots spaced 0.60 m apart to which the following plant species richness treatments were randomly assigned: monocultures ($n = 1$ plot per species, six plots total per block), 3-species polycultures ($n = 20$ plots per block, including 19 of 20 unique combinations of species (one was duplicated accidently), and a 6-species polyculture ($n = 1$ plot per block). Although most biodiversity–ecosystem function studies have constructed diversity treatments using randomly selected assemblages from a local species pool, such an approach assumes that species loss from natural systems is random; yet we know that is often not true (Zavaleta and Hulvey 2004, Bracken et al. 2008). In relatively undisturbed southern California salt marshes, only eight to ten plant species are typically present with high evenness (Zedler and West 2008,

Doherty et al. 2011). The six species we used were among the most abundant native salt marsh plant species in Colorado Lagoon pre-restoration, suggesting they were least likely to be lost in response to ecosystem degradation.

Each 0.60×0.75 m plot was tilled and planted with seedlings (~7.5 cm tall) from eighteen 5 cm x 5 cm pots supplied by the Tree of Life Nursery (San Juan Capistrano, California, USA) or Tidal Influence (Long Beach, California, USA). Seedlings from Tree of Life were grown from diverse seed stock, whereas those from Tidal Influence were propagated from cuttings collected at the site pre-restoration; both methods have been shown to be effective in re-establishing plant cover in restored marshes (Sullivan 2001). Locally collected plants were kept in a greenhouse at CSULB for 6–8 months prior to propagation and planting. As we wanted plants from each pot to contribute similarly to the total percent cover of each plot, the number of seedlings varied among pots. During planting, seedlings were removed from their pots and arranged in a grid with 15-cm spacing between plants from each pot and 15 g of slow-release fertilizer (Osmocote 19-6-12; Scotts, Marysville, Ohio, USA) in each hole (Blair et al. 2013); the location of pots within each plot was randomized. Total plant cover of plots at the start of the experiment was ~10%. No weeding or replanting was done; however, we noted whenever a non-planted species recruited into an experimental plot (rarely, and if not one of the original six species, always *Sueda taxifolia*; woolly seablight).

Sampling

Changes in plant cover within plots were estimated by species to the nearest 5% using a modified version of the Daubenmire method (Daubenmire 1959) in February 2014 and 2016, one and three years post-restoration. (Instances where percent cover was markedly <5%, but not zero were scored as 1%.) We used a non-destructive estimate of productivity due to the ongoing restoration activities occurring at the site; however, plant percent cover is highly correlated with biomass in California salt marshes (e.g., Noto and Shurin 2017). Environmental conditions in experimental plots and species-specific plant leaf traits were measured in February 2014.

Sediment temperature in the top 2 cm was measured in each plot with a digital thermometer and probe (Model 15-077-14; Thermo Fisher Scientific, Waltham, Massachusetts, USA) and redox potential with a handheld pH meter (Model FE20/FG2; Mettler-Toledo, Columbus, Ohio, USA). Sediment samples were collected from each plot with a haphazardly located core (2.24 cm diameter × 2 cm depth) and stored at $-20°C$ until processed. We chose to use a relatively small core volume to minimize disturbance within experimental plots; however, sample volume was kept constant across plots to allow for direct comparisons among treatments. Porewater salinity was measured with the paste method, and bulk density (a proxy for sediment compaction) calculated as the dry mass of a known volume of sediment (Richards 1954); organic matter content (%OM) was calculated as loss on ignition after 16 h at 375°C in a muffle furnace (Ball 1964); and carbon to nitrogen ratios (C:N) determined on dried and ground sediment in a CHN elemental analyzer (Costech 4010; Pioltello, Italy) using a soil standard with 2.01% carbon and 0.192% nitrogen.

Species-specific plant leaf traits were quantified on haphazardly selected individuals from a subset of plots chosen randomly from within each experimental block; only recently mature leaves from the mid-canopy were chosen. Due to species-specific differences in abundance and/or individual size one year post-restoration (e.g., on average, *D. spicata* and *J. carnosa* were less likely to be found in a given plot and many individuals of *D. littoralis* and *D. spicata* were too small to sample), sample sizes varied by species ($n = 6$–22 individuals per species). Photosynthetic rates were measured in the field with an LI-6400XT Portable Photosynthesis System (LI-COR Biosciences, Lincoln, Nebraska, USA) at a light level of 1800 μmol·photon·m^{-2}·s^{-1}, 400 μL·L^{-1}·CO_2, and ambient temperature and humidity; all measurements were taken between 10:00 and 14:00. Afterward, two leaves were harvested from each plant. Leaf mass per area (LMA) was determined by scanning leaves with a flatbed scanner to create a digital image, which was analyzed for leaf area with ImageJ (U.S. National Institutes of Health, Bethesda, MD). One leaf was immediately scanned for leaf area, dried, weighed to determine leaf mass per area (LMA), and then

ground prior to analysis in a CHN elemental analyzer to quantify C:N. The other leaf was frozen and stored at $-80°C$ prior to determination of chlorophyll concentrations. Samples were ground in 80% acetone, centrifuged, and the extract read at 646, 663, and 750 nm on a Genesys 10S spectrophotometer (Thermo Fisher Scientific, Waltham, Massachusetts, USA) after Bonin and Zedler (2008); equations for estimating chlorophyll *a* and *b* were taken from Lichtenthaler (1987).

Data analysis

Effects of salt marsh plant species richness and tidal elevation on change in percent cover in experimental plots one and three years post-restoration were evaluated with two-way analysis of variance (ANOVA) for both total percent cover and percent cover by species. Net diversity effects were partitioned into complementarity and selection effects within experimental blocks as the difference between observed yield in the 6-species polyculture and expected yield based on the performance of each species in monoculture, after Loreau and Hector (2001; see Appendix S1 for details). Effects of tidal elevation on complementarity, selection, and net diversity effects were evaluated with one-way ANOVA. Mean values of complementarity and selection pooled across tidal elevations were compared to a net effect of zero with one-sample *t*-tests. Block, a random factor nested in elevation, did not generally explain much of the observed variation in response variables and so was not included in the final models. Visual inspection of residuals was done for all analyses; data that violated assumptions of normality and/or homogeneity of variances were transformed with a $\ln(x + 1$ or 1.67) function, as appropriate to preserve zeros in the data (each species in the 6-species polycultures had an initial percent cover = 1.67). Post hoc comparisons following ANOVA were done using Tukey's honestly significant difference (HSD).

Descriptive multivariate analyses were done on environmental data from experimental plots and plant leaf traits using principal components analysis (PCA). Pearson product-moment correlation coefficients were generated to quantify linear associations among mean values of environmental variables and elevation, leaf traits

and change in percent cover, and associated principal components. Univariate analyses were done in Minitab 18 (Minitab, State College, Pennsylvania, USA) and multivariate analyses in PRIMER 7 (PRIMER-E, Plymouth, UK). Data (Fitzgerald et al. 2021) are available from Zenodo: http://doi.org/10.5281/zenodo.4780663.

RESULTS

Higher initial plant species richness correlated positively with change in total percent cover in experimental plots both one and three years post-restoration and the magnitude of the effect increased over time. (Fig. 1; Table 1). The most species-rich mixtures were approximately 1.5 times as productive as the average monoculture after one year and more than twice as productive after three years. Similarly, after one year percent cover in the 6-species polyculture was slightly less than that of the most productive monoculture, whereas after three years it was slightly more. Although suggestive of transgressive overyielding (where the mean polyculture is more productive than the highest performing monoculture), the observed effect was not statistically supported (paired t-test on yield by block: $t_9 = 0.54$, $P = 0.604$) likely due to low statistical

power associated with high among-plot variation (Fig. 1B). The identity of the most productive monoculture was different after one vs. three years (*S. pacifica* vs. *F. salina*), and the relative performance of many of the other species also changed over time. Overall, biodiversity effects strengthened from one to three years post-restoration as a function of both a decrease in performance of the average monoculture and a simultaneous increase in performance of the 6-species polyculture (Fig. 1). Surprisingly, other than plots at the lowest elevation having somewhat lower percent cover than plots higher on the shore, there was no consistent effect of tidal elevation on total percent cover in either year (Table 1; Appendix S1: Fig. S1).

Nor was there an effect of tidal elevation on complementarity, selection, or net diversity effects calculated by experimental block (Fig. 2A, C; Appendix S1: Table S1; all $P > 0.692$); overall, net diversity effects calculated as the sum of complementarity and selection effects increased from one to three years post-restoration, consistent with Fig. 1. Pooled across elevations, complementarity increased from one to three years post-restoration while the magnitude of selection effects declined (Fig. 2B, D). The overall mean ($\pm$SE) complementarity effect after one year
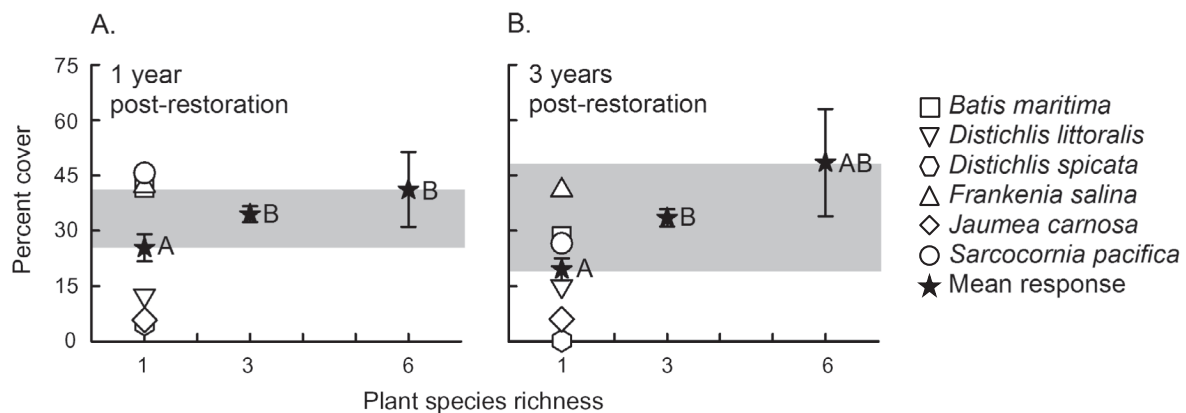

Fig. 1. Effects of salt marsh plant species richness on total percent cover in experimental plots (mean $\pm$ SE), one (A) and three (B) years post-restoration (Table 1; 1 yr: $F_{2,\ 255} = 7.65$, $P < 0.001$; 3 yr: $F_{2,\ 255} = 6.91$, $P < 0.001$; $n = 60$, 200, and 10 plots in the 1-, 3-, and 6-species groups). Plant cover did not vary consistently across tidal elevation in either analysis (Table 1; Appendix S1: Fig. S1). Width of gray horizontal bars denote the net diversity effect (difference in mean performance in 1- vs. 6-species plots) observed in a given year. Different letters denote statistically significant differences at the 0.05-level as defined by Tukey's HSD test following ANOVA.

Table 1. ANOVA summary for change in percent cover in experimental plots one and three years post-restoration.

Source	df	SS	MS	F	P
One year post-restoration					
Elevation	4	10.56	2.64	1.93	0.106
Richness	2	20.94	10.47	7.65	**0.001**
Elevation × Richness	8	3.31	0.41	0.30	0.965
Residual	255	349.20	1.37		
Three years post-restoration					
Elevation	4	19.94	4.99	2.01	0.094
Richness	2	34.32	17.16	6.91	**0.001**
Elevation × Richness	8	11.42	1.43	0.57	0.799
Residual	255	633.70	2.49		

Notes: Tidal elevation and plant species richness were treated as fixed factors. *P*-values for main effects discussed in the text are bolded.

(-3.45 ± 4.37) was not statistically different from zero ($t_4 = 0.79$, $P = 0.474$), whereas the mean effect after three years (15.18 ± 4.47) was different ($t_4 = 3.40$, $P = 0.027$). In contrast, the mean ($\pm$SE) selection effect after one year (18.98 ± 4.97) was different from zero ($t_4 = 3.89$, $P = 0.018$), whereas the mean effect after three years (14.06 ± 8.63) was not ($t_4 = 1.65$, $P = 0.175$). The relative contribution of complementarity and selection effects to the net diversity effect changed from -22% vs. 122% one year post-restoration to 52% vs. 48% three years post-restoration, respectively.

Considering change in percent cover of each plant species individually, after both one and three years most of the experimental species exhibited substantial variation with respect to tidal elevation, but not richness or their interaction (Fig. 3A, C; Appendix S1: Tables S2–S5). In both years, different species did better at specific tidal elevations (e.g., *B. maritima* low, *F. salina* intermediate, and *S. pacifica* high; Fig. 3A, C; Appendix S1: Tables S3, S5). Visualization of mean effects pooled across elevations showed
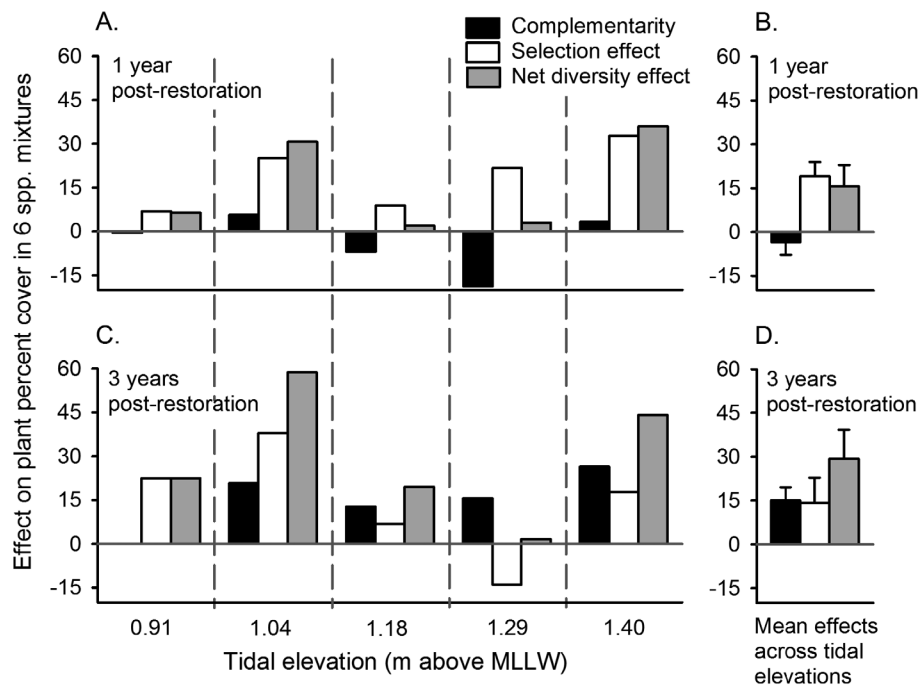

Fig. 2. Partitioning of salt marsh plant species richness effects into complementary and selection effects at five different tidal elevations (*n* = 2 experimental blocks per elevation) and mean effects ($\pm$SE) pooled across elevations one (A, B) and three (C, D) years post-restoration (Appendix S1: Table S1; all *P* > 0.692 for tests of elevation effect by response metric and year). Mean complementarity effects increased from one to three years post-restoration, whereas mean selection effects declined slightly; net diversity effects calculated as the sum of complementarity and selection effects increased over time (see also Fig. 1).
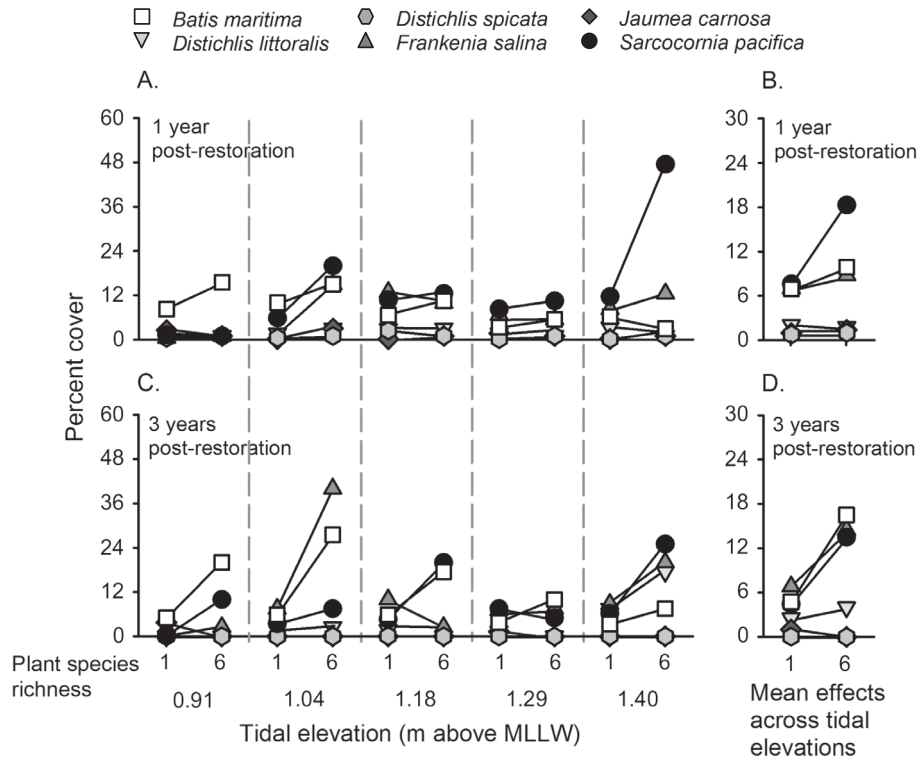
Fig. 3. Plant percent cover by species in 1- and 6-species plots at five different tidal elevations ($n = 2$ experimental blocks per elevation) and mean effects (3-species treatment group and error bars omitted for clarity) pooled across tidal elevations one (A, B) and three (C, D) years post-restoration (see Appendix S1: Tables S2–S3 for statistical analyses).

patterns consistent with a shift from selection effects to complementarity over time—*S. pacifica* in particular performed best in both monoculture and mixtures after one year, whereas several other species (*B. maritima* and *F. salina*) performed as well in monoculture and better in mixtures after three years (Fig. 3B, D).

Of the six environmental variables measured in experimental plots, sediment bulk density ($r = -0.75$, $P < 0.001$), temperature ($r = 0.66$, $P < 0.001$), redox potential ($r = 0.69$, $P < 0.001$), and salinity ($r = 0.66$, $P < 0.001$) correlated strongly with tidal elevation, whereas organic matter content ($r = -0.16$, $P = 0.008$) and C:N ratio ($r = -0.14$, $P = 0.017$) correlated only weakly (all $n = 275$–280). The first two axes from a PCA of environmental variables explained 62.6% of the variance among plots. PC 1 separated tidal elevations based on sediment bulk density, temperature, and redox potential; PC 2

was associated with organic matter content and salinity (Fig. 4A, B; Appendix S1: Table S6). Of the five leaf traits measured across species, only LMA ($r = 0.40$, $P < 0.001$, $n = 77$) was correlated with change in plant percent cover; chlorophyll *a* and *b*, photosynthetic rate, and C:N ratio were not (all $P > 0.121$). The first two axes from a PCA of leaf traits explained 76.4% of the variance among species. PC 1 separated species based on LMA and chlorophyll *a* and *b*; PC 2 was associated with photosynthetic rate and C:N ratio (Fig. 4C, D; Appendix S1: Table S7).

Mean values of PC 1 for environmental variables correlated strongly with tidal elevation after one year (Fig. 5A; $r = -0.99$, $P < 0.001$, $n = 5$ elevations); no new data were collected after three years (Fig. 5B). Mean values of PC 1 for plant leaf traits by species correlated strongly with change in plant percent cover after one year (Fig. 5C; $r = -0.85$, $P = 0.033$, $n = 6$ species), but
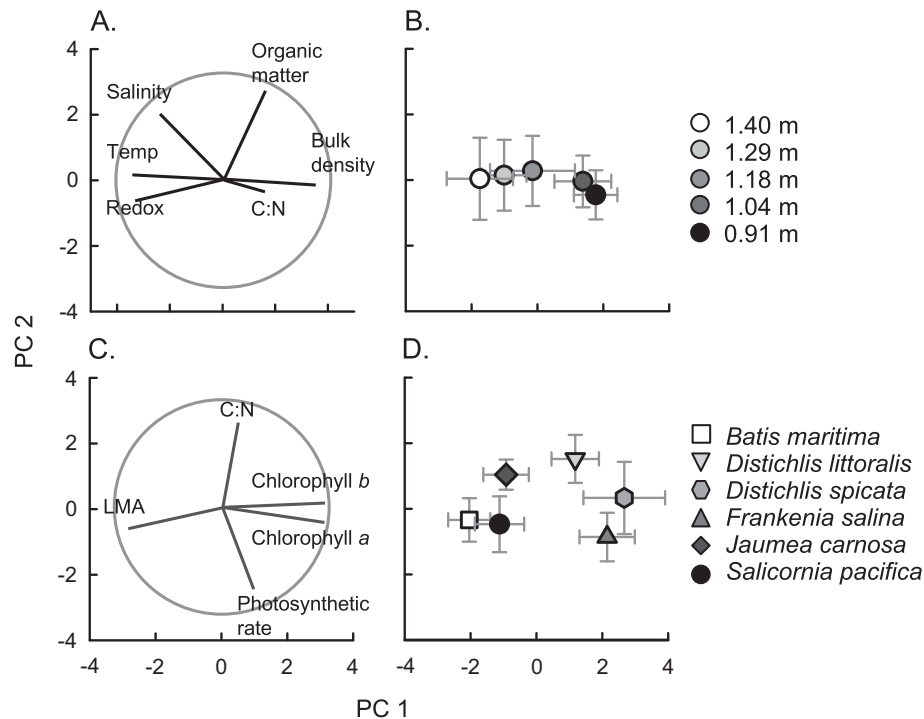
Fig. 4. Principal component analysis (PCA) ordinations of environmental conditions in experimental plots as biplot rays (A) where the length and direction of each vector are defined by its correlations with the first two principal component axes and the radius of the circle is a unit length and by tidal elevation (B) (means ± SD, $n = 45$–51; Appendix S1: Table S4); and of plant leaf traits as biplot rays (C) and by species (D) (means ± SD, $n = 6$–22; Appendix S1: Table S5).

not after three years (Fig. 5D; $r = -0.58$, $P = 0.231$).

Discussion

Introducing salt marsh plants as multispecies assemblages in a coastal wetland restoration accelerated the development of plant biomass relative to monocultures of even the most productive species. Species-rich plantings enhance biomass and nitrogen accumulation (Callaway et al. 2003, Sullivan et al. 2007), maximum height (Keer and Zedler 2004), and canopy complexity (Blair et al. 2013). Nevertheless, many restoration plans still incorporate only single-species plantings or none at all. Perhaps as a consequence, plant assemblages are among the slowest features to recover in restored wetlands and biological structure and biogeochemical functioning are consistently lower than in reference sites (Moreno-Mateos et al. 2012). Our study also provides real-world support for a recent theoretical model predicting strong positive biodiversity effects due to complementarity when functionally different species coexist in a heterogeneous landscape (Hodapp et al. 2016). One potential limitation of our study design is that while the 3-species polycultures included a diverse set of triplets, the 6-species polyculture comprised all experimental species. In other words, all plots assigned to the 6-species treatment had the exact same composition. In theory, it is possible that the positive diversity effects we saw were due to the mix of species we used, rather than to species richness, per se. We do not believe this is likely, however, given that the average percent cover of the 3-species polycultures was also significantly greater than that of the average monoculture after both one and three years.
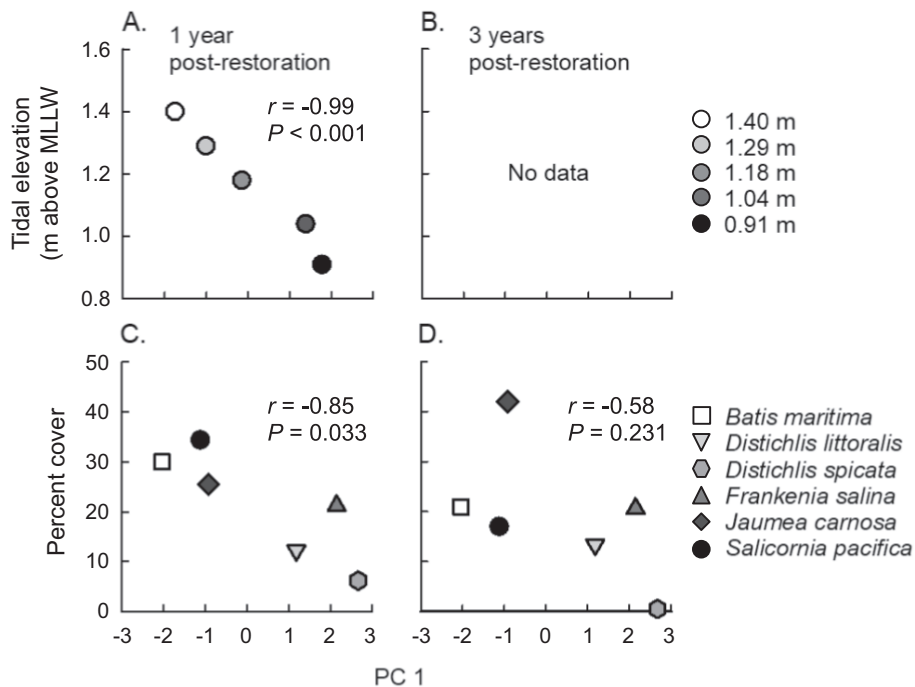
Fig. 5. Correlations between mean values of PC axis 1 of environmental data and tidal elevation (A, B; $n = 5$ elevations) and PC axis 1 of plant leaf traits and percent cover (C, D; $n = 6$ species) in experimental plots one and three years post-restoration. Note that the percent cover reported for *J. carnosa* three years post-restoration, calculated only from plots in which leaf traits were sampled, is quite a bit larger than the value calculated from all plots. Removing this point from the analysis did not change the overall result ($r = -0.60$, $P = 0.285$, $n = 5$ species); none of the other species were so affected.

The magnitude of the positive diversity effects we observed post-restoration strengthened over time, due to a combination of decreasing performance of monocultures and increasing performance of multispecies mixtures, as measured by changes in percent cover. In a comprehensive assessment of the world's largest grassland biodiversity study, Meyer et al. (2016) showed that for 50 ecosystem variables over 11 yr, species-poor communities consistently exhibited a decrease in functioning while species-rich communities exhibited a comparable increase in functioning, leading to an overall increase in the strength of positive diversity effects through time. They hypothesized that a build-up of negative plant–soil feedbacks, incomplete resource capture, and recruitment limitation contributed to deteriorating ecosystem functioning at low biodiversity (see also Marquard et al. 2013). Increasing functioning at high biodiversity was likely due to a combination of niche differentiation,

development of a more diverse soil microbial community associated with successional changes in high-diversity plant assemblages, and facilitation (Meyer et al. 2016). Increasing complementarity over time has also been invoked to explain positive diversity effects in a variety of other ecosystems (Cardinale et al. 2007, Stachowicz et al. 2008*b*). If negative feedbacks in species-poor communities take time to manifest, impacts of biodiversity loss may be substantially greater than suggested by short-term experiments (Stachowicz et al. 2008*b*, Isbell et al., 2015, Meyer et al. 2016).

Positive effects of richness in our experiment were initially due almost exclusively to selection effects—mixtures were dominated by species exhibiting high performance in monoculture (see also Cardinale et al. 2007, Stachowicz et al. 2008*a*). Short-term assembly experiments, such as ours, primarily quantify survival and growth of transplanted individuals, so that fitness

differences among species are likely to overwhelm the expression of any niche differences or facilitation (Carroll et al. 2011, Loreau et al. 2012). The identity of the highest performing species, however, differed after one vs. three years, and neither species was the most productive at all tidal elevations. Cardinale et al. (2007) calculated that across 17 biodiversity experiments with time-series data, the probability that the same species was the best performing monoculture on two consecutive dates was surprisingly low—just 0.25 (14 of 58 intervals), suggesting that over time no single species can consistently produce more biomass than a diverse mixture. Longer-term studies allow for the development of niche differences and population-level processes that include recruitment, survival, and growth of new individuals, making them more likely to show positive diversity effects (Stachowicz et al. 2008a). By the end of our study, complementarity contributed at least as much as selection effects to the generation of net biodiversity effects, indicative of niche partitioning and/ or positive interactions among species becoming relatively more important from one to three years post-restoration (Loreau and Hector 2001, Tilman et al. 2001). The increasing possibility that transgressive overyielding occurred also bolsters the idea that the strength and relative importance of multispecies complementarity increased over time (Cardinale et al. 2007, Marquard et al. 2013. While the trends of increasing diversity effects and complementarity we observed might conceivably reverse over a longer time interval (e.g., Doherty et al. 2011), the environmental variability (across tidal elevations) and natural community interactions (plots were unweeded and dead plants not replaced) inherent in our experimental design may mitigate against this possibility.

Tidal elevation is one of the most important drivers of successional development, species composition, and productivity of plant communities in coastal wetland ecosystems, as environmental conditions vary predictably across this gradient (Sullivan 2001, Zedler et al. 2001). Lower elevation sites in Colorado Lagoon experience frequent flooding (and thus soil waterlogging and hypoxia), whereas higher elevation sites exhibit high soil salinity, temperature, and porosity. Surprisingly, overall diversity effects did not differ consistently across elevations in our study; however, percent cover of individual species did. In other words, high-diversity mixtures were more productive than the average monoculture at all elevations, but the identity of the best performing species in both mixtures and monocultures differed by elevation. This may explain the observed lack of an elevation effect when considering plant species richness—the presence of all species at all elevations meant that at any given elevation, at least some species would do well. Presumably, species-specific combinations of functional traits underlie such variation (Violle et al. 2007). The two species in our study that did best one year post-restoration, *B. maritima* at low and *S. pacifica* at high elevations, were both characterized by high LMA and low leaf chlorophyll concentrations—indicative of a resource conservation strategy likely to be beneficial under stressful conditions (Wright et al. 2004). By three years post-restoration, two additional species also did well, *F. salina* at low and high and *D. littoralis* at high elevations; both were characterized by low LMA and high leaf chlorophyll concentrations and *F. salina* by high photosynthetic rates—indicative of a resource acquisition strategy more suited to benign conditions (Wright et al. 2004). Abiotic conditions in restored coastal wetlands are often quite harsh initially, such that species best suited to withstand environmental extremes are likely to have a competitive advantage. As plant cover increases, habitat amelioration due to the presence of neighbors can alter abiotic conditions enough (e.g., via shading and decreased soil evaporation) to allow less stress-tolerant species to increase in abundance (Bertness et al. 1992, Bertness and Callaway 1994, Whitcraft and Levin 2007). This suggests an additional benefit to using a diverse planting pallet—increased coverage of a broad environmental niche space by a range of functional traits.

Both the magnitude of the net diversity effects we saw and the quickness with which diverse mixtures matched or perhaps exceeded the percent cover of even the single most productive species were somewhat unexpected. Balvanera et al. (2006) found that experiments with maximum richness of fewer than 10 species (such as this one) were much less likely to find positive biodiversity effects than experiments with more

than 20. Similarly, BEF experiments typically take, on average, almost five years before transgressive overyielding begins to appear (Cardinale et al. 2007), yet we saw possible evidence for it after only three years. In natural, relatively undisturbed southern California salt marshes, only eight to ten plant species are typically present with high evenness (Zedler and West 2008, Doherty et al. 2011); nevertheless, species-specific variation among life history and morphological attributes suggest the potential for complementarity effects (Callaway et al. 2003). Confronted with substantial variation in environmental conditions across elevations, high trait diversity should facilitate niche partitioning (Hodapp et al. 2016). Nitrogen uptake by multispecies mixtures of algae has similarly been shown to increase with increasing environmental heterogeneity, due primarily to complementarity (Mandal et al. 2018). Of course, trait variation can provide useful generalizations beyond just BEF patterns, informing our understanding of how environmental change will alter ecosystem functions (Suding et al. 2008), resource use by native vs. invasive species (Funk and Wolf 2016), and community assembly rules (Reich 2014).

Understanding how environmental and species trait variability interact to influence the complementarity and selection mechanisms underlying positive diversity effects should lead to better management decisions and more successful restoration outcomes (Perring et al. 2015). The key question is how to do this, particularly in light of anticipated climate change that sets a moving target for resource managers (Lipton et al. 2018, SCWRP 2018). One possible approach is a trait-based response-and-effect framework for determining how community structure and dynamics will influence ecosystem processes under changing environmental conditions (Suding et al. 2008). Response traits are those that respond to environmental change, whereas effect traits impact ecosystem function. By explicitly focusing on functional rather than compositional goals, a trait-based restoration framework may lead to communities that are more resilient to future perturbations (Funk et al. 2008, Laughlin 2014). Experimental investigations of trait-based model performance considering a range of functional targets in different ecosystems will be a key tool for confronting the increasingly pressing ecological challenge of addressing reductions in biodiversity and associated effects on ecosystem functions.

To better inform restoration policies and practices, a logical next step would be to determine how known BEF relationships provide insight into the mechanisms underlying variation in community composition and ecosystem function (Hillebrand and Matthiesen 2009, Messier et al. 2010). Resource managers of degraded habitats are typically confronted with the goal of increasing ecosystem performance in low diversity systems; restoration projects therefore represent a possibly underutilized opportunity to explore BEF theory. We suggest that, in general, a sustainable restoration plan would incorporate more diverse plantings in lieu of the most productive monoculture. Ultimately, incorporating BEF concepts into broader restoration policies may provide an opportunity to protect communities from species loss and buffer against reduced functionality of restored habitats, even if we do not yet fully understand the specific mechanisms to target (Perring et al. 2015, Moreno-Mateos et al. 2017, Hughes et al. 2018).

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DATA AVAILABILITY

Data are available from Zenodo: http://doi.org/10.5281/zenodo.4780663.

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3664/full