ABSTRACT

THE RELATIONSHIP BETWEEN BIODIVERSITY AND ECOSYSTEM FUNCTION IN A COASTAL WETLAND

By

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Despite reductions in species diversity, few studies in wetlands investigate the relationship between biodiversity and ecosystem function (BEF). My research explores the BEF relationship in a recently restored salt marsh in Long Beach, California. I hypothesized that: (1) increasing plant diversity would result in higher primary productivity and decreased recruitment of native salt marsh plants, (2) observed variation in responses would be correlated with species-specific variation in individual demographic parameters, and (3) variation in demographic parameters and resulting ecosystem processes would be correlated with functional traits. I found that while survival over one year was correlated with elevation, overall percent cover and recruit species richness were positively affected by diversity. Performance patterns reveal variation by species in photosynthetic rate, leaf mass per area and chlorophyll a/b ratios. After one year, I found that the overall diversity patterns were driven by selection effect compared to complementarity.

THE RELATIONSHIP BETWEEN BIODIVERSITY AND ECOSYSTEM FUNCTION IN A COASTAL WETLAND

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CHAPTER 1

INTRODUCTION

Coastal areas such as estuaries and wetlands have been termed critical transition zones (CTZs) because they connect terrestrial, freshwater and oceanic habitats. CTZs perform many key ecosystem functions that include primary production, biogeochemical cycling, provisioning of habitat via biogenic structure, sediment stabilization, and mediation of water flow (Teal, 1962; Levin et al., 1996; Talley and Levin, 1999; Levin et al., 2001; Ewel et al., 2001). Stachowicz et al. (2007) define ecosystem functions to be aggregate aspects of the ecosystem that carry no intrinsic value to humans (which would instead be classified as services), while Christensen et al. (1996) define them to be the interaction of material and energy cycling with organismal relationships. Hooper et al. (2005) report that ecosystem function has often been limited to just include ecosystem properties (e.g., carbon storage), excluding ecosystem goods (e.g., medicines, animal breeding) and services (e.g., regulating climate). For the purposes of this study, I will be focusing on several ecosystem functions (i.e., primary productivity and recruitment) that fall under the more restrictive definition of Hooper et al. (2005).

Since the overall functioning of CTZs affects so many different habitats and organisms, conserving and restoring them is a crucial priority for natural resource

managers. Unfortunately most wetlands world-wide have been degraded to some extent which is associated with reductions in ecosystem functions (Zedler et al., 2001; Hooper et al., 2005); specifically in California, over 90% of original wetlands have been lost or degraded (Dahl, 1990; Zedler et al., 2001). Loss of habitat is often associated with a reduction in species diversity (Tilman et al., 1997; Hooper et al., 2005; Cardinale et al., 2006; Tilman et al., 2006; Stachowicz et al., 2007). This is likely to be of particular concern in wetlands, which are low diversity systems even when fully intact (Zedler et al., 2001; Callaway et al., 2003; Zedler and West, 2008). Restoration is a common tool used to counteract these alterations, with the main goal being to restore target functions or species to a particular habitat. I am investigating how two common restoration techniques, active planting and passive recruitment, differ in how they affect the overall success of restoration, particularly with respect to primary productivity and plant species recruitment.

The species diversity of a community, especially primary producers, is believed to provide the basis for many critical habitat functions. Biodiversity in this context typically refers to the number of species in a community (richness), the distribution of their relative abundances (evenness), and variation in their functional traits (Hooper et al., 2005) which are defined as traits that influence both species responses to environmental conditions as well as influencing ecosystem properties themselves, i.e., response and effect traits (Hooper et al., 2005; Suding et al., 2008). Many studies in terrestrial systems (e.g., Tilman et al., 1997; Tilman, 1999; Hector et al., 1999; Dukes, 2002; Hector et al., 2002; Kennedy et al., 2002; Tilman et al., 2006; Balvanera et al., 2006; Lanta and Leps,

2006; Bai et al., 2007; Thompson et al., 2011) and somewhat fewer in marine systems (e.g., Stachowicz et al., 1999; Reusch et al., 2005; Bruno et al., 2005; Stachowicz et al., 2007) have documented that increases in biodiversity are positively associated with important ecosystem functions (e.g., primary productivity), suggesting that loss of biodiversity will be a potential problem with respect to maintenance of those functions. Unfortunately, until recently almost no studies have been conducted in coastal salt marshes characterized by intrinsically low plant diversity (but see Zedler et al., 2001; Callaway et al., 2003; Zedler and West, 2008), raising the question of whether we can expect to see the same pattern in that system.

This relationship underlies the so-called Biodiversity-Ecosystem Function (BEF) theory. Given the important consequences of biodiversity in terrestrial and marine habitats, extending the theory of BEF to wetlands will provide additional insight into the generality of this relationship. Net diversity effects can be quantitatively partitioned into different species interaction responses: complementarity and selection (Loreau and Hector, 2001). This approach separates the two effects on the basis of an additive partitioning analogous to the Price equation in evolutionary genetics (Price, 1995). Complementarity is the unexpected additive performance of a species in a mixture, compared to its performance in a monoculture, whereas the selection effect refers to the probability that a higher performing species is included (or excluded) from a mixture as diversity increases (Stachowicz et al., 2007). Determination of the role of complementarity versus selection in any BEF study is important to correctly determine which mechanisms cause correlations between biodiversity and ecosystem processes.

Complementarity has been found to be more dominant than selection in a decade-long grassland experiment (Tilman et al., 2006) and in 1-3 year long field experiments in marine systems (Stachowicz et al., 2007; Stachowicz et al., 2008). In contrast, selection effects seem to dominate in shorter-term field experiments or mesocosm experiments, presumably because lack of time or habitat heterogeneity has precluded the development of facilitative interactions among species (Stachowicz et al., 2008).

Many studies have shown that as the diversity of a system increases, so too does the overall utilization of resources, often leading to higher levels of primary production (Tilman et al., 1996; Bracken and Stachowicz, 2006; Zedler et al., 2001; Keer and Zedler, 2002). In coastal wetlands on the west coast of North America, as plant species diversity increased so did productivity, but recruitment into experimental plots decreased, presumably due to a lack of available resources for juvenile plants (Zedler et al., 2001; Callaway et al., 2003; Sullivan et al., 2007; Bonin and Zedler, 2008; Doherty et al., 2011). Beyond species diversity, species identity can also have large effects on the overall functioning of a community (Symstad et al., 1998; Diaz and Cabido, 2001; Engelhardt and Kadlec, 2001; Lavorel and Garnier, 2002; Keer and Zedler, 2002; Callaway et al., 2003). Walker (1992) suggests that the redundancy of certain species is the key to a well-functioning ecosystem (see also Tilman et al., 1996; Steudel et al., 2011). Other studies (e.g., Funk et al., 2008) suggest instead that it is the redundancy of certain traits that may be most important. If it is the trait that enhances function, rather than the presence of a particular species, including individuals with specific traits is more important to restoring the habitat than is the identity of any particular species.

Studying such traits (e.g., plant height, leaf nitrogen content) in high and low performing habitats to connect productivity with individual plant abilities has gained considerable attention in recent years (Lavorel and Garnier, 2002; Callaway et al., 2003; McGill et al., 2006; Funk et al., 2008; Berg and Ellers, 2010; Doherty et al., 2011). According to McGill et al. (2006) and Berg and Ellers (2010), the traits of a species determine their fundamental and realized niches and thus these traits are key to determining how species outcompete for or co-occupy resources. To successfully restore disturbed ecosystems, we have to understand the relationships between diversity, species identity, functional traits, and the ecosystem processes we wish to reproduce.

Here I focus on how BEF relates to two key ecosystem functions: primary productivity and plant species recruitment in a restored coastal wetland. By manipulating local salt marsh plant diversity, my research was designed to address three specific hypotheses. First, that increasing plant species diversity will result in increased primary productivity and decreased plant recruitment in experimental plots. Second, that observed species-specific variation in individual demographic parameters (e.g., survival and growth) will be correlated with variation in plot-level responses. In other words, plant species identity will be an important explanatory variable for interpreting differential levels of ecosystem function in experimental plots. Finally, that variation in plant demographic parameters and resulting ecosystem processes among treatment groups at a given level of species richness will be correlated with species-specific plant functional traits.

CHAPTER 2

MATERIALS AND METHODS

Study Site

My study was conducted at Colorado Lagoon (CL), an urban wetland in Long Beach, California, USA (Fig 1). This lagoon and the surrounding intertidal area recently underwent an extensive restoration including removal of contaminated sediments and increase in tidal flow to nearby Alamitos Bay.

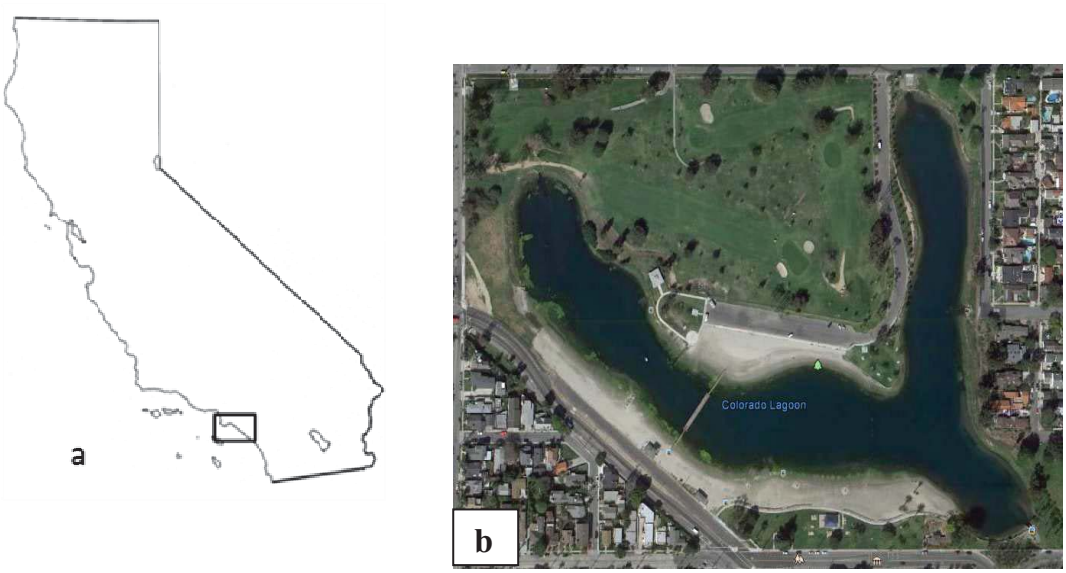

FIGURE 1. Site location: a) California, USA and b) Colorado Lagoon, Long Beach, California, USA. Images courtesy of Google Earth.

Based on primary literature (Bonin and Zedler, 2008; Callaway et al., 2003; Doherty et al., 2011; Sullivan et al., 2007; Zedler et al., 2001) and prior research by California State University at Long Beach (CSULB) graduate student Emily Blair (Blair et al., 2013), I selected the following six native marsh intertidal plant species for inclusion in experimental plantings (Table 1): *Batis maritima* (saltwort; "Bama"), *Jaumea carnosa* (salty susan; "Jaco"), *Distichlis spicata* (saltgrass; "Disp"), *Distichlis littoralis* (shoregrass; "Dili"; formerly *Monanthochloe littoralis), Frankenia salina* (alkali heath; "Frsa"), and *Sarcocornia pacifica* (pickleweed; "Sapa"). These species are common in southern California salt marshes and are often used in active restoration projects.

TABLE 1. Life History and Growth Factors of Six Halophytes

Metrics		Bama	Jaco	Disp	Dili	Frsa	Sapa
Life span	Perennial	x	x	x	x	x	x
Growth form	Succulent	x	x				x
	Upright			x	x	x	x
	Grass			x	x		
	Trailing	x	x				
	Broad-leafed					x	

Note: Modified from Zedler et al., 2001.

I chose not to use *Cressa truxillensis* (alkali weed) or *Isocoma menziesii* (goldenbush), both native marsh species, as Blair et al. (2013) observed high mortality of transplanted individuals in their study.

Experimental Design

I established ten experimental blocks at CL, each containing 28 plots to which treatments were randomly assigned. Each plot (60 cm x 75 cm) contained 18 plants in

standardized positions within the plot for a total of 280 plots and 4,860 plants. Due to limited space and to assess elevation effects, blocks were stacked across tidal heights: 2.98–4.72 ft. above mean low low water (MLLW; reported as "feet" throughout the rest of the document) instead of being placed end to end in one horizontal transect. I used a surveyor's rod and transit level to measure block-specific elevations. All blocks were placed within the middle marsh area (mid-intertidal zone), as defined by Josselyn (1983) to be from mean high water (MHW) to mean higher high water (MHHW). Plots in each block were comprised of six monocultures (1spp), 20 three-species polycultures (3spp; 19 of the 20 possible unique combinations), a six-species polyculture (6spp) and an unplanted control (0spp). As one three-species combination was unintentionally duplicated, not all possible unique combinations were compared for this study.

To generate experimental plants, four of the six species (Sapa, Bama, Jaco, Frsa) were grown in 2" pots in the CSULB greenhouse from field cuttings over summer 2012. The two grasses (Disp and Dili) were purchased from the Tree of Life Nursery (San Juan Capistrano, California; http://www.californianativeplants.com) and then split and propagated at CSULB. Initial planting in CL occurred between October and November 2012. Each plot was planted with 18 plants, in alternating rows of 4 or 3 individuals (Fig 2) with14.8 ml of the slow release fertilizer, Osmocote©, in each hole.

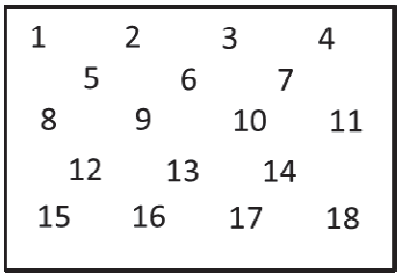

FIGURE 2. Experimental plot design. Each plot contained 18 planted individuals and was aligned with the water on the left side of the plot.

Due to high mortality within two weeks of initial planting, all dead individuals were replaced during a supplementary planting period between December 2012 and January 2013. Initial measurements were taken six weeks after the supplementary planting was completed (February 2013). Plants were not directly watered over the course of the experiment; however non-experimental plants above the plots were watered throughout the study with fresh water and this did trickle down to some blocks. Data on several biotic and environmental parameters were collected at regular intervals throughout the course of this experiment (Table 2).

Biological Measurements

Except for survival, which was recorded for all individual plants, plant traits were measured on a subset of the plants in each plot. Individual-level traits collected included maximum and average plant height, photosynthetic rate, leaf mass per area (LMA), leaf nitrogen content (C/N), and leaf chlorophyll a/b ratio (Table 2). Plot level traits included percent cover, canopy complexity, and recruitment. Plots containing *S. pacifica*, the

TABLE 2. Biological and Environmental Metrics

Sampling Data	Metrics
Feb'13, Apr'13, May'13, Jul'13 (i.e., 6WAT, 12WAT, 18WAT, 24WAT)	• Individual Survival • Recruitment: Abundance, Richness
Feb'13, Aug'13, Feb'14 (i.e., 6WAT, 28WAT, 58WAT)	• Percent Cover, Percent Open space • Maximum and Average Plant Height (6 of 18 plants per plot) • Soil Cores: Salinity, Bulk Density, OM, C/N • Light Reduction by plant canopy • Soil Temperature
Feb'14 (58WAT)	• Canopy Complexity • Photosynthetic Rate • Leaf Samples: C/N, LMA, Chl a/b • Soil Redox Potential

Note: OM = Organic Matter, C/N = Carbon to Nitrogen ratio of soil and leaf samples, LMA = Leaf mass per area, Chl = Chlorophyll a/b.

dominant marsh plant species in this system, will be referred to as S+ going forward, while plots without will be referred to as S- (i.e., plots lacking the marsh dominant). Planted species refers to the six experimental (i.e., initial) species – *B. maritima, J. carnosa, D. spicata, D. littoralis, F. salina,* and *S. pacifica*. Non-planted species refers to any species other than the six experimental species. Plant traits were analyzed for two sets of plants: those collected from all plots and those associated with the subset of plants with photosynthetic measurements ("subset").

All individuals planted at the beginning of the experiment were tagged to allow for monitoring of survival and growth for the first six months, after which measuring

survival and growth at the individual level was no longer possible. To determine survival, each plant was recorded as alive, dead or missing at each sampling time point. Cumulative survival over a year is referred to as survival unless otherwise noted and was analyzed without overgrown plots (those where individual survival was no longer possible to determine due to the high amount of biomass present). For these plots, percent cover by species was recorded in lieu of individual survival. Percent cover was reported for each species, as well as plot open space, using the Daubenmire cover class method, where 0-20% equal class 1, 20-40% equals class 2…80-100% equals class 5 (Daubenmire 1959).

Canopy complexity was assessed at the four corners and in the middle of each plot. At each point, complexity was estimated by measuring maximum and average plant height which were binned into four levels: low = 0-5 cm; medium = 5-25 cm; high = 5-25 cm; and tall = 25+cm. Maximum plant height and average height were recorded to the nearest 0.5 cm on a subset of plants in each plot. Species recruitment was determined by counting the number of new and untagged shoots in each plot. All new shoots were identified to lowest taxonomic level possible and their native vs. non-native status recorded. Cumulative recruitment (abundance, richness) over six months is referred to as recruitment abundance and richness unless otherwise noted.

Photosynthetic rate was measured on individuals across species and elevations with a LI-COR LI-6400XT Portable Photosynthesis System (LI-COR Biosciences, Lincoln, NE) in the field (across site elevations) and in the CSULB greenhouse. I collected all measurements at the same photosynthetic active radiation (PAR) level of

1800 nm, at 400 µml CO_2, at ambient conditions of humidity and temperature, and between 10:00-14:00 each day so measurements could be compared directly (J. L. Funk, pers. comm.). Photosynthetic rate was scaled for percent of leaf in chamber and referred to just as photosynthetic rate going forward unless otherwise noted.

Two sets of leaves were initially collected from the 1st (larger) subset of plants and used for three different analyses. One set of leaves was used to analyze both nitrogen and LMA (these leaves were dried) and the other was used for chlorophyll analysis (these leaves were frozen at -80°C). Separately, two sets of leaves were collected from individuals with associated photosynthetic data (i.e., subset) to analyze nitrogen, LMA, and chlorophyll content. Every attempt was made to select leaves of the same approximate size and from the same section of the plant. Leaves at the top of the plant were not sampled.

Leaf nitrogen content was determined by processing samples in an elemental analyzer (Costech 4010, Pioltello, Italy). Leaves were dried at 60°C and ground to pass a 40-mesh screen using a Wiley mill. Samples were dried once more before being placed in tin foil boats and sent for analysis at Chapman University (Orange, California). I used an apple leaf standard with 2.25% nitrogen. Leaf mass per area (LMA) was determined by scanning leaves with a flatbed scanner to create a digital image, calculating leaf area with ImageJ (U.S. National Institutes of Health, Bethesda, MD; http://imagej.nih.gov/ij/) and then drying the leaves at 60°C for three days before determining dry mass on a Denver Maxx portable balance to 0.001g. Leaf chlorophyll content was determined by thawing frozen leaves, in the dark, overnight at room temperature to determine mass,

grinding the leaves and extracting chlorophyll with 10mL of 100% acetone (Lichtenthaler, 1987). Leaf extract was then centrifuged and a spectrophotometer was used to determine absorbance at 646nm and 663nm, following the protocol reported by Bonin and Zedler (2008). Chlorophyll a, b and their ratio (a/b) was calculated as in Lichtenthaler (1987).

Net diversity using total percent cover after a year was partitioned into complementarity and selection effects for the 6spp plots, as described in Loreau and Hector (2001): $\Delta Y = N\,\overline{\Delta RY}\,\overline{M} + N\,cov(\Delta RY, M)$. The observed yield of the monoculture (1spp) plots was used to determine the expected yield of the polyculture (6spp) plots to assess diversity effects. If there is no difference between expected and observed yield of species in polyculture, based on monoculture yield, then there would be no evidence that increased diversity affected percent cover. If there is a difference in polyculture yield, be it positive or negative, the analysis provided by Loreau and Hector (2001) allows a comparison to determine which process drives the observed effect of diversity, complementarity or selection.

Environmental Measurements

A two-cm deep soil core (31.4 cm^3) was collected haphazardly within each plot. Samples were put on ice in the field and stored at -20 ºC until processed. From these cores, measurements of porewater salinity, bulk density, organic matter and C/N ratio were collected. Porewater salinity was measured using the paste method (Richards, 1954). Bulk density was determined by drying a known volume of soil to determine the

dry mass; bulk density is a measure of sediment compaction (Richards, 1954) and is presented as mass per volume.

Soil temperature (˚C) was taken of the top 2 cm of sediment at haphazard locations within each plot using a Fisher Scientific Thermocouple 15-077-14 Traceable Thermometer. Light readings (PAR; $\mu mol/m^{-2}/s$) were taken at the four corners and the middle of each plot with a LI-190 quantum sensor and LI-250A light meter (LI-COR Biosciences, Lincoln, NE). When a canopy was present, above and below canopy light readings were collected. Light reduction, reported as a percentage, was then calculated by determining the differences in light intensity above and below the canopy at each corner and in the middle of the plot. Redox potential was measured haphazardly within each plot using a Mettler Toledo Five Easy Five Go pH meter (FE20/FG2).

Organic matter (OM) was determined by combusting soil samples at 550°C for two hours in a muffle furnace in the Institute for Integrated Research in Materials, Environments, and Society (IIRMES) facility on campus. The difference in weight of each sample was recorded before and after combustion as it is assumed that the mass difference is representative of the amount of organic carbon in the sediment (Robertson, 2011). About 13-15 mg of sediment was used to quantify sediment percent carbon and nitrogen and their ratio (C/N). The carbon to nitrogen ratio of sediment is widely used as an index of sediment quality and correlates with decomposition rates; high C/N ratios indicate sediments that are dominated by immobilization (versus mineralization) and thus have slower decomposition rates (Megonigal et al., 2004). Samples were dried at 50°C for 24 hours, then ground to a uniform grain size and placed in pre-combusted tin boats

and analyzed for carbon and nitrogen concentrations using a CHN elemental analyzer (Costech 4010, Pioltello, Italy). I used a soil standard with 2.01% carbon and 0.192% nitrogen.

Data Analysis

All univariate statistical analyses were done with Minitab 16 software. All multivariate statistical analyses were done with PRIMER 6 software. Data were tested for normality and equal variances and were log-transformed as necessary. Data were compared among diversity treatments, species identity, and/or across elevations using two-way analyses of variance (ANOVAs). Statistically significant differences among treatment groups were identified with Tukey's HSD pairwise comparisons tests.

Plots that contained *S. pacifica* (S+) and plots that lacked *S. pacifica* (S-) were compared in order to analyze the effect of the marsh dominant. Two-way ANOVAs were run with elevation and ± *S. pacifica* as factors. The following response variables were evaluated with two-way ANOVAs including elevation and treatment and their interaction as factors: aggregate and species-specific survival; aggregate and species-specific percent cover; canopy complexity; average and maximum plant height; recruitment (abundance and richness of both planted and non-planted species); LMA; and all environmental metrics. Percent cover within elevation was analyzed with treatment and species and their interaction as factors. The following response variables were evaluated with two-way ANOVAs including elevation and species and their interaction as factors: species-specific photosynthetic rate; leaf C/N; LMA (subset). Photosynthetic rate and LMA (subset) were analyzed with location and species and their interaction as factors.

Leaf chlorophyll ratio (subset) was analyzed with species and treatment and their interaction as factors. All analyses were not conducted with the same factors (e.g., elevation, species) due to leaf sampling.

A multivariate analysis was conducted on the following leaf traits which are important to survival and percent cover using principle components analysis (PCA): photosynthetic rate, LMA, leaf chlorophyll a and leaf chlorophyll b. Pearson correlation coefficients were generated to evaluate linear associations between survival and percent cover with leaf traits and principle components.

Species-specific observed and expected yields were determined for both monocultures and polycultures using aggregate percent cover at 58 weeks after planting as described in Loreau and Hector (2001). Net diversity effects were calculated and partitioned into complementarity and selection effects (Loreau and Hector, 2001):

$$\Delta Y = N\,\overline{\Delta RY}\,\overline{M} + N\,cov(\Delta RY,\, M)$$

Net diversity effect (ΔY) is the deviation from the total expected yield in mixture. In the 6spp plots, deviation from the expected relative yield was determined for each species (ΔRY_i) and compared to the species-specific yield in monoculture (M_i).

CHAPTER 3

RESULTS

Biological Measurements

Survival

Aggregate survival, cumulative for the experiment, differed statistically by elevation but not by planting diversity (Fig 3, Table 3). Survival was lowest at 2.98 ft. (the lowest elevation) compared to higher elevations. The interaction between diversity and elevation was not significant. There were differential patterns of survival among species, compared to the aggregate pattern (Fig 4, Table 3). There were statistically significant interactions between diversity and elevation for *J. carnosa*, *D. spicata*, and *F. salina* (Fig 4b, 4c & 4e), and perhaps for *D. littoralis* ($p = 0.055$; Fig 4d). *Batis maritima* survival differed by elevation, with higher survival in plots below 3.86 ft. (Fig 4a), while *S. pacifica* survival differed both by elevation and treatment, with highest survival at elevations greater than 3.86 ft. (Fig 4f).

Plot Level

Aggregate percent cover at one year after planting was significantly higher in initially higher diversity plots (3 and 6 spp) than control and initially lower diversity plots (0 and 1 spp), but did not differ significantly by elevation (Fig 5, Table 4). There was no interaction between elevation and treatment. Percent cover, within elevation, was

significant for both diversity treatment and species at the 0.05 level, except at 3.40 ft. where only species was significant (Figure 6, Table 4). The interaction between treatment and species was not significant at any elevation (Table 4). At 2.98 ft. overall percent cover was higher in the 6spp plots compared to the 1spp plots and *B. maritima* had statistically more cover than *D. littoralis* or *D. spicata* (Fig 6a). At 3.40 ft. *B. maritima* and *F. salina* had significantly higher cover than *D. littoralis, J. carnosa* and *D. spicata* (Fig 6b). At 3.86 ft. overall percent cover was higher at the 3 and 6spp plots compared to the 1spp plots and *F. salina* and *S. pacifica* had statistically more cover than *D. littoralis, D. spicata,* and *J. carnosa* (Fig 6c). At 4.22 ft. overall percent cover was higher in the 6spp plots compared to the 1spp plots and *S. pacifica* had statistically more cover than *D. littoralis, J. carnosa and D. spicata* (Fig 6d). At 4.59 ft. overall percent cover was higher in the 3 and 6 spp plots compared to the 1spp plots and *S. pacifica* had significantly more cover than *B. maritima, D. littoralis, D. spicata* and *Jaumea carnosa* (Fig 6e).

There was a statistically significant interaction between elevation and plots containing or lacking *S. pacifica* (S+, S-, respectively) for percent cover (Fig 7, Table 4). Percent cover was significantly higher in S+ plots at the elevations 3.86 and 4.59 ft. compared to at the lowest elevation (i.e., 2.98 ft.) and in S- plots at 4.22 ft.

Species-specific percent cover varied by elevation and diversity except *J. carnosa*, which did not vary significantly with either parameter (Fig 8, Table 5). The interaction of elevation and treatment was significant only for *D. spicata*. *Batis maritima* had higher cover in the 1spp treatments compared to the 3spp and 6spp treatments and

statistically lower cover at the highest elevation at 4.59 ft. (Fig 8a). *Distichlis littoralis* had highest cover in the 1spp treatments compared to the 3spp and 6spp treatments (Fig 8d). *Frankenia salina* had significantly higher cover in the 1spp plots compared to the 6 spp plots and statistically lower cover at the lowest elevation at 2.98 ft. compared to the elevations at 3.40, 3.86 and 4.59 ft. (Fig 8e). *Sarcocornia pacifica* had significantly lower cover at the lowest elevation (at 2.98 ft.) compared to the elevations above 3.86 ft. (Fig 8f).

Canopy complexity and average and maximum plant heights were significantly different across elevation, but not among treatments (Fig 9, Table 6). The interaction of elevation and treatment was not significant for any of the response variables. Plots located at the lowest elevation at 2.98 ft. were the least complex and had the lowest average and maximum plant heights compared to other plots (Fig 9a, 9c, 9e). Plots that contained *S. pacifica* had on average more canopy layers and were taller than plots without *S. pacifica* (Fig 9b, 9d, 9f).

Twelve weeks after planting, there were differences in the abundance recruits of planted species by treatment, with the 1spp and 3spp treatments having more recruits compared to the 0spp treatments (Fig 10a, Table 7). The 6spp treatments were not different from the other treatments, due to high variability among plots. There were no significant interactions between elevation and treatment for either the planted and non-planted species recruit abundance. There were significant differences in richness of recruits of planted species across elevation and among treatments (Fig 10e & 10f, Table 7). The 3spp and 6spp treatments had higher recruit richness of planted species than the

1spp treatments, which had higher recruit species richness than the 0spp treatments (Fig 10e, Table 7). There was no interaction between elevation and treatment. There were no differences in recruit species richness of non-planted species across elevation or treatment, nor a significant interaction (Fig 10g & 10h, Table 7).

Individual Level

Photosynthetic rate was different among species and between locations (greenhouse and field; Fig 11, Table 8). The interaction between location and species was not significant. All rates were higher in the greenhouse compared to the field but the difference between photosynthetic rate at the two locations varied by species. *Frankenia salina* had higher photosynthetic rates than *D. littoralis, B. maritima,* and *J. carnosa* (Fig 11, Table 8).

In the field, species' photosynthetic rates were different from each other, but not across elevation (Fig 12, Table 8). Due to sampling limitations, the interaction of elevation and species could not be tested. *Frankenia salina* had higher photosynthetic rates on average than *B. maritima* and *J. carnosa*; however they were not different from those of *S. pacifica, D. spicata,* or *D. littoralis* (Fig 12, Table 8). Preliminary data from leaves also sampled for photosynthetic rate suggest that leaf C/N ratios are different by species but not across elevation (Fig 13, Table 8). *Jaumea carnosa* had higher C/N ratios compared to *B. maritima, S. pacifica* and *F. salina*.

LMA differed among species, but not across elevation or treatment (Fig 14, Table 8). On average *F. salina* and *D. littoralis* had significantly smaller LMA ratios than *S. pacifica, D. spicata, B. maritima* or *J. carnosa* (Fig 14, Table 8). LMA ratios of the

subset differed by species, with *S. pacifica* having higher C/N ratios compared to *F. salina, D. littoralis* and *D. spicata.* There were no statistically significant differences between locations (i.e., the field and greenhouse) and no significant interaction between species and location (Fig 15, Table 8). In the field, there were no differences between elevations (Fig 16, Table 8). The interaction could not be tested. An outlier more then 2 standard deviations from the mean was removed (Fig 16, Table 8).

The interaction between species identity and location (i.e., the field and greenhouse) was statistically significant in preliminary analysis of the leaf chlorophyll a/b ratios in the subset of individuals (Fig 17, Table 8). *Sarcocornia pacifica* in the greenhouse and *F. salina* in the field had higher chlorophyll ratios compared to *B. maritima* (in the field and in the greenhouse) and *J. carnosa* and *D. spicata*, in the field (Fig 17). While there were no statistical species specific differences between field and greenhouse locations, *B. maritima* and *D. littoralis* field chlorophyll a/b ratios were higher than the greenhouse ratios (Fig 17). In the field, chl a/b ratios were significantly different among species, but not diversity treatments (Fig 18, Table 8). Due to sampling limitations, differences across elevation could not be tested. *Frankenia salina* had higher chlorophyll a/b ratios than *B. maritima, J. carnosa, D. spicata* and *D. littoralis* (Fig 18).

The first two components explained 79.9% of the variance (Fig 19, Table 9). Axis 1 separated species based on chlorophyll a and chlorophyll b. Axis 2 separated species based on photosynthetic rate and LMA. Leaf traits represented by PCA axis 2 correlated strongly with survival ($r = 0.835$; $P = 0.039$; Fig 20) and percent cover ($r =$

0.921; $P = 0.009$; Fig 21). Leaf traits represented by PCA axis 1 did not correlate with survival or percent cover.

Net Diversity

Net diversity effects varied across elevation and were driven largely by selection effects, not complementarity (Fig 22).

Environmental Measurements

Soil salinity, bulk density and temperature varied significantly with elevation (Fig 23a-c, Table 10&11). Six weeks after planting, plots with the highest salinity and highest bulk density were found at 4.59 ft. (Fig 23a & 23b) as compared to all other lower elevation plots. The plots with the lowest soil temperature were found at 3.40 ft. (Fig 23c) as compared to other elevations. Fifty-eight weeks after planting, plots with the highest salinity extended from 4.22 to 4.59 ft. instead of being confined to the highest elevation at 4.59 ft. (Fig 23a), while sediment in plots at 2.98 and 3.40 ft. had the highest bulk density (Fig 23b). Plots with the highest soil temperatures were found at between 3.86 and 4.59 ft. (Fig 23c).

Light reduction by the plant canopy did not vary significantly across elevation or treatment but the pattern of reduction changed over the course of the experiment (Fig 23d). Fifty-eight weeks after treatment, elevations located above 3.40 ft. tended to have higher light reduction values compared to the lowest elevation at 2.98 ft. (Fig 23d). Percent sediment organic matter did not differ significantly by elevation or treatment; however overall sediment organic values were higher by the end of the experiment (Fig 23e). Fifty-eight weeks after planting, soil redox potential was significantly higher in

plots at 4.22 and 4.59 ft. and lowest at 2.98 ft. (Fig 23f). Sediment C/N was not significantly different among elevations or treatments (Fig 23g). There was no interaction between elevation and treatment for any of the environmental factors.

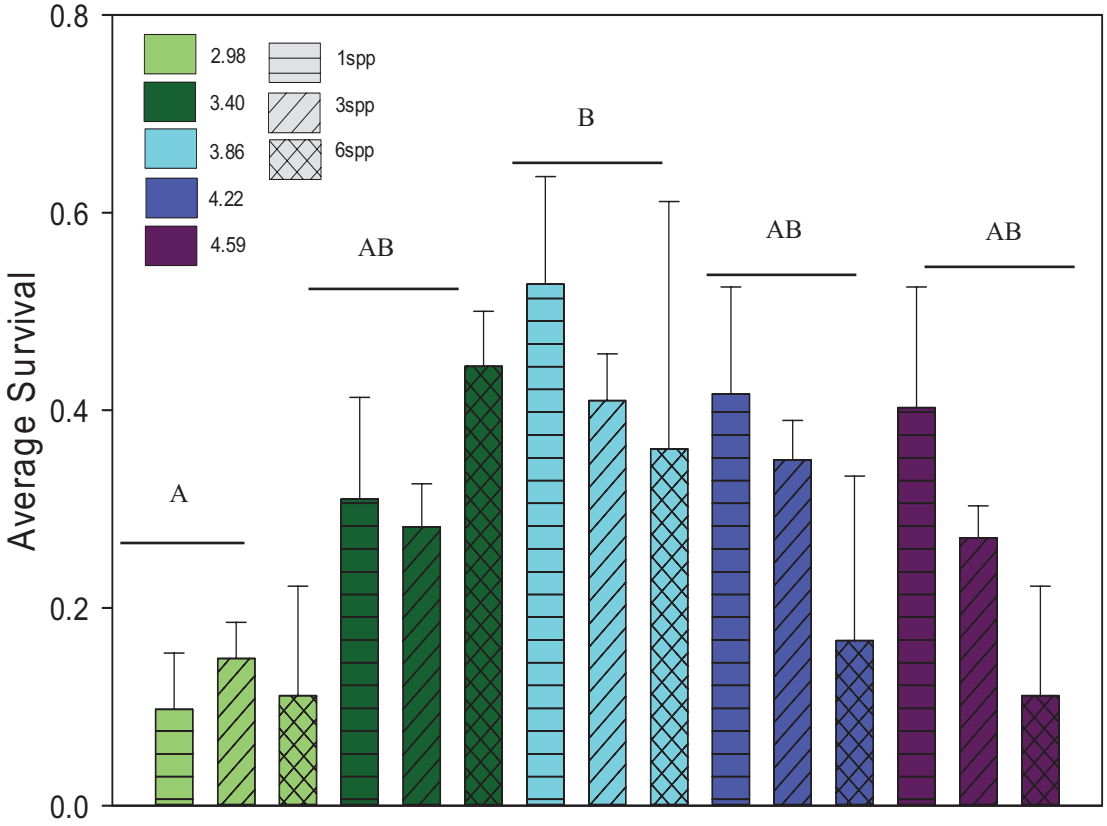

FIGURE 3. Mean (± 1 SE) aggregate survival: across elevation and treatment (n = 280 plots). Differences among elevations (measured in feet) as determined by Tukey's pairwise comparison tests are represented by different letters.

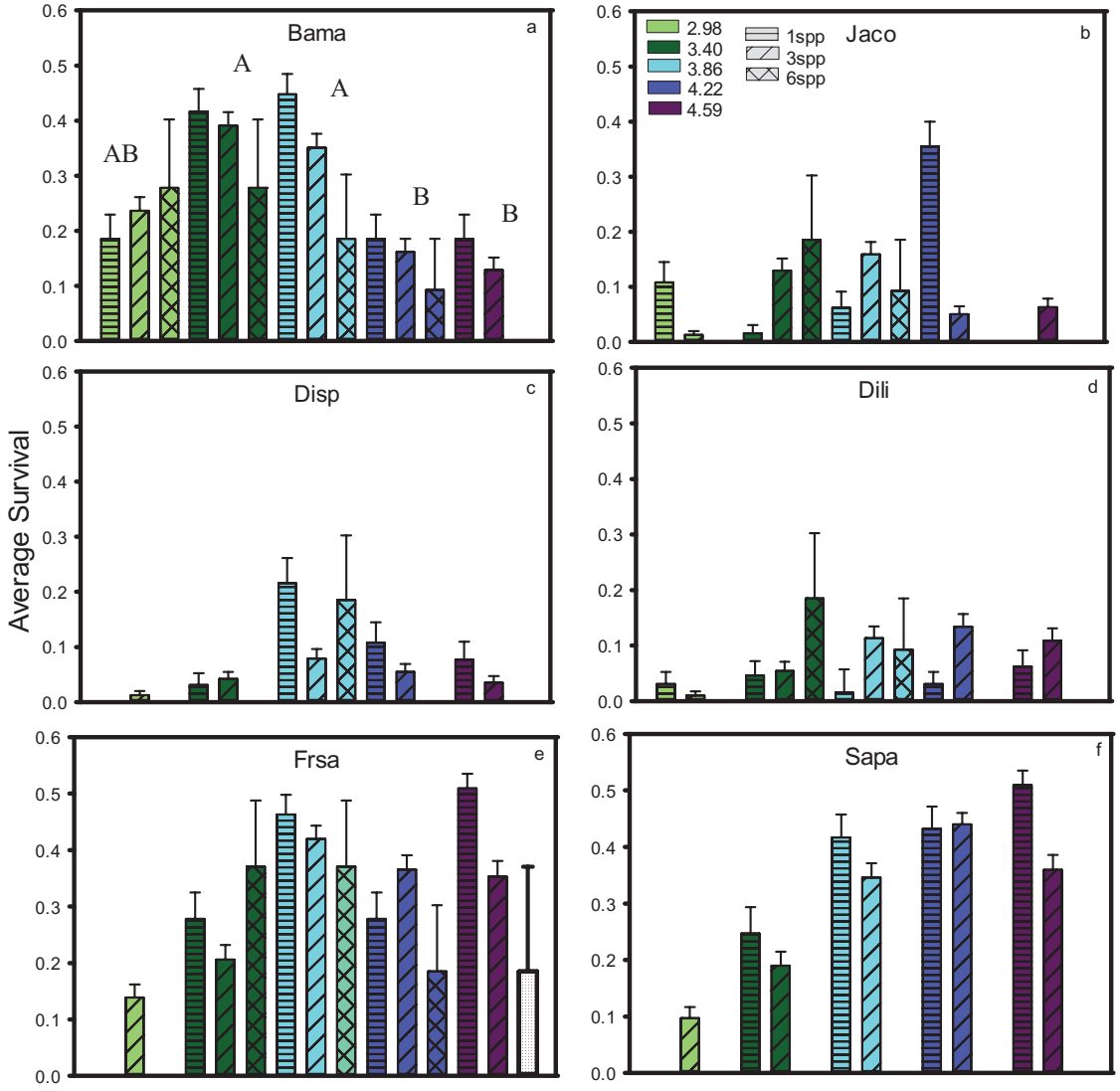

FIGURE 4a-f. Mean (± 1 SE) species-specific survival: by elevation and diversity level (as indicated in the legend). Differences among elevations as determined by Tukey's pairwise comparison tests are represented by different letters.

TABLE 3. Aggregate and Species-Specific Survival

Metric	Source	*DF*	*adj SS*	*adj MS*	*F*	*P*
Aggregate Survival	Elevation	4	0.798	0.199	2.56	0.039
	Treatment	2	0.202	0.101	1.30	0.275
	Elev*Treat	8	0.365	0.046	0.59	0.789
	Residual	255	19.84	0.078		
Bama Survival	Elevation	4	0.018	0.004	6.85	< 0.001
	Treatment	2	0.003	0.002	2.56	0.078
	Elev*Treat	8	0.005	0.001	0.97	0.462
	Residual	762	0.506	0.001		
Jaco Survival	Elevation	4	0.003	0.001	2.45	0.045
	Treatment	2	0.001	0.001	1.63	0.196
	Elev*Treat	8	0.036	0.005	12.95	< 0.001
	Residual	834	0.293	< 0.001		
Disp Survival	Elevation	4	0.006	0.002	6.51	< 0.001
	Treatment	2	0.002	0.001	5.02	0.007
	Elev*Treat	8	0.005	0.001	2.44	0.013
	Residual	834	0.209	< 0.001		
Dili Survival	Elevation	4	0.003	0.001	2.04	0.087
	Treatment	2	< 0.001	< 0.001	0.88	0.413
	Elev*Treat	8	0.006	0.001	1.92	0.055
	Residual	720	0.259	< 0.001		
Frsa Survival	Elevation	4	0.033	0.008	13.64	< 0.001
	Treatment	2	0.002	0.001	1.25	0.287
	Elev*Treat	8	0.019	0.002	3.94	< 0.001
	Residual	714	0.436	0.001		
Sapa Survival	Elevation	4	0.139	0.035	59.99	< 0.001
	Treatment	2	0.008	0.004	6.82	0.001
	Residual	753	0.436	0.001		

Note: Results of separate two-factor univariate ANOVAs of biological and plant trait metrics with the following as factors: Elevation and Treatment. Significant *p*-values (< 0 .05) are underlined. Sample size: n = 4860 (cumulative species); n = 600 (Bama, Sapa), n = 660 (Jaco, Disp), n = 540 (Dili, Frsa). Due to sampling issues, individual survival was not collected for all plots but only affected Sapa as the interaction can't be run.

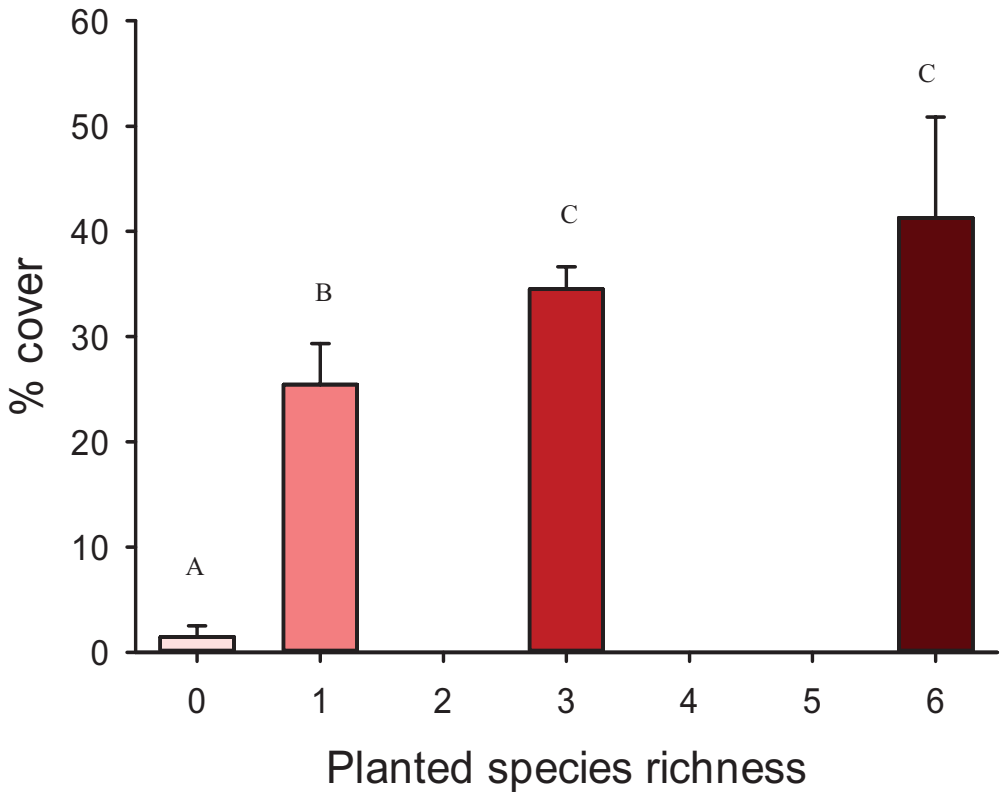

FIGURE 5. Mean (± 1 SE) aggregate percent cover: across diversity treatment (1spp, 3spp, 6spp). Differences among diversity treatment noted by Tukey's pairwise comparisons are shown by different letters.

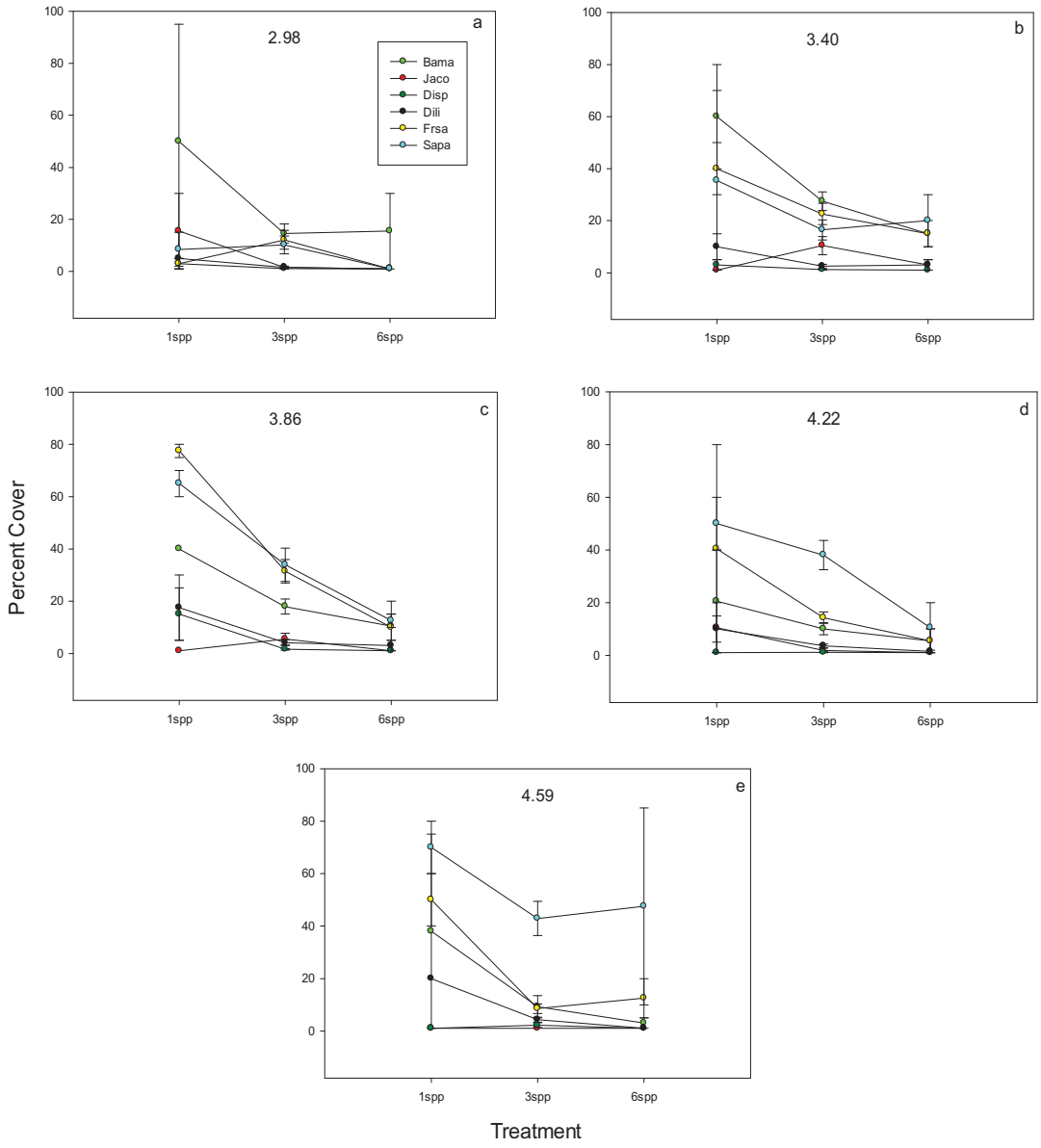

FIGURE 6a-e. Mean (± 1 SE) total percent cover by elevation: (graphs a-e) by species (as shown in the legend) and diversity treatment (1spp, 3spp, 6spp). Lines between the treatments are included to help interpret change between the treatments (not as an indicator of continuous data).

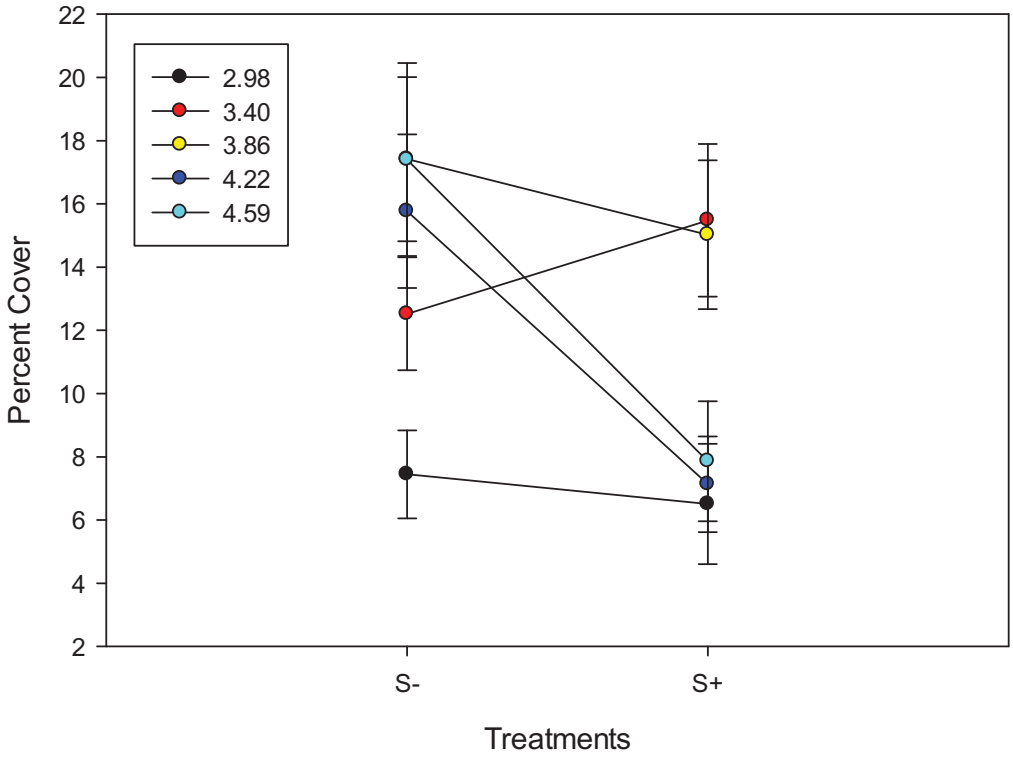

FIGURE 7. Mean (± 1 SE) total percent cover of S-/+ plots: (i.e., plots without or with the marsh dominant species) at each elevation (as indicated in the legend). Lines between the treatments are included to help interpret change between the treatments (not as an indicator of continuous data).

TABLE 4. Percent Cover: Aggregate, by Elevation, and by the Marsh Dominant

Metric	Source	*DF*	*adj SS*	*adj MS*	*F*	*P*
Aggregate Percent Cover	Elevation	4	12.386	3.097	1.79	0.132
	Treatment	2	32.802	16.401	9.47	< 0.001
	Elev*Treat	8	4.387	0.548	0.32	0.959
	Residual	255	441.62	1.732		
Species Cover by Treatment @ 2.98	Treatment	2	6.062	3.031	3.55	0.032
	Species	5	12.935	2.587	3.03	0.013
	Treat*Spp	10	5.827	0.583	0.68	0.739
	Residual	126	107.55	0.854		
Species Cover by Treatment @ 3.40	Treatment	2	2.439	1.220	1.33	0.268
	Species	5	42.736	8.547	9.33	< 0.001
	Treat*Spp	10	7.865	0.787	0.86	0.574
	Residual	126	115.49	0.917		
Species Cover by Treatment @ 3.48	Treatment	2	13.938	6.969	8.42	< 0.001
	Species	5	45.183	9.037	10.92	< 0.001
	Treat*Spp	10	6.236	0.624	0.75	0.673
	Residual	126	104.29	0.828		
Species Cover by Treatment @ 4.22	Treatment	2	6.575	3.288	4.90	0.009
	Species	5	29.279	5.856	8.73	< 0.001
	Treat*Spp	10	4.630	0.463	0.69	0.732
	Residual	126	84.56	0.671		
Species Cover by Treatment @ 4.59	Treatment	2	8.918	4.459	6.10	0.003
	Species	5	57.180	11.436	15.65	< 0.001
	Treat*Spp	10	8.209	0.821	1.12	0.350
	Residual	126	92.10	0.731		
S+/- Percent Cover	Elevation	4	47.328	11.832	8.03	< 0.001
	S+/-	1	11.752	11.752	7.98	0.005
	Eleve*S+/-	4	12.131	3.033	2.06	0.085
	Residual	710	1045.98	1.473		

Note: Results of separate two-factor univariate ANOVAs of biological and plant trait metrics with the following factors: Treatment and Species; and Elevation and S-/+. Significant *p*-values (< 0 .05) are underlined. Sample size: n = 280.

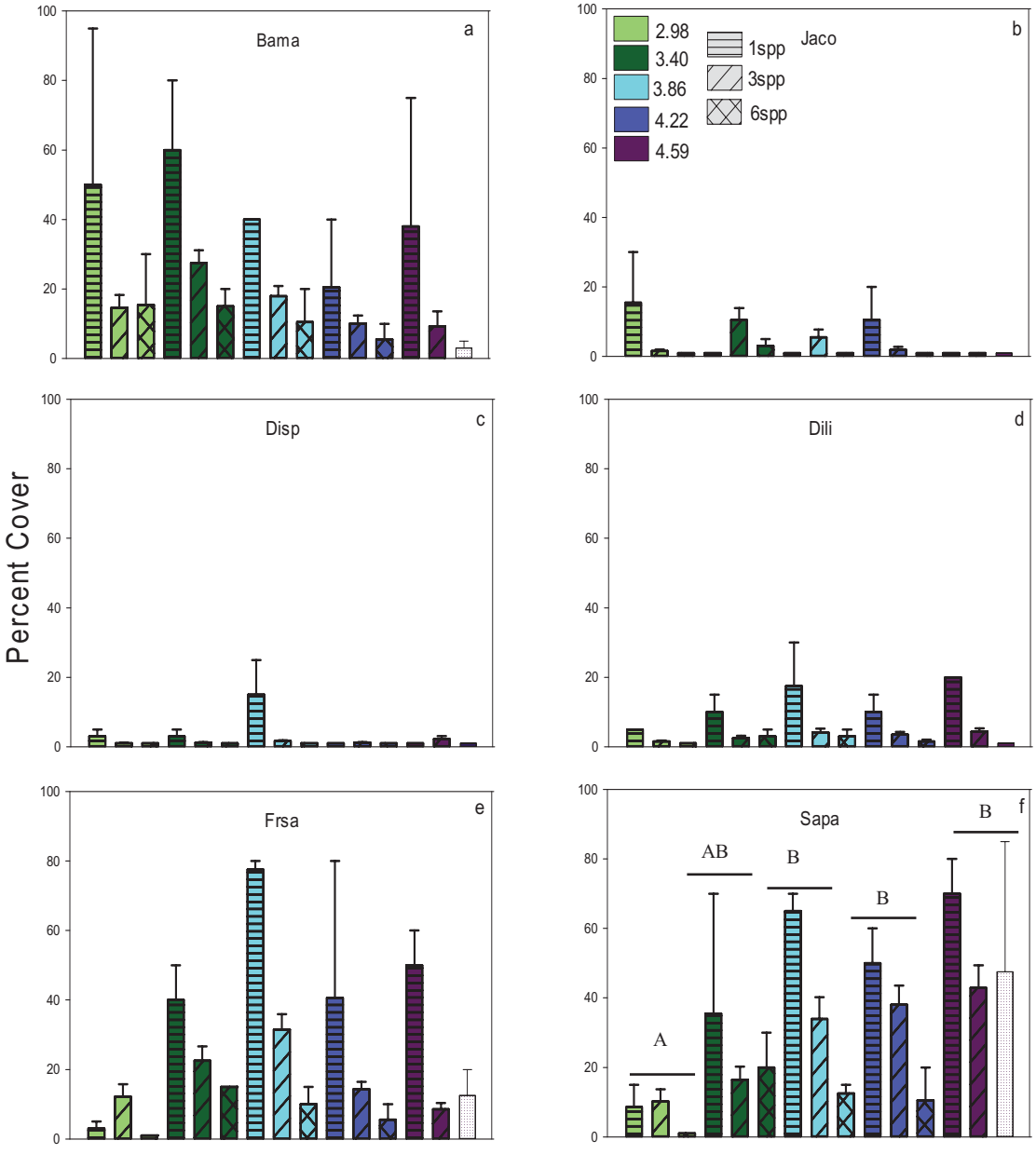

FIGURE 8a-f. Mean (± 1 SE) species-specific percent cover: by elevation and treatment level (as indicated in the legend). Differences among elevations as determined by Tukey's pairwise comparison tests are represented by different letters.

TABLE 5. Species-Specific Percent Cover

Metric	Source	*DF*	*adj SS*	*adj MS*	*F*	*P*
Bama Cover	Elevation	4	13.741	3.435	2.88	0.026
	Treatment	2	8.766	4.383	3.67	0.029
	Elev*Treat	8	1.399	0.175	0.15	0.997
	Residual	105	125.45	1.195		
Jaco Cover	Elevation	4	1.623	0.406	0.65	0.627
	Treatment	2	0.802	0.401	0.64	0.527
	Elev*Treat	8	6.602	0.825	1.33	0.237
	Residual	115	71.543	0.622		
Disp Cover	Elevation	4	2.279	0.570	4.39	0.002
	Treatment	2	2.357	1.178	9.09	< 0.001
	Elev*Treat	8	4.040	0.505	3.90	< 0.001
	Residual	115	14.908	0.130		
Dili Cover	Elevation	4	2.188	0.055	1.38	0.248
	Treatment	2	14.414	7.207	18.13	< 0.001
	Elev*Treat	8	1.515	0.189	0.48	0.870
	Residual	95	37.75	0.397		
Frsa Cover	Elevation	4	22.776	5.694	6.01	< 0.001
	Treatment	2	7.398	3.699	3.90	0.023
	Elev*Treat	8	9.879	1.235	1.30	0.251
	Residual	95	90.01	0.947		
Sapa Cover	Elevation	4	25.946	6.486	4.64	0.002
	Treatment	2	5.747	2.874	2.06	0.133
	Elev*Treat	8	5.991	0.749	0.54	0.827
	Residual	105	146.79	1.398		

Note: Results of separate two-factor univariate ANOVAs of biological and plant trait metrics with the following as factors: Elevation and Treatment. Significant *p*-values (< 0 .05) are underlined. Sample size: n = 280.

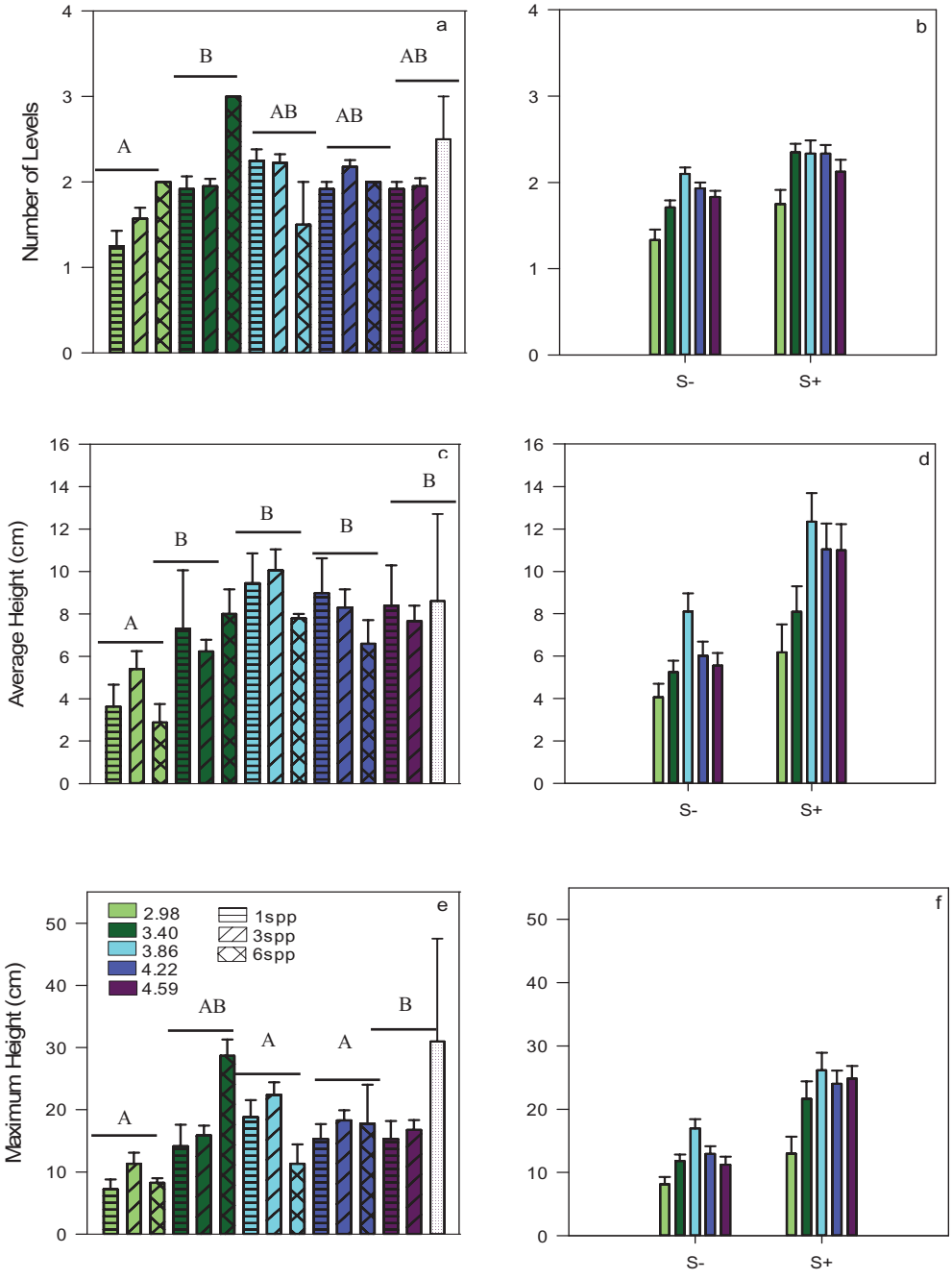

FIGURE 9a-f. Mean (± 1 SE) canopy complexity: (including average and maximum plant height) across elevation and treatment, without or with the marsh dominant (i.e., S-/+), as indicated in the legend. Differences among elevations as determined by Tukey's pairwise comparison tests are represented by different letters. Note the different scales among panels.

TABLE 6. Canopy Complexity

Metric	Source	*DF*	*adj SS*	*adj MS*	*F*	*P*
Canopy Complexity	Elevation	4	3.735	0.934	2.75	0.029
	Treatment	2	1.342	0.671	1.98	0.141
	Elev*Treat	8	4.565	0.571	1.68	0.103
	Residual	255	86.58	0.340		
Average Height	Elevation	4	12.48	3.12	6.09	< 0.001
	Treatment	2	0.13	0.07	0.13	0.877
	Elev*Treat	8	1.82	0.23	0.44	0.894
	Residual	383	196.10	0.51		
Maximum Height	Elevation	4	1307.10	326.80	2.86	0.024
	Treatment	2	455.70	227.90	1.99	0.138
	Elev*Treat	8	1062.20	132.80	1.16	0.322
	Residual	264	30155.60	114.20		
Canopy Complexity- S- vs. S+	Elevation	4	14.614	3.654	11.76	< 0.001
	S-/+	1	10.432	10.432	33.57	< 0.001
	Elev*S	4	1.278	0.320	1.03	0.393
	Residual	260	80.80	0.311		
Average Height: S- vs. S+	Elevation	4	28.99	7.25	15.58	< 0.001
	S-/+	1	16.05	16.05	34.51	< 0.001
	Elev*S	4	1.08	0.27	0.58	0.679
	Residual	388	180.46	0.47		
Maximum Height S- vs. S+	Elevation	4	22.78	5.70	15.65	< 0.001
	S-/+	1	18.66	18.66	51.27	< 0.001
	Elev*S	4	1.86	0.46	1.27	0.280
	Residual	269	97.89	0.36		

Note: Results of separate two-factor univariate ANOVAs of biological and plant trait metrics with the following factors: Elevation and Treatment; and Elevation and S-/+. Significant *p*-values (< 0 .05) are underlined. Sample size: n = 280.

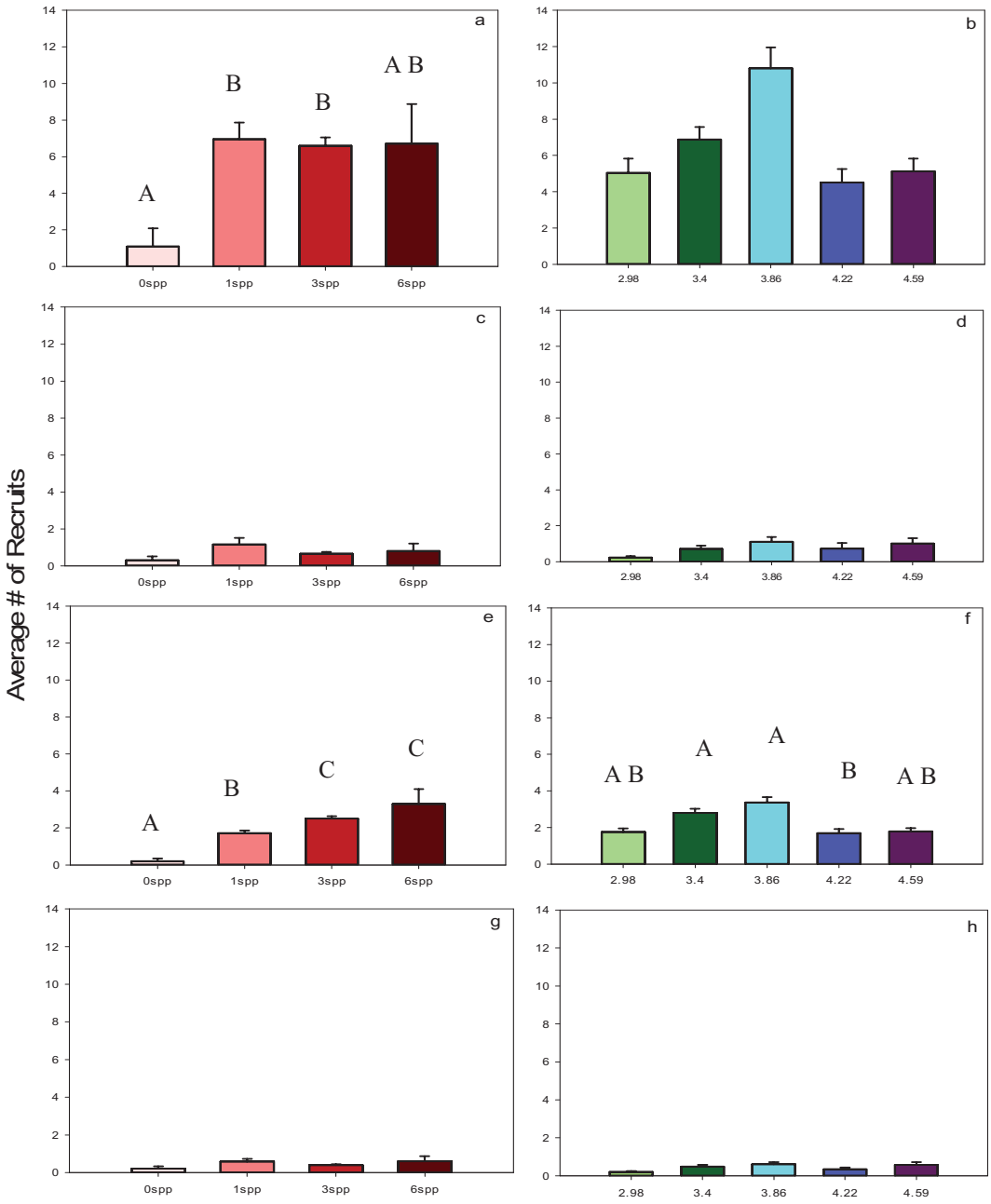

FIGURE 10a-h. Mean (± 1 SE) recruitment: Abundance and richness. Recruitment of planted species abundance by treatment (a) and elevation (b) and non-planted species abundance by treatment (c) and elevation (d). Mean (± 1 SE) recruitment of planted species richness by treatment (e) and elevation (f) and non-planted species richness by treatment (g) and elevation (h). Differences among elevations as determined by Tukey's pairwise comparison tests are represented by different letters.

TABLE 7. Recruitment: Abundance and Richness by the Marsh Dominant

Metric	Source	*DF*	*adj SS*	*adj MS*	*F*	*P*
Abundance	Elevation	4	297.45	74.36	1.92	0.108
12WAT-	Treatment	3	305.37	101.79	2.62	0.051
Planted	Elev*Treat	12	214.59	17.88	0.46	0.936
	Residual	260	10091.04	38.81		
Abundance	Elevation	4	11.56	2.89	0.90	0.464
12WAT-	Treatment	3	14.06	4.69	1.46	0.226
Non-planted	Elev*Treat	12	22.31	1.86	0.58	0.858
	Residual	260	834.37	3.21		
Richness	Elevation	4	38.44	9.61	3.85	0.005
12WAT-	Treatment	3	83.28	27.76	11.13	< 0.001
Planted	Elev*Treat	12	43.25	3.60	1.44	0.146
	Residual	260	648.68	2.50		
Richness	Elevation	4	3.20	0.80	1.25	0.290
12WAT-	Treatment	3	2.38	0.79	1.24	0.294
Non-planted	Elev*Treat	12	8.01	0.67	1.05	0.408
	Residual	260	166.05	0.37		
Abundance	Elevation	4	1324.18	331.04	8.57	<0.001
12WAT-	S-/+	1	56.22	56.22	1.45	0.229
Planted	Elev*S	4	120.78	30.20	0.78	0.538
S- vs. S+	Residual	270	10434.38	38.65		
Abundance	Elevation	4	22.80	5.70	1.78	0.132
12WAT-	S-/+	1	1.17	1.17	0.37	0.546
Non-planted	Elev*S	4	7.15	1.79	0.56	0.692
S- vs. S+	Residual	270	862.41	3.19		
Richness	Elevation	4	131.50	32.88	11.77	<0.001
12WAT-	S-/+	1	16.87	16.87	6.04	0.015
Planted	Elev*S	4	4.10	1.03	0.37	0.832
S- vs. S+	Residual	270	754.32	2.79		
Richness	Elevation	4	5.19	1.30	2.06	0.087
12WAT-	S-/+	1	3.71	3.71	5.88	0.016
Non-planted	Elev*S	4	2.32	0.58	0.92	0.452
S- vs. S+	Residual	270	170.41	0.63		

Note: Results of separate two-factor univariate ANOVAs of biological and plant trait metrics with the following factors: Elevation and Treatment; and Elevation and S-/+. Significant *p*-values (< 0 .05) are underlined. Sample size: n = 280.

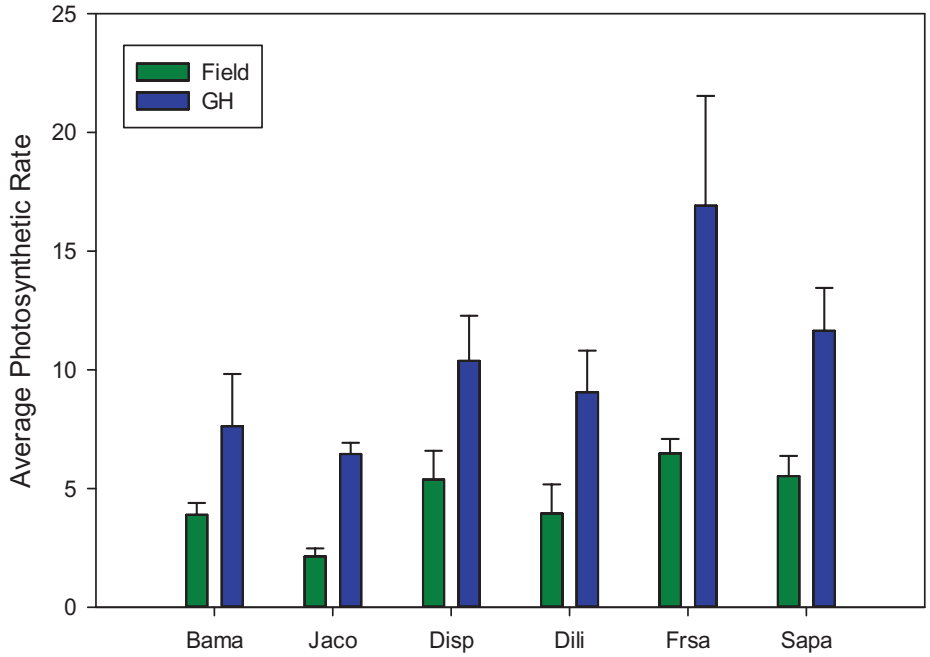

FIGURE 11. Mean (± 1 SE) photosynthetic rate: Greenhouse and field. Differences between location and among species were significant.

TABLE 8. Leaf Traits by Species

Metric	Source	*DF*	*adj SS*	*adj MS*	*F*	*P*
Photosynthetic Rate	Location	1	493.17	493.17	46.77	< 0.001
	Species	5	349.42	69.88	6.63	<0.001
	Loc*Spp	5	78.33	15.67	1.49	0.200
	Residual	112	1180.95	10.54		
Photosynthetic Rate-Species	Elevation	4	39.01	9.75	1.01	0.404
	Species	5	214.45	42.89	4.46	0.001
	Residual	96	923.59	9.62		
Leaf C/N-LiCor	Elevation	4	48.89	12.22	1.28	0.286
	Species	5	460.04	92.01	9.65	< 0.001
	Residual	70	667.68	9.54		
LMA	Elevation	4	2.52	0.63	1.35	0.250
	Treatment	2	0.34	0.17	0.37	0.694
	Species	5	73.12	14.62	31.29	< 0.001
	Residual	594	277.65	0.47		
LMA-LiCor	Location	1	0.68	0.68	1.46	0.230
	Species	5	11.40	2.28	4.93	0.001
	Loc*Spp	5	1.32	0.26	0.57	0.722
	Residual	81	37.44	0.46		
---	Elevation	3	0.86	0.29	0.52	0.671
	Species	5	20.06	4.01	7.25	< 0.001
	Residual	66	36.49	0.55		
Chl a/b LiCor	Location	1	0.26	0.26	2.41	0.123
	Species	5	3.49	0.70	6.52	< 0.001
	Loc*Spp	5	1.31	0.26	2.45	0.037
	Residual	124	13.29	0.11		
---	Species	5	6.77	1.35	11.92	< 0.001
	Treatment	3	0.37	0.12	1.09	0.357
	Residual	127	14.43	0.11		

Note: Results of separate two-factor univariate ANOVAs of biological and plant trait metrics with the following factors: Location and Species; and Elevation and Species. Significant *p*-values (< 0 .05) are underlined. Due to sampling effort interaction calculations are only provided when possible. Sample size: n = 124 (subset: both GH and Field); n=106 (subset, Field only); n=606.

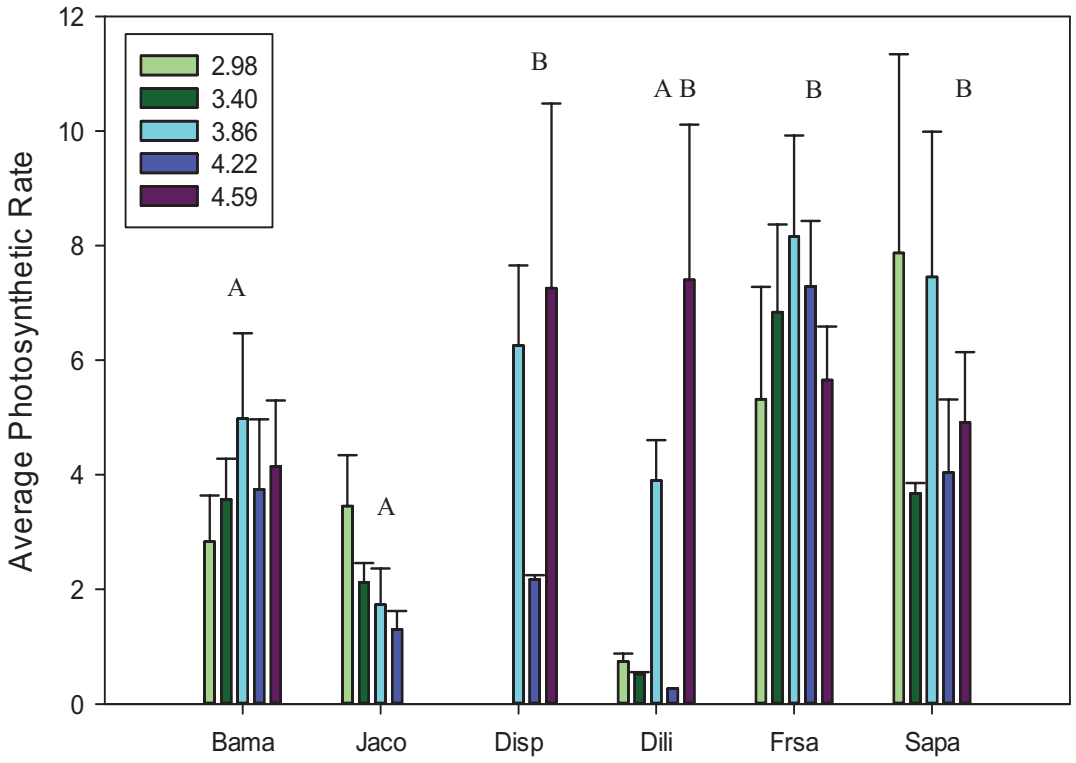

FIGURE 12. Mean (± 1 SE) photosynthetic rate among species and elevation. Differences among species as determined by Tukey's pairwise comparison tests are represented by different letters.

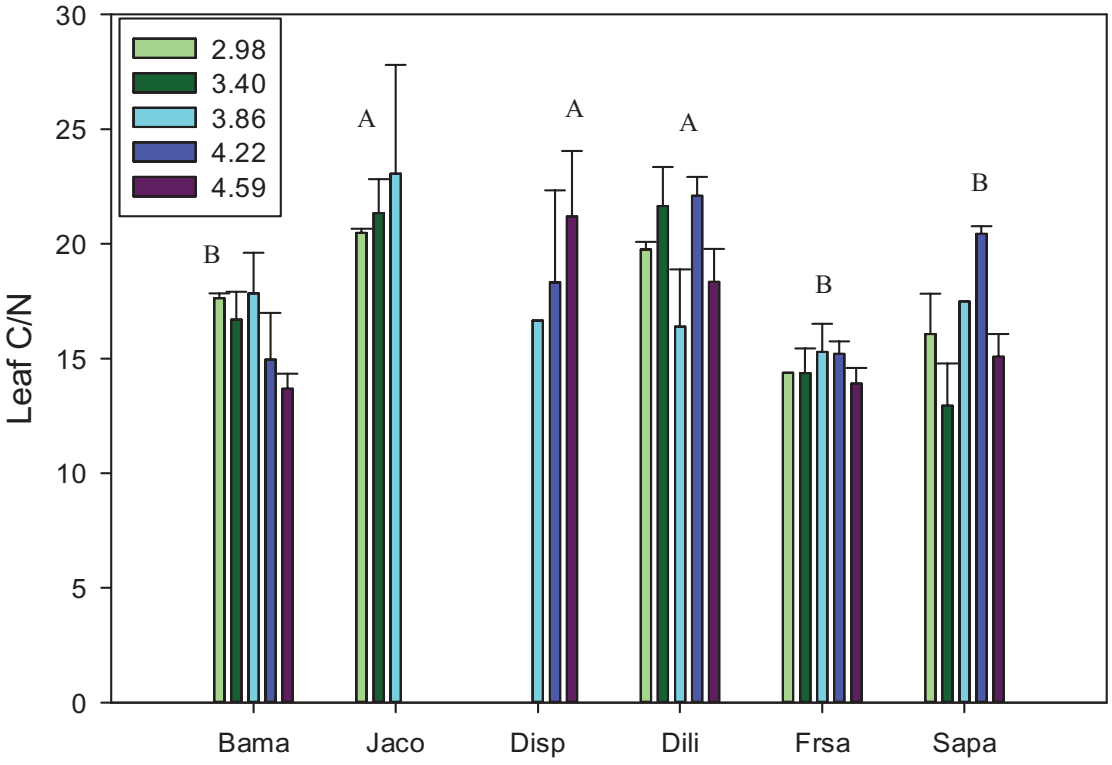

FIGURE 13. Mean (± 1 SE) species-specific leaf C/N: across elevation. Differences among species as determined by Tukey's pairwise comparison tests are represented by different letters.

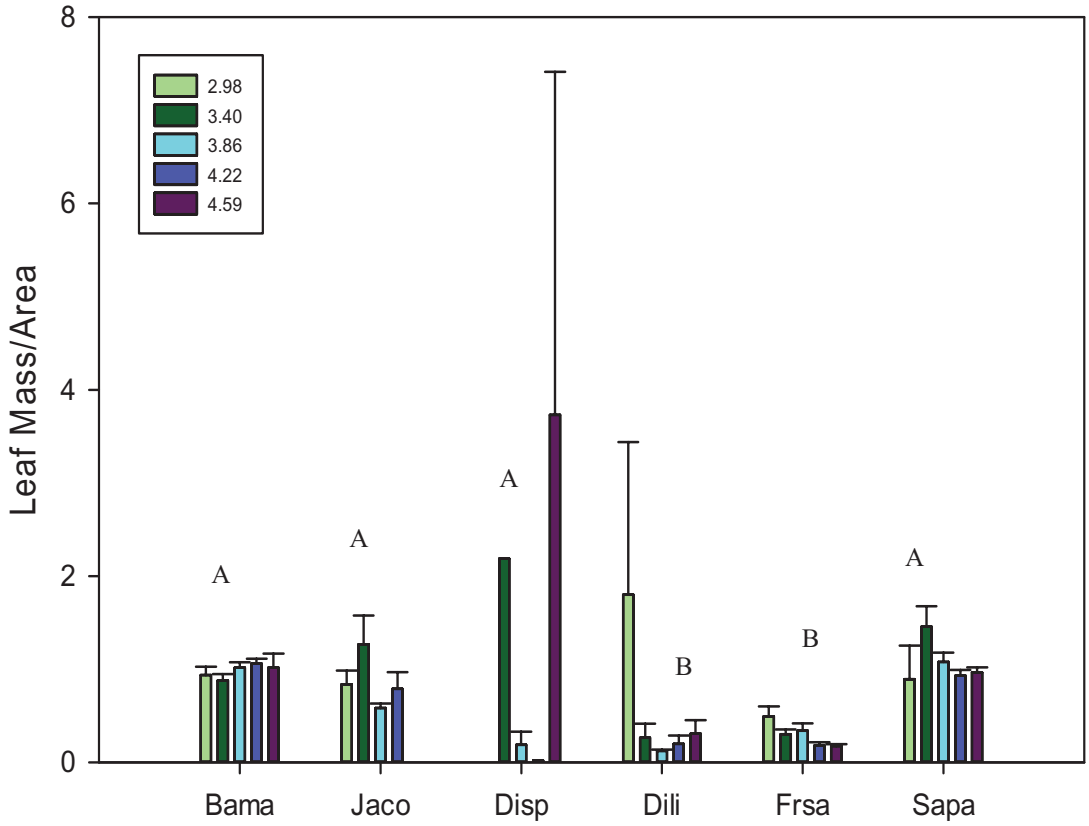

FIGURE 14. Mean (± 1 SE) species-specific LMA: leaf mass per area across elevation (as shown in the legend). Differences among species as determined by Tukey's pairwise comparison tests are represented by different letters.

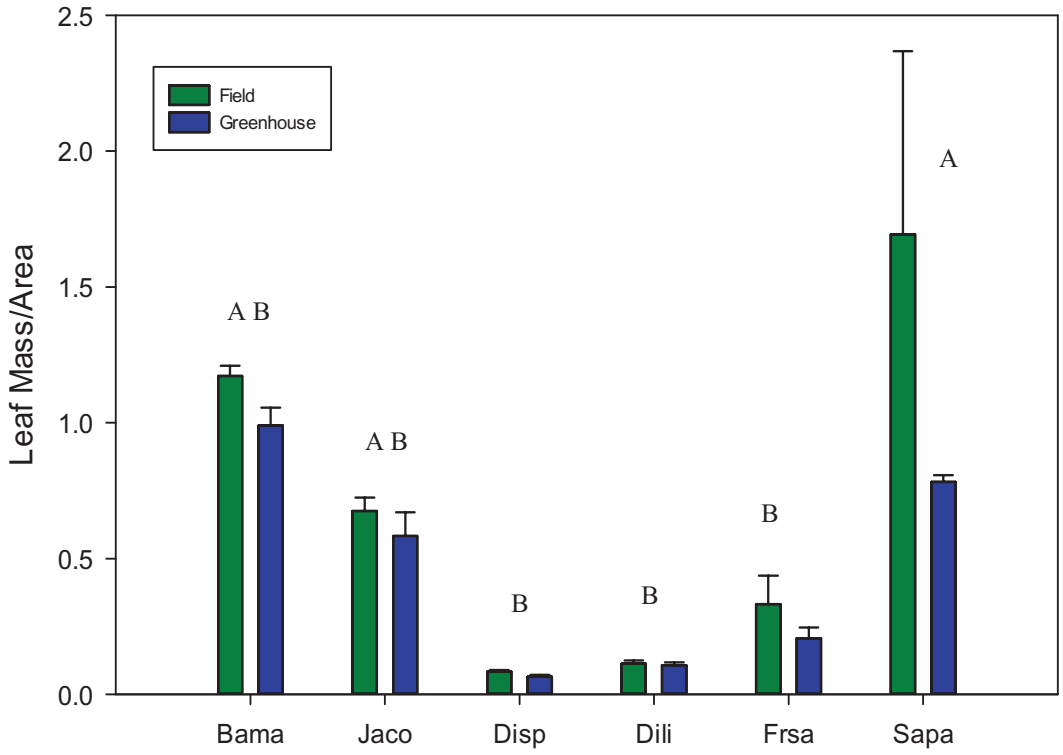

FIGURE 15. Mean (± 1 SE) species-specific LMA in greenhouse and field locations. Differences among species as determined by Tukey's pairwise comparison tests are represented by different letters. Differences in LMA between locations were not significant.

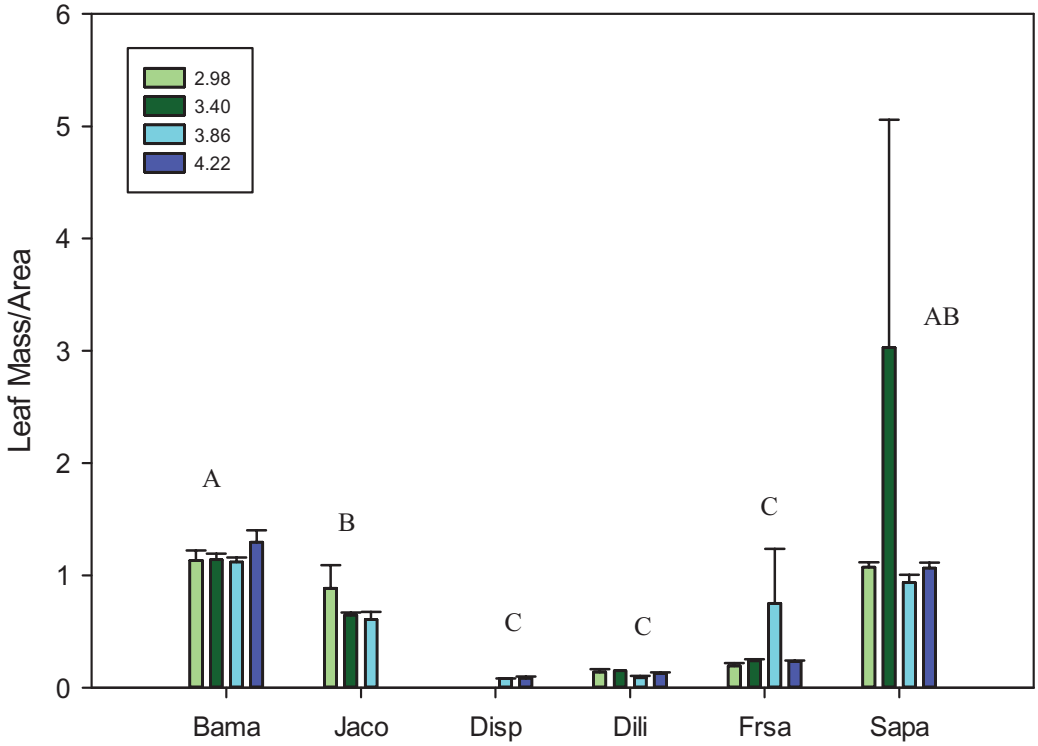

FIGURE 16. Mean (± 1 SE) species-specific LMA for the subset: leaf mass per area across elevation (as shown in the legend). Differences among species as determined by Tukey's pairwise comparison tests are represented by different letters.

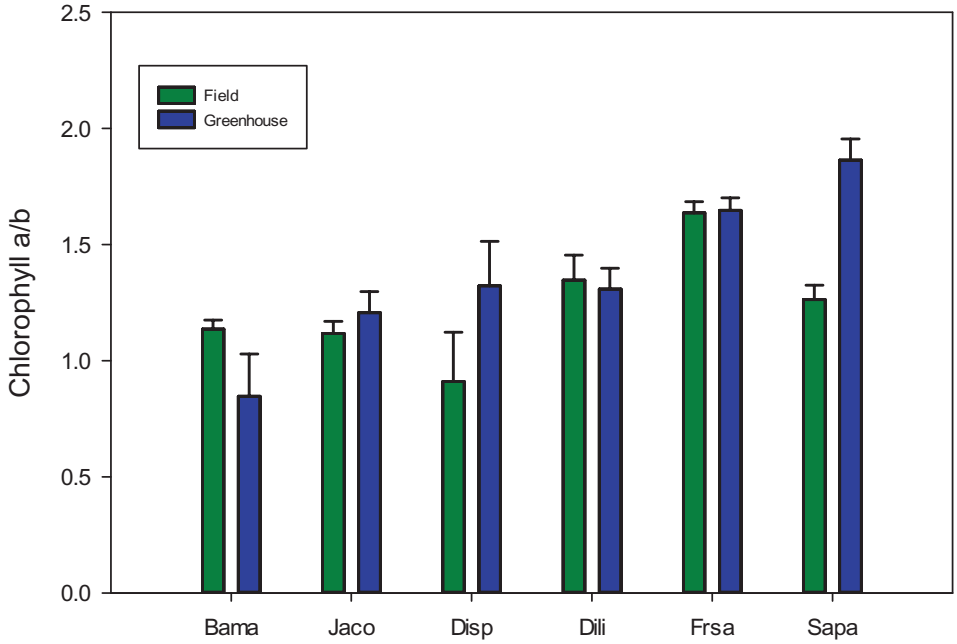

FIGURE 17. Mean (± 1 SE) species-specific chlorophyll a/b for the subset: field and greenhouse locations. The interaction between location and species was significant.

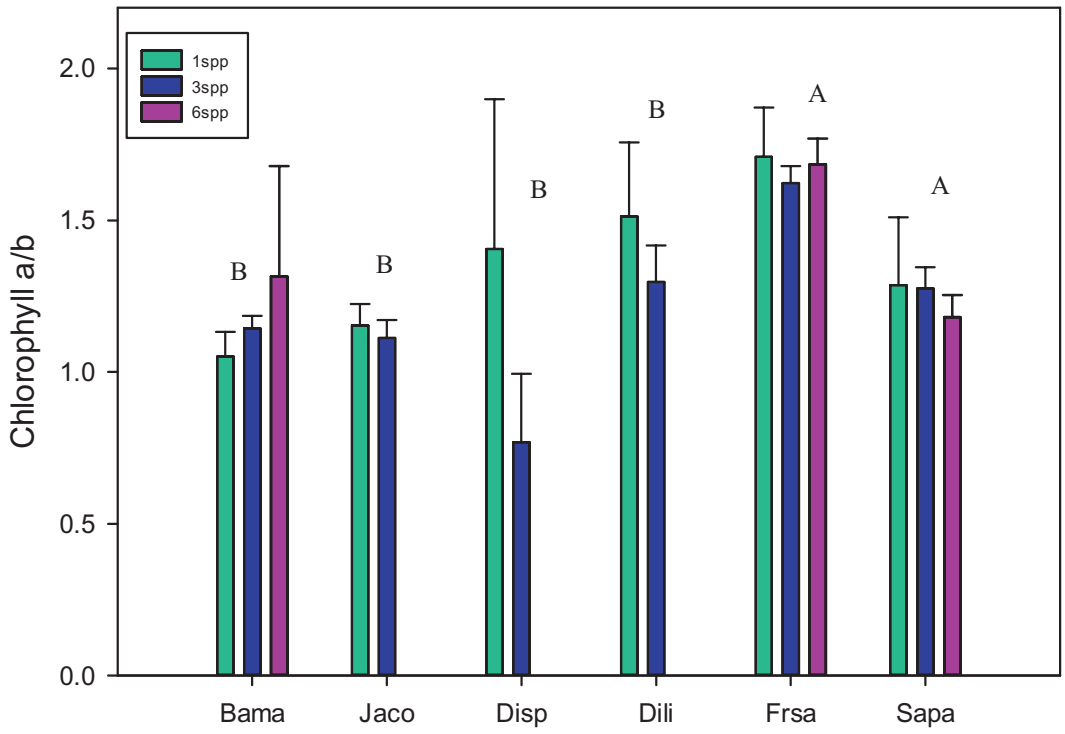

FIGURE 18. Mean (± 1 SE) species-specific chlorophyll a/b: across diversity treatments. Differences among species as determined by Tukey's pairwise comparison tests are represented by different letters. No significant difference was found among treatments (1spp, 3spp, 6spp).

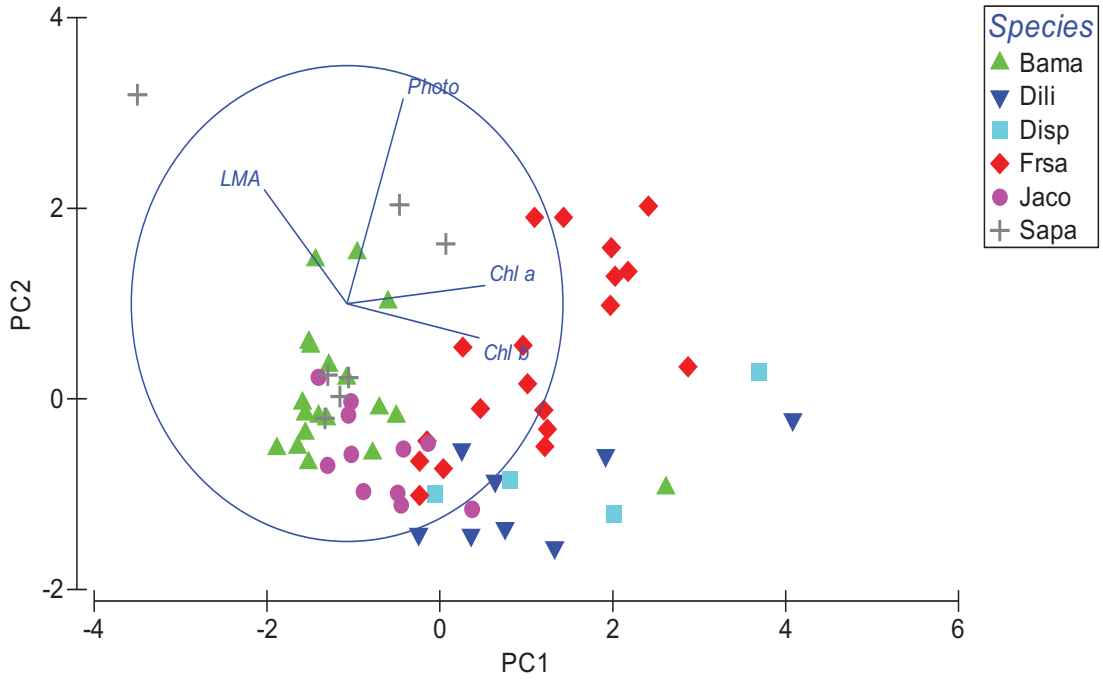

FIGURE 19. Principle components analysis (PCA) of species-specific leaf traits. PCA axis 1 represents species differences by chlorophyll a and chlorophyll b. PCA axis 2 represents species differences in photosynthetic rate and LMA.

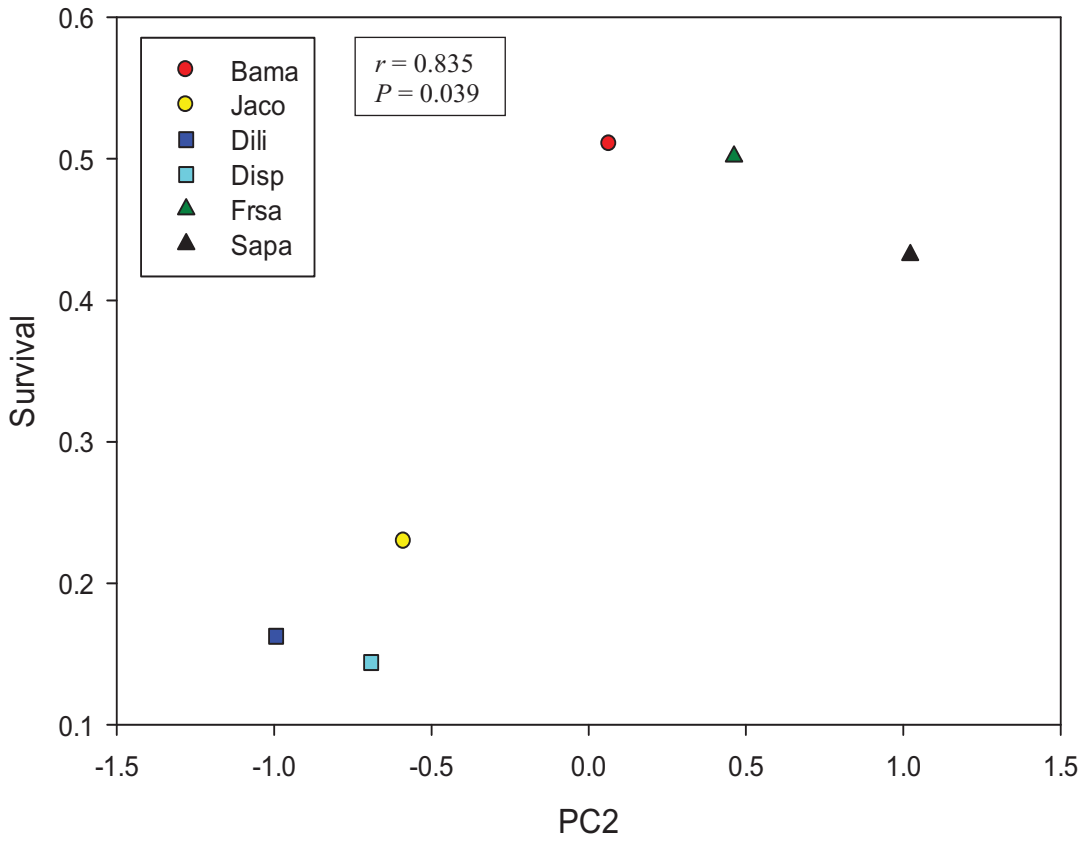

FIGURE 20. The relationship between survival and PCA axis 2. The PCA axis 2 represents species differences in photosynthetic rate and leaf mass per area (LMA).

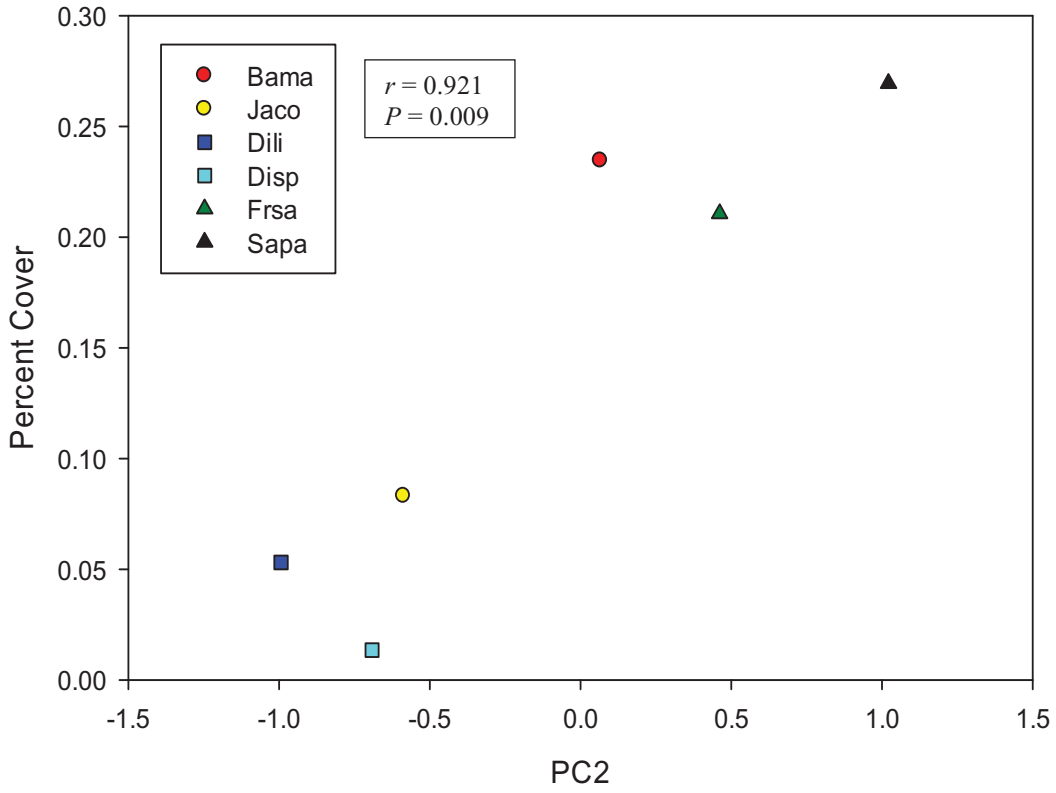

FIGURE 21. The relationship between percent cover and PCA axis 2. The PCA axis 2 represents species differences in photosynthetic rate and leaf mass per area (LMA).

TABLE 9. PCA of Species' Leaf Traits

	PCA Axis	
	1	2
Photosynthetic Rate	0.260	0.862
Leaf mass per area	-0.384	0.480
Leaf chlorophyll a	0.640	0.077
Leaf chlorophyll b	0.613	0.144

Note: The first two PCA axes explained 79.9% of the variation among species. Results of a PCA ordination for 5 leaf traits for six species. Sample size: n = 116.

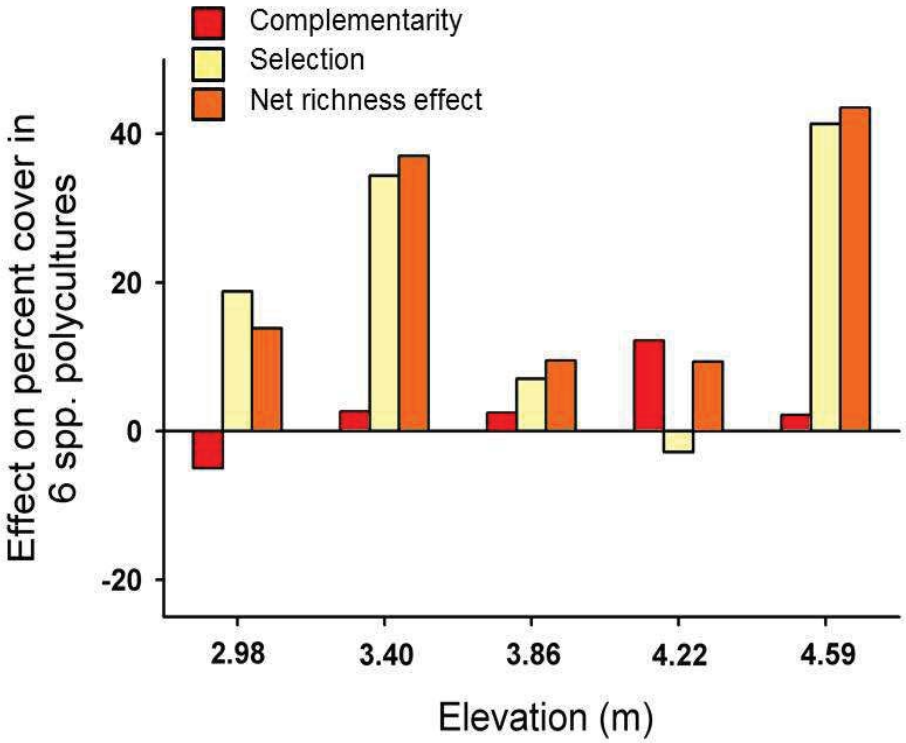

FIGURE 22. Net diversity effect: for percent cover across elevation. Selection, not complementarity, effect drove the net diversity effect after one year.

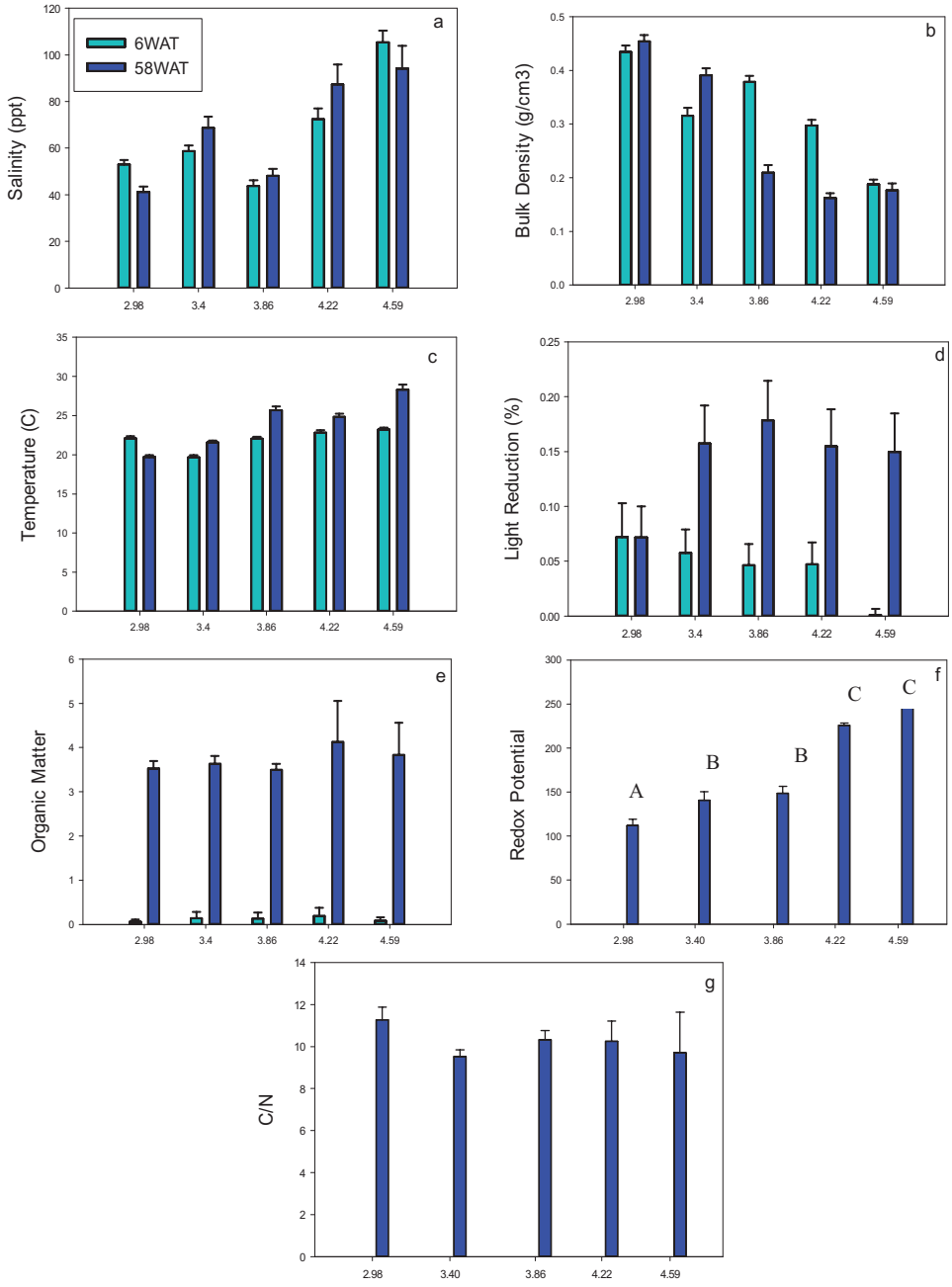

FIGURE 23a-g. Mean (± 1 SE) environmental measurements: across elevation at six and 58WAT: a) Salinity; b) Bulk density; c) Temperature; d) Light reduction; e) Organic matter; f) Redox potential; g) Soil C/N. Differences among elevations as determined by Tukey's pairwise comparison tests are represented by different letters. Note the different scales among panels.

TABLE 10. Environmental Measurements at 6WAT

Metric	Source	*DF*	*adj SS*	*adj MS*	*F*	*P*
Salinity-6WAT	Elevation	4	3.83	0.96	6.67	< 0.001
	Treatment	3	0.10	0.03	0.23	0.879
	Elev*Treat	12	1.24	0.10	0.72	0.734
	Residual	260	37.37	0.14		
Bulk Density-6WAT	Elevation	4	0.53	0.13	16.74	< 0.001
	Treatment	3	0.03	0.01	1.35	0.259
	Elev*Treat	12	0.01	< 0.001	0.12	1.000
	Residual	260	2.04	0.01		
Soil Temperature-6WAT	Elevation	4	144.73	36.18	7.82	< 0.001
	Treatment	3	3.58	1.19	0.26	0.856
	Elev*Treat	12	30.52	2.54	0.55	0.880
	Residual	260	1202.73	4.63		
Light Reduction-6WAT	Elevation	4	0.01	< 0.001	0.13	0.971
	Treatment	3	0.06	0.02	0.75	0.521
	Elev*Treat	12	0.15	0.01	0.48	0.925
	Residual	260	6.54	0.03		
Organic Matter-6WAT	Elevation	4	1.11	0.28	0.30	0.879
	Treatment	3	6.09	2.03	2.18	0.091
	Elev*Treat	12	6.17	0.51	0.55	0.878
	Residual	260	241.96	0.93		

Note: Results of separate two-factor univariate ANOVAs of environmental metrics with the following factors: Elevation and Treatment. Significant *p*-values (< 0 .05) are underlined. Sample size: n = 280.

TABLE 11. Environmental Measurements at 58WAT

Metric	Source	*DF*	*adj SS*	*adj MS*	*F*	*P*
Salinity-58WAT	Elevation	4	9.03	2.26	10.45	< 0.001
	Treatment	3	0.28	0.09	0.43	0.735
	Elev*Treat	12	1.66	0.14	0.64	0.806
	Residual	260	56.18	0.22		
Bulk Density-58WAT	Elevation	4	1.17	0.29	34.73	< 0.001
	Treatment	3	0.01	< 0.001	0.43	0.732
	Elev*Treat	12	0.08	0.01	0.84	0.614
	Residual	260	2.19	0.01		
Soil Temperature-58WAT	Elevation	4	663.04	165.76	15.50	< 0.001
	Treatment	3	56.22	18.74	1.75	0.157
	Elev*Treat	12	35.24	2.94	0.27	0.993
	Residual	260	2779.85	10.69		
Light Reduction-58WAT	Elevation	4	0.25	0.06	0.97	0.424
	Treatment	3	0.25	0.08	1.29	0.278
	Elev*Treat	12	0.71	0.06	0.93	0.521
	Residual	260	16.49	0.06		
Organic Matter-58WAT	Elevation	4	2.79	0.70	0.04	0.997
	Treatment	3	22.80	7.60	0.45	0.720
	Elev*Treat	12	146.40	12.20	0.72	0.735
	Residual	260	4427.27	17.03		
Redox Potential-58WAT	Elevation	4	293756.00	73439.00	24.22	< 0.001
	Treatment	3	1147.00	382.00	0.13	0.945
	Elev*Treat	12	26827.00	2236.00	0.74	0.714
	Residual	260	788284.00	3032.00		
Soil C/N-58WAT	Elevation	4	26.67	6.67	0.57	0.688
	Treatment	3	2.70	0.90	0.08	0.973
	Residual	76	8.95.95	11.79		

Note: Results of separate two-factor univariate ANOVAs of environmental metrics with the following factors: Elevation and Treatment. The interaction for Soil C/N was not possible due to preliminary status of analysis. Significant *p*-values (< 0 .05) are underlined. Sample size: n = 280.

CHAPTER 4

DISCUSSION

Initial Planting Diversity and Elevation are Very Important for Plant Productivity

In my experiment, initial planting diversity was positively correlated with total percent cover at one year after planting. Similar positive relationships between diversity and productivity have previously been found mainly in terrestrial ecosystems (McNaughton, 1977; Brown and Ewel, 1988; Ewel et al., 1991; Tilman, 1996; Hooper and Vitousek, 1997; Tilman, 1997), but also in more recent evaluations of marine (Stachowicz et al., 2007; Stachowicz et al., 2008) and wetland systems (Callaway et al., 2003; Sullivan et al., 2007). Initial planting diversity was also positively correlated with species richness of recruits of my six planted species. Working in grasslands, Tilman (1997) found that initially high diversity plots remained more diverse over four years, but also resisted invasion better than plots with lower initial diversity. While recruitment of non-planted species into my plots was low compared to recruitment of planted species there was no recruitment of non-native species into experimental plots after six months, as all non-planted species that recruited were native California marsh species. It would be interesting to note which non-native species were present after two years, and in which experimental treatments, as I suspect Colorado Lagoon is not unique to wetlands and therefore should be susceptible to the recruitment of invasive species. Other studies have

shown that overall plant species diversity is retained in restored wetlands that start with higher initial planting diversity (Keer and Zedler, 2002; Zedler et al., 2001; Zedler and West, 2008). Incorporating high diversity planting can therefore lead to enhancement of specific target functions (e.g., increasing percent cover, canopy complexity) over time.

In contrast to the results for percent cover and recruitment, I found that plant survival was strongly related to tidal elevation, with no significant effect of initial planting diversity. Previous studies have suggested that elevation is an important factor in restored wetlands (Levin et al., 1996; Zedler et al., 2001; Levin and Talley, 2002). As different marsh plant species are adapted to different intertidal zones (i.e., high, middle, low), preferentially planting species in order to maximize survival in this already rather harsh habitat should be explicitly incorporated into restoration practice. My plants were relatively small when planted (i.e., grown in 2" pots), compared to what is often used in restorations. Smaller plants are more easily pulled up by birds and other foragers and the softer sediment in lower elevations may also have been a factor contributing to lower survival.

Species-Specific Patterns are Different from the Aggregate Patterns

Species-specific survival and percent cover patterns were often quite different from the aggregate pattern. The aggregate survival pattern suggested that average survival was highest above 2.98 ft.; however, species-specific patterns did not always match this result. My data provide more evidence in support of locationally-targeted planting of species within a marsh. With the exception of *Distichlis littoralis*, all of my species exhibited statistically significant differences in survival either across elevation

(*Batis maritima* and *Sarcocornia pacifica*) or in the interaction between elevation and treatment (*Jaumea carnosa, D. spicata* and *Frankenia salina*). The species with the highest survival differed across elevation: *B. maritima* did best low on the shore (2.98 and 3.40 ft.), *Frankenia salina* did best at the middle shore heights (3.86 and 4.22 ft.), whereas *S. pacifica* did best high on the shore (4.59 ft.). The grasses *D. littoralis* and *D. spicata* exhibited lower survival overall, but did comparatively better at the mid-intertidal elevations. Ignoring location-specific performance capacity of different species would most likely reduce the effectiveness of intertidal restorations. Other studies have found that individual species perform differently than the aggregate pattern (Zedler et al., 2001; Sullivan et al., 2007; Doherty et al., 2011; Tilman, 1997). For instance Zedler et al. (2001) noted performance differences across elevational zones by the marsh dominant (*Sarcocornia pacifica*, previously *Salicornia virginica*) and other native species (*Limonium californicum, Salicornia bigelovii,* and *Suaeda esteroa*), while Sullivan et al. (2007) and Doherty et al. (2001) focused on combinations of species that perform better or worse than the monocultures.

In my study, aggregate percent cover increased with diversity (the three and 6spp plots had higher cover than the 0spp and the 1spp plots); however, species-specific percent cover patterns increased by a combination of elevation, treatment and interaction effects instead of diversity, suggesting that the interaction between plant species yields a more complex relationship than just summing up expected yield of all species in mixture. My results suggest that planting species with certain neighbors, and at particular elevations, is an important aspect that should be taken into account when restoring

wetlands. By focusing on the overall picture (i.e., aggregate percent cover or survival), the importance and effect of species interactions is lost. It is important as a manager to acknowledge the potential for species performance differences within the intertidal zone to influence marsh restoration success. Studies in grassland systems suggest that the effect of diversity is not consistent, but rather is highly variable depending on the species in mixture (Huston et al., 2000). Identity differences in mixture can therefore result in differential performance among species (Tilman et al., 1997). In other words, just planting halophytes in the mid-intertidal zone (as defined by Josselyn, 1983) because they are salt-tolerant is not an effective management plan if your overall goal is to achieve maximum plant cover. It would be best to identify the maximal performance zone for each species (and in different species combinations) prior to planting to increase overall survival and plant cover.

Net Diversity is Driven by Selection, Varies by Elevation

I found that overall net diversity effects varied across elevation (Fig 22). A net diversity effect is determined by the additive effects of both complementarity (when interspecific interactions allow species to capture resources in ways that are complementary in space or time) and selection (the probability of including or excluding a high performing species) effects (Loreau, 2000; Loreau and Hector, 2001; Stachowicz et al., 2007; Stachowicz et al., 2008; Reusch et al., 2005; Hooper et al., 2005). Generally, complementarity effects are positive (Loreau and Hector, 2001), whereas selection effects can be either negative or positive (Troumbis et al., 2000; Loreau, 2000; Loreau and Hector, 2001). While both processes can contribute to a net diversity effect, I found that

selection effects were more dominant in my experimental plots than complementary effects. This suggests that there is at least one species that is outperforming the others and that the observed increases in performance (productivity and richness of recruits) is due to the chance presence of one or more higher performing species in mixture.

I separately evaluated the effect the marsh dominant's absence and presence had on percent cover at each elevation and found that plots with *S. pacifica* had significantly lower percent cover at the elevations at 2.98 and 3.40 ft. (Fig 6). This coincided with survival patterns of *S. pacifica* and are perhaps not surprising. These patterns follow the "inverse-sampling effect" sensu Loreau (2000), which suggests that selecting against a high performing species in mixture could reduce function even with an increase in species diversity. I also assessed *S. pacifica*'s (the marsh dominant) effect on the number of canopy layers and average and maximum plant height. For each of these parameters, I found that both elevation and presence of *S. pacifica* were important, but the interaction was not. These patterns followed the patterns found in survival and percent cover; where the marsh dominant was absent, I saw a general but not universal decline in plot-level performance metrics. Despite being the marsh dominant, *S. pacifica* did not perform well at the lower elevations (below 3.40 ft.), therefore without this dominant, tall marsh species in the lower elevations, there was a reduction in the height and canopy complexity of those plots. When present, the marsh dominant in this system provides additional function compared to the other species (i.e., increased complexity), therefore the inclusion of *S. pacifica,* either by passive or active means, is beneficial to the marsh system. Despite being weed-like in recruitment and growth, *S. pacifica* also has an

optimal elevation within the intertidal zone, providing further evidence that location of species' planting in restorations should be determined sensibly.

There is evidence in different habitats that selection effects are likely to be most important in the short term (Huston et al., 2000; Tilman et al., 1997; Reusch et al., 2005; Stachowicz et al., 2007; Loreau and Hector, 2001); however, over time complementarity effects eventually dominate ecosystems (Tilman et al., 2006; Stachowicz et al., 2007; Stachowicz et al., 2008). My experiment ran for one calendar year, which is longer than most marine studies of diversity effects (typically done with algae; Stachowicz et al., 1999; Stachowicz et al., 2007), but is relatively short-term compared to many terrestrial plant studies (Tilman et al., 2006) and potentially short-term for wetland plant lifespans. Over time, I expect that my plots will continue to exhibit a positive diversity effect, but whether the underlying mechanism will remain selection, or will shift to complementarity, is an open question. Continued monitoring of my plots will provide a valuable addition to the study of coastal wetland restorations, as there are few (if any) long-term monitoring studies currently established that focus on diversity effects (as discussed in Zedler et al., 2001).

Presence of Plants Regardless of Initial Diversity Increases Diversity

When comparing experimental and control plots, I found that minimal recruitment occurred into the control plots. These results supported management plans that emphasize effectiveness of active planting compared to passive restoration strategies (Blair et al., 2013; Keer and Zedler, 2002; Whitcraft and Levin, 2007). Active planting allows wetlands to achieve higher plant cover much quicker than natural re-vegetation

(Zedler, 2000). While their overall abundances were low, all non-planted species that recruited into my plots were native to California. This supports previous findings that propose planting in restored marshes influences species composition (Zedler et al., 2001; Whitcraft and Levin, 2007). Actively planting directly influences which species are initially present and therefore subsequently influences which species can most easily recruit to other parts of the marsh.

Species Identity Matters, as Observed Effects are Plant-Trait Related

Species identity was shown to be an important contributing factor to performance (survival, percent cover), particularly since species-specific patterns did not mimic the aggregate performance. Multiple studies have observed that identity differences are related to and drive variation in trait responses (Stachowicz et al., 2007; Keer and Zedler, 2002; Doherty et al., 2011; Steudel et al., 2011; Loreau and Hector, 2001). I found that species-specific photosynthetic rate and leaf mass per area (LMA) explained variation in survival and percent cover. Therefore pairing species together that have inherently lower photosynthetic rates and/or LMA ratios could reduce overall survival and percent cover; which would not be ideal if your overall management goal was to increase plant cover over time. Restorations that mix species with higher and lower photosynthetic rates, or LMA ratios, together may therefore be expected to perform better. My results provide further evidence that identity is an important factor when determining the overall functioning of a wetland.

Environmental Factors are Largely Related to Elevation

Differences in plant performance were associated with environmental factors as well as variation in neighbor abundance (i.e. treatment). Species responded differently to environmental factors (i.e., redox potential, percent light reduction) associated with differences in elevation (Blair et al., 2013; Hooper et al., 2005). For example, *B. maritima* survived and grew best at the lowest elevation, unlike the other five species. The lowest elevation was associated with the most compacted sediment and lower salinity and temperature values. Since Colorado Lagoon was an un-vegetated intertidal mudflat prior to planting, environmental factors could have been an important factor determining species survival (Zedler, 2000; Bedford et al., 1999; Iversen et al., 2012). For example, the lack of initial plant cover to alleviate some of the harsher environmental aspects (i.e., salinity, temperature, soil aeration) may explain the low recruitment levels I observed in my unplanted control plots (Bertness et al. 1992).

Overall Conclusions

By evaluating the BEF question in a coastal wetland habitat, my study provides evidence that relationships between species diversity and ecosystem function are often positive and can explain observed variation in ecological processes. After one year, I found that initial planting diversity and elevation were important predictors of productivity in a wetland as measured through survival and percent cover. Species identity also matters, as species-specific performance patterns differed from the aggregate survival and percent cover patterns. I linked differences in leaf traits by species to

variation in productivity and found that diversity patterns in percent cover were mainly driven by selection effect rather than complementarity.

Differences in species presence (determined by species-specific variation in survival) at each elevation suggested that the selection effect may be due to the inclusion more than one high performing species. Future restorations should carefully consider location and species identity when incorporating species diversity into active re-vegetation plans for coastal wetlands. More informed restorations would allow for trait and species similarity within the planting palette, in order to reduce large cover and/or diversity loss due to unforeseen natural or anthropogenic damages. By explicitly incorporating species identity and location into wetland restoration, we can presumably allow those habitats to be more functional than they would be otherwise.

The experimental manipulation of marsh plant species in Colorado Lagoon has allowed for further scientific exploration of the BEF question. Current analysis focuses on aggregate and species specific patterns; it would be interesting to compare functional group differences instead (i.e., runner vs. uprights; grass vs. succulent) that may be more applicable for other systems (Funk et al., 2008; Doherty et al., 2011; Traut, 2005; Zedler et al., 2001). As all possible three-species combinations were planted instead of random subsets, I will eventually be able to analyze which species are relatively high- and low-performers, and how that might vary depending on the other species in their plots. This information will be beneficial for future restoration projects in southern California because it could provide evidence to avoid certain combinations that may reduce rather than enhance function in marshes. It is important that all habitat restoration be as

informed as possible, otherwise our attempts at amending past degradation may not be as beneficial as assumed.

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LITERATURE CITED

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