

Introduction:

Some of the most prominent ecological experiments in the past two decades have examined the effect of diversity on ecosystem functioning by manipulating the species richness of plant communities (Tilman and Downing 1994, Hector et al. 1999, Tilman et al. 2006). The collective conclusion of these experiments, namely that biodiversity and ecosystem functioning (BEF) are positively related, became the founding principle of BEF theory (Hooper et al. 2005). Because it links diversity to tangible functions, BEF theory is used to justify both conservation (Egoh et al. 2007) and restoration of diversity (Naeem 2006). BEF models predict that diversity and functioning are related by positive linear (Bradshaw 1997) or positive asymptotic (Naeem 2006) trends in restored ecosystems. Though such models are widely supported by tightly-controlled BEF experiments (Balvanera et al. 2006), they are rarely tested in restored field sites.

The goal of ecological restoration is to return degraded systems to their natural origins (Bradshaw 1997). Thus, it is the natural processes such as disturbance and competition, present in developing restorations but absent in BEF experiments, which require field testing of experimentally-derived BEF models. Three field studies indicate that BEF theory is not universally applicable: (1) in a natural grassland (Thompson et al. 2005), (2) across several ecosystem states (Jelinski et al. 2007), and (3) in a former BEF experiment after the cessation of weeding controls (Pfisterer et al. 2004). To my knowledge, diversity has been shown to enhance functioning in only one restored field site, a young salt marsh at Tijuana Estuary known as the Tidal Linkage (Callaway et al. 2003). Therefore, field studies are needed to test if the restoration of diversity increases function, to assess changes in BEF relationships as sites mature, and to quantify the functions enhanced by diversity. I propose to address both needs by testing the applicability of the BEF models in the Tidal Linkage site 12 years after its restoration and by measuring the effect of species richness on multiple functions.

Site History:

The Tidal Linkage is a 0.7-ha site that was excavated from disturbed upland in 1997 and planted with eight native marsh plain seedlings in randomly-drawn assemblages of 0, 1, 3, or 6 species per plot for a total of 87 2x2-m plots. These species richness treatment plots were maintained for two years after planting by weeding and replacement of some seedlings. Positive correlations between species richness and ecosystem functioning were observed in 1999-2000 for the following functions: canopy layering (Keer and Zedler 2002), resistance to invasion (Lindig-Cisneros and Zedler 2002), N accumulation, shoot biomass, and root biomass (Callaway et al. 2003). Thus, BEF theory was supported by all functions.

Project Progress:

Following observations that the Tidal Linkage had lost diversity over time (Zedler and West 2008), I returned to the site in 2008 to assess the relationship between species richness and both aboveground net primary productivity (ANPP) and shoot biomass in the original plots created by Callaway et al. My 2008 species richness data portray a simplified Tidal Linkage plant community: two of the original species, *Salicornia virginica* (Sv) and *Jaumea carnosa* (Jc), now comprise 88% of all shoot biomass while three short-lived species, including locally-rare *Suaeda esteroa*, are scarcely present (Figure 1). Though ANPP was not comparable with earlier data from the site and showed no correlation with species richness, shoot biomass has changed a great deal since 2000 becoming more homogeneous across species richness treatments and increasing overall at the site (Figure 2). The positive relationship between species richness and shoot biomass reported by Callaway et al. (2003) can be attributed almost entirely to positive sampling effects associated with Sv and Jc (Sullivan et al. 2007), meaning plots with high

species richness yielded more shoot biomass because they more likely included the two highly productive species. Hence, in nine years without weeding controls, Sv and Jc outcompeted other species and increased their abundance, thereby creating a less diverse, more productive plant community at the Tidal Linkage and reversing the positive relationship between species richness and shoot biomass in 2000 to a negative relationship in 2008 (Figure 3, $p < 0.001$).

Figures:

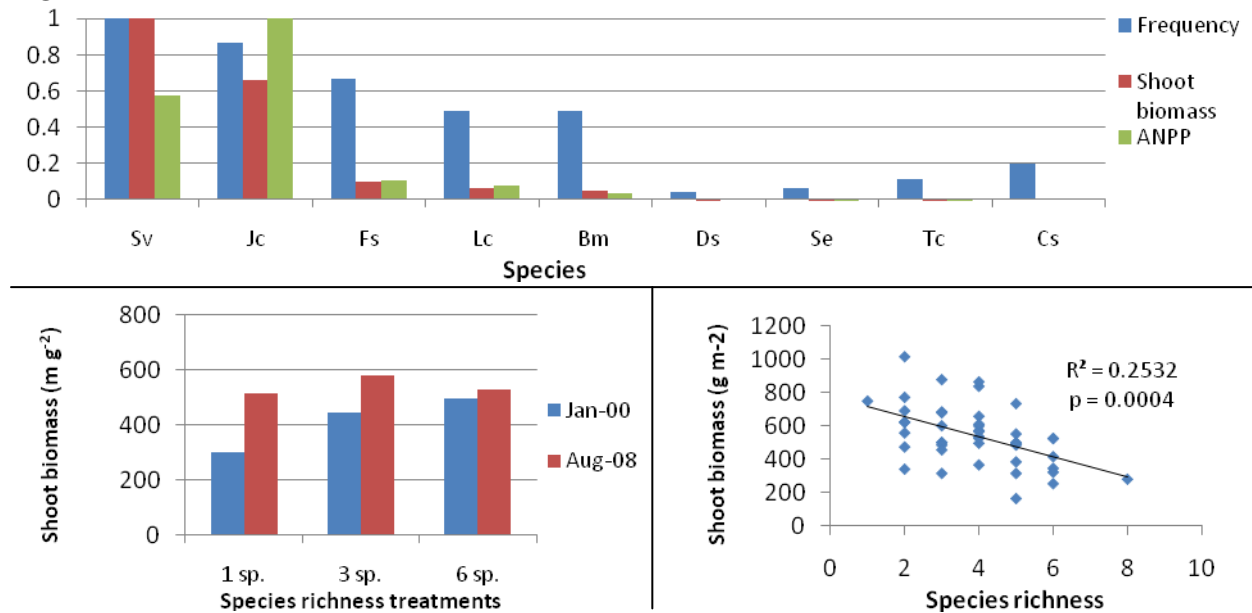


Figure 1 (top). Normalized frequency, shoot biomass, and ANPP from 45 0.25-m² plots by species: *Salicornia virginica* (Sv), *Jaumea carnosa* (Jc), *Frankenia salina* (Fs), *Limonium californicum* (Lc), *Batis maritima* (Bm), *Distichlis spicata* (Ds), *Suaeda Esteroa* (Se), *Triglochin concinna* (Tc), and *Cuscuta salina* (Cs).

Figure 2 (bottom left). Mean shoot biomass of 3 species richness treatments established in 1997 and measured in 2000 and 2008, treatment n=15.

Figure 3 (bottom right). Regression of shoot biomass and species richness in 2008, n=45.

Proposed Project Description:

My 2008 shoot biomass data from the Tidal Linkage do not support BEF theory, but they do not discount the fact that high diversity accelerated the development of several functions as shown by Callaway et al. (2003). Also, the benefits of current diversity might be hidden; for example, if Sv and Jc populations were damaged it might reveal the capacity of non-dominant species to replace the lost community biomass. BEF theory explains such benefits of diversity with the portfolio hypothesis, which states that large pools of species are more likely to include at least one species that can withstand a given disturbance (Naeem 2006). BEF experiments support the portfolio hypothesis by measuring the stability of shoot biomass across diversity treatments (Mulder et al. 2001, Tilman et al. 2006). I have found no previous tests of BEF theory measuring stability as a function in restored field sites, though it is likely just as important to restoration practitioners as ANPP, the most frequently measured function (Balvanera et al. 2006). In the Tidal Linkage, the portfolio hypothesis leads me to expect greater recovery of ANPP by species-rich plots, from which, I removed shoot biomass in 2008; therefore, I propose to test the effect of diversity on stability by measuring the recovery of ANPP in 2009.

Zedler and West (2008) suggest reestablishing *Suaeda esteroa* (Se) and other species that have decreased in abundance at Tijuana Estuary to avoid losing them and their unique features. Se is productive early in the growing season, can re-colonize disturbance patches, and functions

as a territory-defense perch for the endangered Belding's Savannah Sparrow (Zedler et al. 2001). Though *Se* recruited in large numbers during its first and second seasons at the Tidal Linkage (Lindig-Cisneros and Zedler 2002), it now occurs in only 7% of plots and comprises only 1% of all ANPP (Figure 1). *Se* seedlings might require unique microsite environments, as does a European *Suaeda* (Tessier et al. 2000). Based on work by Morzaria-Luna et al. (2004), I hypothesize that canopy openings and wrack deposits facilitate *Se* recruitment by mulching seedlings, and so, I will expose *Se* seedlings to these factors in an experimental reestablishment at the Tidal Linkage.

Methods:

In 2009 I will repeat my aboveground biomass harvesting methods used in 2008 to ensure a reliable comparison of ANPP data. Methods are as follows: relocate 15 0.25-m² plots of each species richness treatment (1, 3, and 6); record species present, canopy layering (as in Keer and Zedler 2002), and maximum height of each species then collect all shot biomass; separate annual v. perennial biomass (to determine ANPP); combust samples of biomass at 550°C (for ash content). Recovery of ANPP will be measured as the fraction of pre-disturbance ANPP (2008) recovered as post disturbance ANPP (2009) after one year. I will use regression analysis to analyze 2008 species richness v. recovery of ANPP (2009 ANPP/2008 ANPP).

To test the hypothesis that wrack mulching increases *Se* establishment, I will grow *Se* seedlings (from seeds already collected from Tijuana Estuary) then transplant them into 0.1-m² subplots in the center of the 0.25-m² plots I will have cleared to assess recovery of ANPP. Wrack will be laid out in various thicknesses and arrangements to create four treatments of slightly different disturbance-levels that might suit *Se* establishment, as follows: 2 cm of wrack spread throughout the 0.25-m² plot, 6 cm of wrack placed in the ring around the area planted with *Se*, 6 cm of wrack placed in the ring around the area planted with *Se*, and a control with no wrack; wrack will be held in place with string as in Bertness and Ellison (1987). I will measure survival and recruitment in May 2009 and assess treatment effects with ANOVA.

Project Significance:

Since my proposed study is the first to investigate the effect of diversity on stability in a restored site, it will add novel information to restoration ecology. If I find a positive correlation between diversity and stability, a compelling argument will be made for the restoration of diversity, as increased human land use has led to more disturbances in tidal marshes in California (Peterson et al. 2008) and around the world (Hooper et al. 2005). The positive BEF relationships measured at the Tidal Linkage in 2000 are the strongest field-based support of BEF theory in restorations, but they do not appear to withstand the test of time. My proposed field study of the relationship between species richness and stability will further our development of BEF theory and expand my 2008 data on the maturing Tidal Linkage.

My experiment to reestablish *Se* will advance knowledge of how to restore a rare species at Tijuana Estuary. If I learn how to restore *Se*, one component of diversity and its unique set of features, will become restorable region wide.

In the summer of 2008 I conducted the Tidal Linkage study mentioned above and a parallel study in Curtis Prairie, Madison, WI. I will continue that parallel by measuring recovery of ANPP at those same locations plus a Wisconsin floodplain that underwent record flooding last year. After completing my M.S. degree, I plan to pursue a Ph.D. with a similar theme, specifically, I would like to embed diversity treatments into several mitigation wetlands in the Madison, WI area then chart the development of several functions the wetlands. After my doctorate, I intend to practice mitigation or restoration utilizing experimental approaches.

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