Herbivory and presence of a dominant competitor interactively affect salt marsh plant diversity

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Abstract

Question: Do herbivory and the presence of a dominant grass competitor interactively affect herbaceous communities and assembly rules in a SW Atlantic salt marsh?

Location: Upper salt marsh, Mar Chiquita coastal lagoon, Argentina.

Methods: We performed a field factorial experiment over 4 yr to evaluate the separate and interactive effects of (1) herbivory and (2) competition with the dominant grass species (i.e. *Spartina densiflora*) on the salt marsh subordinate plant community. The factorial design includes dominant grass removal and herbivory manipulation.

Results: Our results show that herbivory and presence of the dominant competitor interactively affect subordinate plant cover and diversity. Results further indicate that, in the presence of the dominant competitor, patch-to-patch variation in subordinate species composition is lower than expected at random, a result consistent with the expected outcomes of deterministic exclusion following light competition. Removal of the dominant grass nevertheless led to patch-to-patch dissimilarity in subordinate species composition, far from the dissimilarity expected at random, indicating increased importance of deterministic processes that drive communities to diverge.

Conclusion: Our results show that the conditional effect of herbivory on plant diversity can be determined by the presence of a single plant species. Dominant plant species, in addition, may not only affect plant species diversity by determining the number and identity of subordinate species in a given patch (i.e. α-diversity) but also by affecting spatial variability through habitat homogenization.

Introduction

Understanding the ecological processes that determine biological diversity is one of the major goals of community ecology (Levine & HilleRisLambers 2009). Early ecological theory interpreted local species diversity as a consequence of stochastic and historical accumulation of species through colonization and extinction dynamics (see MacArthur 1965; MacArthur & Wilson 1967). Later, with the rise of population ecology, with a focus on negative interactions, local diversity started to be perceived either as a result of competition/niche partitioning processes (MacArthur 1972; Auerbach & Shmida 1987), as a result of a top-down control performed by consumers (Hairston et al. 1960; Paine 1966; McNaughton 1985), or as a

combination of disturbance and competition (Dayton 1971; Platt 1975). After three decades of intense theoretical and empirical work, there is now increasing acceptance that diversity of natural communities is determined by a combination of different stochastic (including colonization/extinction dynamics, ecological drift and dispersal dynamics; see Chase et al. 2009) and deterministic (including competition, trophic interactions, physical stress and facilitation, among others) forces acting and interacting together.

Among the deterministic forces that can affect community structure, interspecific competition for a limiting resource can act as a strong filter, determining which species of the regional pool can be present, thus establishing local communities with limited memberships (Grime

1973; Kunstler et al. 2012). If species in the regional pool differ in their competitive ability for different resources, local communities will be occupied by the subset of species that are competitively superior in the context of the local resource conditions (Tilman 1982; Keddy & Shipley 1989). One of the most clear-cut examples of competitive exclusion occurs in plant productive systems, where above-ground competition for light is intense. In these systems, light availability is reduced by fast-growing taller species that preempt the resource (Grime 1973; Tilman 1982). The lack of ground-level light usually drives the exclusion of all but a few subordinate species that, through specific adaptations, are capable of tolerating extremely low resource levels (Hautier et al. 2009).

Herbivory is also recognized as a deterministic filter that can affect the structure of plant communities (Olff & Ritchie 1998). Herbivory effects on plant diversity, however, can vary from positive (by removing plant biomass and decreasing light competition, herbivores allow subordinate species to survive) to negative (by consuming palatable species, herbivores can generate low diversity patches dominated by the subset of non-palatable or herbivore-resistant species). The contrasting effects of herbivores on different systems are thought to be driven by levels of productivity (i.e. competition intensity; Olff & Ritchie 1998; Proulx & Mazumder 1998; Osem et al. 2002) and size of herbivores (i.e. small herbivores are usually more selective; Olff & Ritchie 1998; Edwards & Crawley 1999; Bakker et al. 2006). The effect of herbivory on plant community assembly is, thus, strongly tied to the levels of plant competition (Olff & Ritchie 1998; Bakker et al. 2006). Although the effect of herbivory on plant diversity under different competition intensities has previously been explored either in productivity gradients (Bakker et al. 2006) or by manipulating soil fertility (Borer et al. 2014), experimental evidence from studies that jointly and directly manipulate the presence of dominant competitors and herbivores is scarce. This is especially important in systems where there is a clear dominant competitor (which practically monopolizes the resources) because competition intensity is set by this single species.

Competition and herbivory were traditionally seen as niche-based processes, but their effect on plant diversity can be mediated by both deterministic (i.e. related to niche) and neutral processes (Tilman 2004; Adler & Drake 2008; Orrock & Watling 2010). Competitive exclusion, for instance, can be either deterministic or neutral in terms of the identity of excluded species (Segre et al. 2014). Deterministic exclusion occurs when the identity of the excluded species is related to its capacity to tolerate low resource levels, whereas neutral exclusion occurs when the identity of the excluded species is random (Segre et al. 2014). For example, as productivity increases, the loss of

short plant species as a group is deterministic, but which of those species disappears in a given patch can be random (Alberti et al. 2017). Similarly, consumers can deterministically reduce the number of species by removing non-tolerant species (Chase et al. 2009; Germain et al. 2013), but they can also increase the importance of neutral processes by relaxing competitive exclusion (Segre et al. 2014; Alberti et al. 2017). Thus, the interaction between competition and herbivory can potentially affect plant species diversity not only as direct deterministic forces but also by influencing the relative importance of deterministic and neutral processes in community assembly.

Here we evaluated how herbivory and the presence of a dominant grass competitor affect herbaceous diversity and assembly rules in a SW Atlantic salt marsh. Salt marshes are environments that experience strong abiotic forces (Ewing 1983; Bertness 1998) and are commonly dominated by a single species. The presence of the dominant species can, nevertheless, sometimes buffer environmental conditions and facilitate the survival of other herbaceous subordinate species (Bertness & Shumway 1993; Hacker & Bertness 1999; Callaway & Pennings 2000). Plant species diversity is thus usually a balance between competitive and facilitative processes with the dominant species (Bertness & Shumway 1993; Callaway & Pennings 2000). Although subordinate species usually depend on the presence of herbivores that generate and maintain patches with low dominant cover (Bakker et al. 1993; Gough & Grace 1998; Kuijper & Bakker 2003; Daleo et al. 2014), they can also be negatively affected by strong herbivore pressure (Ungar 1998). We hypothesize that the presence of the dominant plant species negatively affects subordinate cover but positively affects subordinate diversity (as the dominant halophyte ameliorates environmental stress – the major deterministic filter – allowing most of the species present in the regional species pool to survive). We also hypothesize that, by decreasing cover of the dominant species, herbivores positively affect subordinate cover and diversity (by concomitantly increasing light availability). Finally, we hypothesize that in the absence of the dominant species, herbivores will become a deterministic filter, decreasing subordinate cover and diversity.

Methods

Study site

The study was performed in an extensive salt marsh located at the mouth of the Mar Chiquita coastal lagoon (Argentina; 37°32′ S, 57°19′ W). This lagoon is affected by semi-diurnal microtides (<1 m) and is characterized by bare mudflats in the low intertidal zone followed by marshes of the cordgrass *Spartina densiflora* at intermediate elevations. An extended plant community, characterized

by a matrix of *S. densiflora* inter-mixed with other halophytes (such as *Sarcocornia perennis*, *Limonium brasiliense* and the saltgrass *Distichlis spicata*) as well as herb species (such as *Cressa truxillensis*, *Acmella decumbens*, *Conyza bonariensis*, *Apium sellowianum* and *Picris echioides*, among others) can be found in the upper salt marsh (Alberti et al. 2011; Daleo et al. 2014). We focus on the assemblage of these herbaceous subordinate species. In this zone, the dominant herbivores are wild guinea pigs (*Cavia aperea*), which exert strong control on plant production, diversity and successional trajectories (Alberti et al. 2011; Daleo et al. 2014; Pascual et al. 2017) by consuming not only the dominant cordgrass *S. densiflora* but also other subordinate plant species (Vicari et al. 2002; Alberti et al. 2011; Daleo et al. 2014).

Experimental set up

We conducted a fully factorial experiment to evaluate the separate and interactive effect of competition with the dominant grass species (i.e. *S. densiflora*) and herbivory on the subordinate plant community. Our factorial design includes dominant grass removal (with and without *S. densiflora* removal) and herbivory manipulation (with and without herbivore exclusion). Given the variability and patchy nature of herbivory pressure, herbivory manipulation was implemented in a split-plot design (i.e. dominant competitor removal factor was implemented using 0.7 × 1.5-m plots that were then divided into two 0.7 m × 0.7-m subplots with a 0.1 m buffer between them). This plot size is consistent with the size of natural patches observed in the field (Alberti et al. 2011). Each treatment combination was replicated six times (for a total of 12 plots and 24 subplots). Dominant competitor removal was implemented by removing *S. densiflora* above-ground biomass and rhizomes using scissors, minimizing the impact on sediment structure (see Daleo et al. 2014). This removal was implemented at the beginning of the experiment in Jan 2010, and repeated every 3 mo (when necessary) during the first year. Subsequent maintenance of treatments consisted in the removal of sporadic seedlings if present. Herbivore exclusion subplots were surrounded with a plastic mesh (10 mm opening) fence 0.6-m high supported by iron stakes. Similar exclosures have been widely used in this system, and the use of cage controls revealed that there are no associated cage artifacts (Alberti et al. 2007, 2010; Daleo et al. 2007, 2009, 2014). The experiment ran for over 4 yr (from Jan 2010 to Apr 2014). At the end of the experiment, cover was visually estimated at each plot to the nearest 1% for each species. Cover was estimated independently for each species (thus, total summed cover can exceed 100% for multilayer canopies). The complete list of plant species found at the end of the experiment is given in Table 1. To evaluate if the effects of herbivory and competition on plant diversity are mediated by light availability (see Borer et al. 2014), photosynthetic active radiation (PAR) was measured above the vegetation and at the soil surface in each plot. PAR availability at the soil surface was estimated as the ratio between PAR at the soil surface and PAR above the vegetation.

Statistical analyses

The effects of herbivory and competition on subordinate plant cover and species richness, as well as on PAR availability, were modelled using LMEM with the *lmer* function from the *lme4* package (Bates et al. 2015) in R 3.1.2 (R Core Team 2014). Herbivory and competition were treated as fixed factors, whereas plot was treated as random factor to reflect the split-plot nature of the design. Visual inspection of residual plots did not reveal any obvious deviations from homoscedasticity or normality. The final model was selected using the likelihood ratio test (always consistent with the AIC criterion) following Zuur et al. (2009). The effect of herbivory on dominant plant cover was analysed with a paired *t*-test.

To discriminate whether the effects of experimental treatments on subordinate diversity were due to differences in the underlying assembly mechanisms (i.e. the relative contribution of neutral and deterministic forces), we used a null model approach based on the Raup-Crick metric (Raup & Crick 1979). Raup-Crick metric modification, proposed by Chase et al. (2011), provides a metric that ranges from −1 to 1, with negative values indicating communities sharing more species than expected at random, positive values indicating communities sharing fewer species than expected at random, and zero values indicating communities that share exactly the number of species as expected at random. As this metric becomes less similar to 0 (either positive or negative), the relative importance of deterministic processes increases (because the community structure is less likely explained by chance). Values approaching −1 (more similar than expected at random) reflect treatments that allow replicates to converge (homogeneous environmental filtering), while values approaching 1 (less similar than expected at random) reflect processes that allow replicates to diverge (heterogeneous environmental filtering). It is important to note that this null model approach was not intended to disentangle or manipulate the neutral and deterministic processes *per se* but only to evaluate if the community assembly process is more deterministic or more neutral. This was done through exploring whether replicates of a treatment are more or less similar to expectations from a null model obtained by randomly sampling species from the regional pool (Chase et al. 2011).

Table 1. List of herbaceous species observed in the experiment. Presence was estimated as the number of subplots (total = 24) where a given species was present.

| Species Name	Family	% Cover (Mean ± SE)	Presence
Apium sellowianum	Apiaceae	6.75 ± 1.28	19
Carduus acanthoides	Asteraceae	0.21 ± 0.21	1
Carduus nutans	Asteraceae	0.21 ± 0.21	1
Conyza bonariensis	Asteraceae	1.00 ± 0.47	10
Gamochaeta americana	Asteraceae	1.08 ± 0.50	5
Hypochaeris radicata	Asteraceae	2.17 ± 0.73	11
Pluchea sagittalis	Asteraceae	2.71 ± 1.04	6
Senecio selloi	Asteraceae	1.37 ± 0.57	6
Sonchus asper	Asteraceae	0.42 ± 0.42	1
Atriplex montevidensis	Chenopodiaceae	0.83 ± 0.83	1
Sarcocornia perennis	Chenopodiaceae	6.96 ± 2.10	16
Cressa truxillensis	Convolvulaceae	2.54 ± 1.27	8
Carex vixdentata	Cyperaceae	1.67 ± 0.53	9
Melilotus officinalis	Fabaceae	0.72 ± 0.47	4
Blackstonia perfoliata	Gentianaceae	0.08 ± 0.08	1
Plantago myosurus	Plantaginaceae	0.54 ± 0.36	3
Limonium brasiliense	Plumbaginaceae	0.42 ± 0.31	2
Cortaderia selloana	Poaceae	2.46 ± 1.38	5
Distichlis spicata	Poaceae	4.08 ± 1.41	12
Imperata brasiliensis	Poaceae	0.21 ± 0.21	1
Polypogon monspeliensis	Poaceae	6.62 ± 3.19	8
Poa lanigera	Poaceae	9.17 ± 3.84	7
Polygala pulchella	Polygalaceae	1.29 ± 0.72	4
Samolus valerandi	Primulaceae	0.25 ± 0.15	3
Unidentified grass	Poaceae	0.50 ± 0.42	2

A null model was constructed by performing a probability-based randomization, in which randomly generated species composition and cover were assembled for each sampling unit (i.e. subplot) by sampling from the total species pool (estimated as the list of species observed in all sampling units) under four constraints: (1) the number of species of the randomly generated sample equals the number of species actually observed in the subplot, (2) the probability of occurrence (i.e. probability of being present in a subplot) for a given species was proportional to its observed total occurrence frequency (i.e. the proportion of subplots where this species was actually observed), (3) the total abundance of the randomly generated sample equals the total abundance actually observed in the subplot, and (4) the abundance probability for each species in the randomly generated sample was proportional to its observed total abundance. For all possible pairs of subplots, species composition of each subplot was probabilistically generated 9999 times. Bray-Curtis dissimilarity index between subplots was measured for each iteration, and the resulting metric was the proportion of iterations in which the index was smaller or equal to the actual observed Bray-Curtis dissimilarity index between that pair of subplots (Chase et al. 2011; Stegen et al. 2013). Finally, the metric was standardized to range from −1 to 1 by subtracting 0.5 and multiplying by 2 (Chase et al. 2011). Hereafter we call this

metric the RC metric. Given that all pair-wise combinations of subplots were calculated, the resulting distance matrix, based on the deviations from the species compositions expected by chance, can be analysed using the same set of statistical methods used for many other pair-wise indices of dissimilarity (see Chase et al. 2011). To evaluate the effects of herbivory and competition on the balance between neutral and deterministic processes governing herbaceous plant community assembly, an analysis of multivariate homogeneity of group dispersions (Anderson et al. 2006), based on the dissimilarity matrices constructed with RC metric (using 1999 permutations), was performed. Significant results indicate that at least one treatment differs from another in its RC metric (i.e. differs in the relative importance of deterministic and neutral processes in community assembly). We performed this analysis using the *betadisper* and *permutest* functions from *vegan* package (Oksanen et al. 2015) in R.

Results

Changes in subordinate species cover and richness

After 4 yr of the experiment, the net effect of *S. densiflora* on subordinate herbaceous species cover was clearly negative, suggesting a strong competitive interaction (see Fig. 1a). Removal of *S. densiflora* increased subordinate
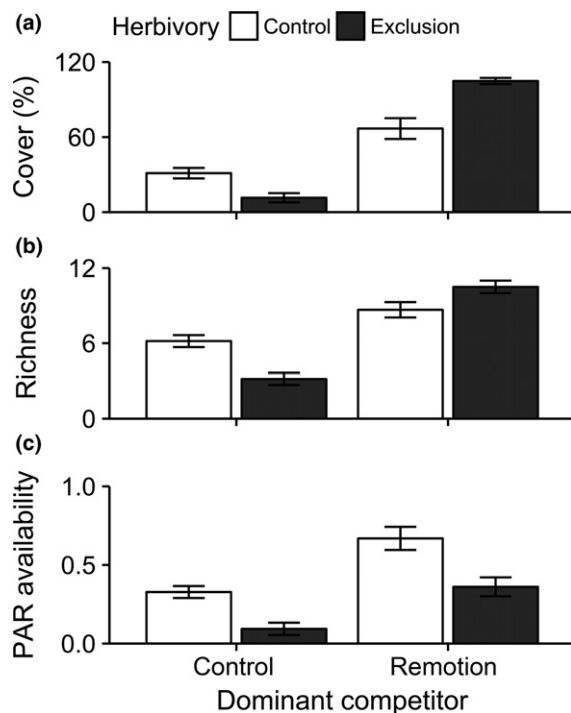
Fig. 1. Effect of competition with the dominant grass *S. densiflora* and herbivory on subordinate plant species cover (**a**) and richness (**b**) as well as on PAR availability (**c**). Bars are means ± SE.

plant species cover by 114% when herbivores were present, but this increase reached 812% when herbivores were excluded (Competition × Herbivory: $\chi_1 = 23.3$, $P = 0.0001$; Fig. 1a). In plots dominated with *S. densiflora*, herbivory exclusion significantly increased *S. densiflora* cover from nearly 60% to >90% (paired *t*-test, $t = 2.6$, $df = 11$, $P < 0.05$) but decreased subordinate herbaceous cover from about 30% to about 10% (see Fig. 1a). In contrast, when *S. densiflora* was removed, exclusion of herbivores increased subordinate herbaceous cover from about 65% to almost 100% (C × H: $\chi_1 = 23.3$, $P < 0.0001$; Fig. 1a). The same pattern was observed for subordinate species richness: removal of *S. densiflora* increased subordinate species richness to a higher degree when herbivores were absent (232%) than when herbivores were present (41%; C × H: $\chi_1 = 21.8$, $P < 0.0001$; Fig. 1b). The effect of herbivores on subordinate species richness was dependent on the presence of *S. densiflora*: while herbivory exclusion decreased subordinate richness by about 50% when *S. densiflora* was present, it increased it by 20% when *S. densiflora* was removed (Fig. 1b). As expected, removal of *S. densiflora* increased PAR availability at ground level by around 140% (C: $\chi_1 = 14.2$, $P < 0.0001$; Fig. 1c) and herbivory exclusion decreased it by about 50% (H: $\chi_1 = 20.2$, $P < 0.0001$; Fig. 1c) but there was no interaction between factors (C × H: $\chi_1 = 0.82$, $P = 0.37$; Fig. 1c).

Changes in dissimilarity and the balance between neutral and deterministic forces

The relative contribution of neutral and deterministic forces (RC metric) differed among treatments (pseudo-$F_{3,20} = 5.06$, $P = 0.0095$; Fig. 2). Pair-wise comparisons showed that there were two different groups determined by the presence or absence of *S. densiflora*, without an apparent effect of herbivory (see Fig. 2). In other words, independent of the presence of herbivores, removal of the dominant competitor led to a significant increase in RC metric from negative to positive values. Thus, we further conducted separate analyses of multivariate homogeneity of group dispersions, one for each main effect (i.e. competition and herbivory). The analyses showed that competition significantly affected RC metric (pseudo-$F_{1,22} = 22.4$, $P = 0.0005$) but there was no effect of herbivory (pseudo-$F_{1,22} = 0.12$, $P = 0.64$). Although species compositions were more similar than expected at random when *S. densiflora* was present (RC = -0.33 ± 0.07), they were less similar than expected at random in plots where *S. densiflora* was removed (RC = 0.58 ± 0.06). To evaluate whether the net deviation from purely neutral communities was the same between treatments with and without *S. densiflora* (regardless of the contrasting direction in the deviation), we used the absolute value of RC metric to examine
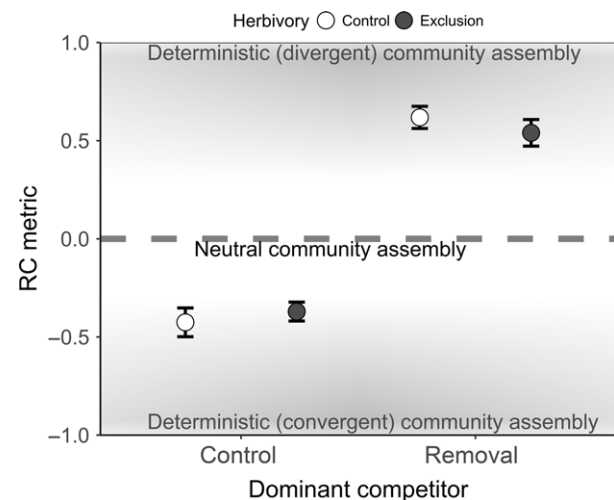
Fig. 2. Mean (±SE) Raup-Crick metric (RC metric) within-treatment. This metric ranges from −1 to 1 and indicates whether a pair of plots are less similar (approaching 1), as similar (approaching 0), or more similar (approaching −1) than a pair of plots randomly assembled by sampling species from the regional pool. Differences between treatments are evaluated using the analysis of multivariate homogeneity of group dispersions, in which non-Euclidean distances between objects and group centroids are handled by reducing the original distances to principal coordinates.

multivariate homogeneity of group dispersions. This analysis showed that the absolute deviation from neutral communities did not differ significantly between the two treatments (pseudo-$F_{1,22}$ = 2.46, P = 0.16).

Discussion

Our results show that herbivory and competition interactively affected subordinate plant communities; whereas exclusion of herbivores increased dominance of *S. densiflora* and decreased the cover and richness of subordinate species, removal of *S. densiflora* positively affected both variables. Nonetheless, the subordinate plant community reached its highest cover and richness when both *S. densiflora* was removed and herbivores were excluded simultaneously. Results further indicate that competition with the dominant grass made patch-to-patch subordinate species composition more similar than expected at random, a result consistent with the expected outcomes of deterministic exclusion following light competition. The removal of the dominant grass, however, led to higher divergence than expected at random in subordinate species composition. The absolute deviation from neutral communities, indeed, was similar in the presence or absence of *S. densiflora*, suggesting that the balance between deterministic and neutral processes is similar in both situations.

Effect of competition and herbivory on subordinate cover and species richness

Salt marshes are systems characterized by the presence of strong environmental limiting factors for plant growth, such as salinity and anoxia (Pennings & Bertness 2001). Once established, however, stress-tolerant plant species can facilitate the survival of other less tolerant herbaceous species by buffering harsh environmental conditions (Callaway & Pennings 2000). However, dominant species can also decrease resource availability for subordinate species (Bertness & Shumway 1993; Hacker & Bertness 1999). Thus, salt marsh plant diversity is usually a balance between competitive and facilitative processes (Hacker & Bertness 1999). Our results show that competition for light seems to play a larger role than facilitation in our system, as removal of the dominant grass led to significant increases in light availability as well as in subordinate plant cover and richness. Herbivory exclusion, in turn, increased dominance, decreased light availability and decreased both subordinate cover and richness. Nevertheless, the effects of both factors were not additive but interactive: when they occurred simultaneously, removal of the dominant competitor and exclusion of herbivores drove higher subordinate biomass and richness. These results suggest that: (1) the net effect of *S. densiflora* on subordinate plants is negative (the dominant grass competitively excludes some subordinate species); (2) herbivores have an indirect positive effect on subordinate growth by decreasing *S. densiflora* dominance and increasing light availability (see Borer et al. 2014); and (3) without *S. densiflora*, herbivores have a negative effect on subordinate species.

Herbivores can either increase plant species diversity by decreasing light competition (Olff & Ritchie 1998; Borer et al. 2014) or decrease it by consumption and eradication of palatable species (see Olff & Ritchie 1998). As pointed out earlier, these contrasting effects are thought to be driven by levels of productivity (i.e. if the intensity of light competition is high, the net effect of herbivores on plant diversity is positive; Olff & Ritchie 1998; Osem et al. 2002; Bakker et al. 2006; Hillebrand et al. 2007) and size of herbivores (i.e. small herbivores are more selective than large herbivores and can differentially affect more palatable species; Olff & Ritchie 1998; Edwards & Crawley 1999; Bakker et al. 2006). Our results show that the outcome of herbivory on plant diversity can also be influenced by the presence of a single dominant plant species: when the dominant competitor was present, herbivory decreased (probably light) competition strength, allowing subordinate species to survive, but in the absence of the dominant competitor, herbivory removed some species from the system, decreasing diversity. Thus, the intensity of competition, determined by fertility gradients or by the presence or not of a single plant species, may still hold as the main control of the effect of herbivores on plant diversity.

For a long time, the only important factors in determining salt marsh community structure were thought to be abiotic stress and nutrient competition (Pomeroy & Wiegert 1981; Adam 1993), but herbivory is now also considered as a force strong enough to influence salt marsh functioning (Silliman et al. 2005; Jefferies et al. 2006). Herbivory can play a major role in determining salt marsh plant diversity by slowing down successional dynamics and suppressing re-colonization of the dominant marsh grasses, thus allowing subordinate species to survive in disturbed patches (Bakker et al. 1993; Kuijper & Bakker 2003; Daleo et al. 2014). Here we show that even in undisturbed patches herbivores can decrease dominance, positively affecting plant diversity.

Effects of herbivory and competition on the role of stochastic and deterministic forces in salt marsh plant assembly

Communities assemble through a combination of neutral processes that make environmentally similar communities diverge, and deterministic processes that make environmentally similar communities converge (Chase et al. 2009). One might think that biological interactions

associated with the niche concept, such as competition or predation/herbivory, would act as clear deterministic biological filters that, by decreasing the number of species that can exist in a given locality, drive community convergence (Chase 2007). There is, nevertheless, increasing evidence that those interactions can drive either convergence or divergence of environmentally similar communities (see Chase et al. 2009; Segre et al. 2014). Consumers (i.e. predators or herbivores), for example, can increase the importance of deterministic processes (i.e. increasing convergence of prey assemblages) by driving sensitive species to extinction (stochastic variation in species composition is less likely to occur in smaller, consumer-filtered species pools; see Chase et al. 2009; Alberti et al. 2017). But consumers can also increase the importance of neutral processes (increasing divergence) by decreasing the dominance of competitively superior species, by decreasing the number of individuals that can live in a given locality (Orrock & Fletcher 2005) or even by increasing the probability of random local extinctions (Ryberg & Chase 2007; Chase et al. 2009). Similarly, competition usually drives decreases in the number of species in a given locality. But this competitive exclusion can be either deterministic (species not capable of tolerating low resource levels are excluded) or neutral (the identity of excluded species is random; Segre et al. 2014). Our results show that the presence of the dominant plant *S. densiflora* decreases the number of subordinate species and leads species assemblages to converge, a result compatible with the expected outcomes of deterministic exclusion following light competition (see Segre et al. 2014). However, we also found that RC metric was higher than expected at random when *S. densiflora* was removed, indicating an increased importance of processes that drive community divergence far from the null model expectation (see Myers et al. 2015). In this context, in a recent work, Guo et al. (2014) argued that the higher β-diversity (i.e. difference in species composition or divergence between patches) observed in NW Atlantic salt marshes is related to high heterogeneity of microhabitats that act as strong deterministic forces. Thus, the decrease in RC metric in the presence of *S. densiflora* may not only be related to deterministic competition but also to decreases in the importance of habitat heterogeneity as a filter (see also Myers et al. 2015). Clonal plants, such as *S. densiflora*, have a clear advantage in heterogeneous habitats (Hutchings & Bradbury 1986; Wijesinghe & Handel 1994) and their presence may be capable of buffering environmental conditions as well as driving light availability to become the main limiting factor. Hence, the presence of this dominant plant may negatively affect subordinate species diversity not only by decreasing the number of species present in a give patch (i.e. α-diversity) through

competition, but also by decreasing patch-to patch variation in species composition through habitat homogenization.

In summary, the results show that competition and herbivory can interact to set plant community composition; the presence of a single species can change the sign of the herbivory effect upon subordinate plant communities. Results also suggest that the presence of dominant plant species can affect plant species diversity not only by removing species through competitive exclusion but also by decreasing environmental heterogeneity.

Acknowledgements

References

Adam, P. 1993. *Saltmarsh ecology*. Cambridge University Press, Cambridge, UK.

Adler, P.B. & Drake, J.M. 2008. Environmental variation, stochastic extinction, and competitive coexistence. *The American Naturalist* 172: E186–E195.

Alberti, J., Escapa, M., Daleo, P., Iribarne, O., Silliman, B.R. & Bertness, M. 2007. Local and geographic variation in grazing intensity by herbivorous crabs in SW Atlantic salt marshes. *Marine Ecology Progress Series* 349: 235–243.

Alberti, J., Méndez Casariego, A., Daleo, P., Fanjul, E., Silliman, B., Bertness, M. & Iribarne, O. 2010. Abiotic stress mediates top-down and bottom-up control in a Southwestern Atlantic salt marsh. *Oecologia* 163: 181–191.

Alberti, J., Canepuccia, A., Pascual, J., Pérez, C. & Iribarne, O. 2011. Joint control by rodent herbivory and nutrient availability of plant diversity in a salt marsh–salty steppe transition zone. *Journal of Vegetation Science* 22: 216–224.

Alberti, J., Bakker, E.S., Klink, R., Olff, H. & Smit, C. 2017. Herbivore exclusion promotes a more stochastic plant community assembly in a natural grassland. *Ecology* 98: 961–970.

Anderson, M.J., Ellingsen, K.E. & McArdle, B.H. 2006. Multivariate dispersion as a measure of beta diversity. *Ecology Letters* 9: 683–693.

Auerbach, M. & Shmida, A. 1987. Spatial scale and the determinants of plant species richness. *Trends in Ecology & Evolution* 2: 238–242.

Bakker, J.P., de Leeuw, J., Dijkema, K.S., Leendertse, P.C., Prins, H.H.T. & Rozema, J. 1993. Salt marshes along the coast of The Netherlands. *Hydrobiologia* 265: 73–95.

Bakker, E.S., Ritchie, M.E., Olff, H., Milchunas, D.G. & Knops, J.M.H. 2006. Herbivore impact on grassland plant diversity depends on habitat productivity and herbivore size. *Ecology Letters* 9: 780–788.

Bates, D., Maechler, M., Bolker, B., Walker, S., Christensen, R.H.B., Singmann, H. Dai, B. & Grothendieck, G. 2015. lme4: Linear Mixed-Effects Models using "Eigen" and S4.

Bertness, M.D. 1998. *The ecology of Atlantic shorelines*. Sinauer Associates, Sunderland, MA, US.

Bertness, M.D. & Shumway, S.W. 1993. Competition and facilitation in marsh plants. *The American Naturalist* 142: 718–724.

Borer, E.T., Seabloom, E.W., Gruner, D.S., Harpole, W.S., Hillebrand, H., Lind, E.M., Adler, P.B., Alberti, J., Anderson, T.M., (. . .) & Yang, L.H. 2014. Herbivores and nutrients control grassland plant diversity via light limitation. *Nature* 508: 517–520.

Cabrera, A.L. & Zardini, E.M. 1993. *Manual de la flora de los alrededores de Buenos Aires*. Editorial Acme, Buenos Aires, AR.

Callaway, R.M. & Pennings, S.C. 2000. Facilitation may buffer competitive effects: indirect and diffuse interactions among salt marsh plants. *The American Naturalist* 156: 416–424.

Chase, J.M. 2007. Drought mediates the importance of stochastic community assembly. *Proceedings of the National Academy of Sciences of the United States of America* 104: 17430–17434.

Chase, J.M., Biro, E.G., Ryberg, W.A. & Smith, K.G. 2009. Predators temper the relative importance of stochastic processes in the assembly of prey metacommunities. *Ecology Letters* 12: 1210–1218.

Chase, J.M., Kraft, N.J.B., Smith, K.G., Vellend, M. & Inouye, B.D. 2011. Using null models to disentangle variation in community dissimilarity from variation in α-diversity. *Ecosphere* 2: art24.

Daleo, P., Fanjul, E., Méndez Casariego, A., Silliman, B.R., Bertness, M.D. & Iribarne, O. 2007. Ecosystem engineers activate mycorrhizal mutualism in salt marshes. *Ecology Letters* 10: 902–908.

Daleo, P., Silliman, B., Alberti, J., Escapa, M., Canepuccia, A., Peña, N. & Iribarne, O. 2009. Grazer facilitation of fungal infection and the control of plant growth in south-western Atlantic salt marshes. *Journal of Ecology* 97: 781–787.

Daleo, P., Alberti, J., Pascual, J., Canepuccia, A. & Iribarne, O. 2014. Herbivory affects salt marsh succession dynamics by suppressing the recovery of dominant species. *Oecologia* 175: 335–343.

Dayton, P.K. 1971. Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. *Ecological Monographs* 41: 351–389.

Edwards, G.R. & Crawley, M.J. 1999. Herbivores, seed banks and seedling recruitment in mesic grassland. *Journal of Ecology* 87: 423–435.

Ewing, K. 1983. Environmental controls in Pacific Northwest intertidal marsh plant communities. *Canadian Journal of Botany* 61: 1105–1116.

Germain, R.M., Johnson, L., Schneider, S., Cottenie, K., Gillis, E.A. & MacDougall, A.S. 2013. Spatial variability in plant predation determines the strength of stochastic community assembly. *The American Naturalist* 182: 169–179.

Gough, L. & Grace, J.B. 1998. Herbivore effects on plant species density at varying productivity levels. *Ecology* 79: 1586–1594.

Grime, J.P. 1973. Competitive exclusion in herbaceous vegetation. *Nature* 242: 344–347.

Guo, H., Więski, K., Lan, Z. & Pennings, S.C. 2014. Relative influence of deterministic processes on structuring marsh plant communities varies across an abiotic gradient. *Oikos* 123: 173–178.

Hacker, S.D. & Bertness, M.D. 1999. Experimental evidence for factors maintaining plant species diversity in a New England salt marsh. *Ecology* 80: 2064–2073.

Hairston, N.G., Smith, F.E. & Slobodkin, L.B. 1960. Community structure, population control, and competition. *The American Naturalist* 94: 421–425.

Hautier, Y., Niklaus, P.A. & Hector, A. 2009. Competition for light causes plant biodiversity loss after eutrophication. *Science* 324: 636–638.

Hillebrand, H., Gruner, D.S., Borer, E.T., Bracken, M.E.S., Cleland, E.E., Elser, J.J., Harpole, W.S., Ngai, J.T., Seabloom, E.W., Shurin, J.B. & Smith, J.E. 2007. Consumer versus resource control of producer diversity depends on ecosystem type and producer community structure. *Proceedings of the National Academy of Sciences of the United States of America* 104: 10904–10909.

Hutchings, M.J. & Bradbury, I.K. 1986. Ecological perspectives on clonal perennial herbs. *BioScience* 36: 178–182.

Jefferies, R.L., Jano, A.P. & Abraham, K.F. 2006. A biotic agent promotes large-scale catastrophic change in the coastal marshes of Hudson Bay. *Journal of Ecology* 94: 234–242.

Keddy, P.A. & Shipley, B. 1989. Competitive hierarchies in herbaceous plant communities. *Oikos* 54: 234–241.

Kuijper, D.P.J. & Bakker, J.P. 2003. Large-scale effects of a small herbivore on salt-marsh vegetation succession – A comparative study on three Wadden Sea islands. *Journal of Coastal Conservation* 9: 179–188.

Kunstler, G., Lavergne, S., Courbaud, B., Thuiller, W., Vieilledent, G., Zimmermann, N.E., Kattge, J. & Coomes, D.A. 2012. Competitive interactions between forest trees are driven by species' trait hierarchy, not phylogenetic or functional similarity: implications for forest community assembly. *Ecology Letters* 15: 831–840.

Levine, J.M. & HilleRisLambers, J. 2009. The importance of niches for the maintenance of species diversity. *Nature* 461: 254–257.

MacArthur, R.H. 1965. Patterns of species diversity. *Biological Reviews* 40: 510–533.

MacArthur, R.H. 1972. *Geographical ecology: patterns in the distribution of species*. Princeton University Press, Princeton NJ, US.

MacArthur, R.H. & Wilson, E.O. 1967. *The theory of island biogeography*. Princeton University Press, Princeton, NJ, US.

McNaughton, S.J. 1985. Ecology of a grazing ecosystem: the ser-engeti. *Ecological Monographs* 55: 259–294.

Myers, J.A., Chase, J.M., Crandall, R.M. & Jiménez, I. 2015. Disturbance alters beta-diversity but not the relative importance of community assembly mechanisms. *Journal of Ecology* 103: 1291–1299.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P. Stevens, M.H.H. & Wagner, H. 2015. vegan: community ecology package. R package version 2.3-0. http://CRAN.R-project.org/package=vegan

Olff, H. & Ritchie, M.E. 1998. Effects of herbivores on grassland plant diversity. *Trends in Ecology & Evolution* 13: 261–265.

Orrock, J.L. & Fletcher, R.J.J. 2005. Changes in community size affect the outcome of competition. *The American Naturalist* 166: 107–111.

Orrock, J.L. & Watling, J.I. 2010. Local community size mediates ecological drift and competition in metacommunities. *Proceedings of the Royal Society of London series B: Biological Sciences* 277: 2185–2191.

Osem, Y., Perevolotsky, A. & Kigel, J. 2002. Grazing effect on diversity of annual plant communities in a semi-arid rangeland: interactions with small-scale spatial and temporal variation in primary productivity. *Journal of Ecology* 90: 936–946.

Paine, R.T. 1966. Food web complexity and species diversity. *The American Naturalist* 100: 65–75.

Pascual, J., Alberti, J., Daleo, P. & Iribarne, O. 2017. Herbivory and trampling by small mammals modify soil properties and plant assemblages. *Journal of Vegetation Science* 28: 1028–1035.

Pennings, S.C. & Bertness, M.D. 2001. Salt marsh communities. In: Bertness, M.D., Gaines, S.D. & Hay, M. (eds.) *Marine community ecology*, pp. 289–316. Sinauer Associates, Sunderland, MA, US.

Platt, W.J. 1975. The colonization and formation of equilibrium plant species associations on badger disturbances in a tall-grass prairie. *Ecological Monographs* 45: 285–305.

Pomeroy, L.R. & Wiegert, R.G. 1981. *The ecology of a salt marsh*. Springer, New York, NY, US.

Proulx, M. & Mazumder, A. 1998. Reversal of grazing impact on plant species richness in nutrient-poor vs. nutrient-rich ecosystems. *Ecology* 79: 2581–2592.

Raup, D.M. & Crick, R.E. 1979. Measurement of faunal similarity in paleontology. *Journal of Paleontology* 53: 1213–1227.

Ryberg, W.A. & Chase, J.M. 2007. Predator-dependent species-area relationships. *The American Naturalist* 170: 636–642.

Segre, H., Ron, R., De Malach, N., Henkin, Z., Mandel, M. & Kadmon, R. 2014. Competitive exclusion, beta diversity, and deterministic vs. stochastic drivers of community assembly. *Ecology Letters* 17: 1400–1408.

Silliman, B.R., van de Koppel, J., Bertness, M.D., Stanton, L.E. & Mendelssohn, I.A. 2005. Drought, snails, and large-scale die-off of Southern U.S. salt marshes. *Science* 310: 1803–1806.

Stegen, J.C., Lin, X., Fredrickson, J.K., Chen, X., Kennedy, D.W., Murray, C.J., Rockhold, M.L. & Konopka, A. 2013. Quantifying community assembly processes and identifying features that impose them. *The ISME Journal* 7: 2069–2079.

Tilman, D. 1982. *Resource competition and community structure*. Princeton University Press, Princeton, NJ, US.

Tilman, D. 2004. Niche tradeoffs, neutrality, and community structure: a stochastic theory of resource competition, invasion, and community assembly. *Proceedings of the National Academy of Sciences of the United States of America* 101: 10854–10861.

Ungar, I.A. 1998. Are biotic factors significant in influencing the distribution of halophytes in saline habitats? *Botanical Review* 64: 176–199.

Vicari, R.L., Fischer, S., Madanes, N., Bonaventura, S.M. & Pancotto, V. 2002. Tiller population dynamics and production on *Spartina densiflora* (Brong) on the floodplain of the Paraná River, Argentina. *Wetlands* 22: 347–354.

Wijesinghe, D.K. & Handel, S.N. 1994. Advantages of clonal growth in heterogeneous habitats: an experiment with *Potentilla simplex*. *Journal of Ecology* 82: 495–502.

Zuur, A., Ieno, E.N., Walker, N., Saveliev, A.A. & Smith, G.M. 2009. *Mixed effects models and extensions in ecology with R*. Springer Science & Business Media, New York, NY, US.