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# Hierarchical organization of a Sardinian sand dune plant community

Valentina Cusseddu, Giulia Ceccherelli, Mark Bertness

Coastal sand dunes have attracted the attention of plant ecologists for over a century, but they have largely relied on correlations to explain dune plant community organization. We experimentally examined longstanding hypotheses that sand binding, interspecific interactions, abiotic factors and seedling recruitment are drivers of sand dune plant community structure in Sardinia, Italy. Removing foundation species from the fore, middle and back dune habitats over 3 years led to erosion and habitat loss on the fore dune and limited plant recovery that increased with dune elevation. Reciprocal species removals in all zones suggested that interspecific competition is common, but that dominance is transient, particularly due to sand burial disturbance in the middle dune. A fully factorial 2-year physical factor manipulation of water, nutrient availability and substrate stability revealed no significant proximate response to these abiotic factors in any dune zone. In the fore and middle dune, plant seeds are trapped under adult plants during seed germination, and seedling survivorship and growth generally increase with dune height in spite of increased herbivory in the back dune. Sand and seed erosion lead to limited seed recruitment on the fore dune while high summer temperatures and allelopathy lead to competitive dominance of woody plants in the back dune. Our results suggest that Sardinian sand dune plant communities are hierarchically organized, structured by sand binding foundation species on the fore dune, sand burial in the middle dune and increasingly successful seedling recruitment, growth and competitive dominance in the back dune.

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Hierarchical organization of a Sardinian sand dune plant community

Valentina Cusceddu<sup>1</sup>, Giulia Ceccherelli<sup>1</sup> and Mark D. Bertness<sup>2</sup>

*<sup>1</sup>Department of Science for Nature and Environmental Resources, University of Sassari,  
Italy;*

*<sup>2</sup>Department of Ecology and Evolutionary Biology, Brown University  
Providence, Rhode Island, USA;*

Corresponding Author:

Valentina Cusceddu<sup>1</sup>

Via Piandanna 4, 07100, Sassari, Italy

e-mail address: vcusceddu@uniss.it

19 *Abstract* (246 words). Coastal sand dunes have attracted the attention of plant ecologists for  
20 over a century, but they have largely relied on correlations to explain dune plant community  
21 organization. We experimentally examined longstanding hypotheses that sand binding,  
22 interspecific interactions, abiotic factors and seedling recruitment are drivers of sand dune  
23 plant community structure in Sardinia, Italy. Removing foundation species from the fore,  
24 middle and back dune habitats over 3 years led to erosion and habitat loss on the fore dune  
25 and limited plant recovery that increased with dune elevation. Reciprocal species removals in  
26 all zones suggested that interspecific competition is common, but that dominance is transient,  
27 particularly due to sand burial disturbance in the middle dune. A fully factorial 2-year  
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29 significant proximate response to these abiotic factors in any dune zone. In the fore and  
30 middle dune, plant seeds are trapped under adult plants during seed germination, and seedling  
31 survivorship and growth generally increase with dune height in spite of increased herbivory  
32 in the back dune. Sand and seed erosion lead to limited seed recruitment on the fore dune  
33 while high summer temperatures and allelopathy lead to competitive dominance of woody  
34 plants in the back dune. Our results suggest that Sardinian sand dune plant communities are  
35 hierarchically organized, structured by sand binding foundation species on the fore dune,  
36 sand burial in the middle dune and increasingly successful seedling recruitment, growth and  
37 competitive dominance in the back dune.

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**INTRODUCTION**

43 Understanding the biotic and abiotic mechanisms that generate spatial patterns in natural  
44 communities is a major goal of ecology and is critical for developing ecology into a  
45 predictive science that can inform ecosystem management and contribute to conservation  
46 (Morin 2011). Many natural communities are structured and defined by foundation species,  
47 *sensu* Dayton (1975). Foundation species are operationally defined as common, abundant  
48 species that build and maintain habitats, ameliorating potentially limiting physical and  
49 biological stressors, thus providing habitat for other species (Jones et al. 1994, Bruno and  
50 Bertness 2001, Ellison et al. 2005, Angelini et al. 2011). Examples of foundation species-  
51 dependent ecosystems include forests, coral reefs, salt marshes, mangroves, mussel and  
52 oyster reefs, which are all built and maintained by numerically dominant habitat forming  
53 foundation species (Bruno and Bertness 2001). Amelioration of potentially limiting physical  
54 and/or biotic conditions is a hallmark of foundation species-based ecosystems. Coastal sand  
55 dunes are physically harsh habitats for the halophytic plants that dominate them and are best  
56 understood as foundation species-based ecosystems (Olf et al. 1993).

57 Recently, it has been suggested that foundation species-based ecosystems are commonly  
58 hierarchical, where the amelioration of potentially limiting stresses is responsible for  
59 ecosystem establishment and maintenance, but that other species interactions are often  
60 responsible for generating the most conspicuous, but superficial spatial patterns in these  
61 communities (Bruno and Bertness 2001, Bruno et al. 2003, Altieri et al. 2007, Angelini et al.  
62 2011). While this model of community organization appears to be widespread (Bruno and  
63 Bertness 2001), most evidence for hierarchical organization is anecdotal or correlative with  
64 few explicit experimental tests (for exceptions see Altieri et al. 2007, Angelini and Silliman  
65 2014). This is the case in spite of the potential importance of hierarchical community  
66 organization to conservation and management strategies. Plant communities that occur at the

67 land/sea interface, like sand dune, salt marsh, sea grass and mangrove communities, provide  
68 **functions?** important ecological services including stabilizing shorelines from erosion and storm  
69 damage, harboring animal diversity, providing nursery habitats to threatened avifauna,  
70 marine turtles, and shellfish, as well as processing nutrient-rich terrestrial runoff (Barbier et  
71 al. 2013). Provisioning of these services relies on informed management facing increasing  
72 threats. Sand dunes, however, are generally not conservation priorities and not managed to  
73 protect their ecosystem services (Ehrenfeld 1990, Everard et al. 2010).

74 Most research on sand dune communities has been descriptive and reliant on dated  
75 correlative literature (e.g. Cowles 1899, Oosting and Billings 1942, Mack and Harper 1977).  
76 Experimental work has been restricted to small scale sand burial, seed dispersal and  
77 disturbance studies (Maun and Perumal 1999, Franks and Peterson 2003, Miller et al. 2010),  
78 field studies of annuals, nurse plant effects and comparisons among chronosequences as a  
79 proxy for successional shifts in plant species interactions (Lichter 2000, Franks 2003,  
80 Cushman et al. 2010), experimental grazer studies (Huntzinger et al. 2008) and greenhouse  
81 studies of the importance of plant/mycorrhizal associations (Gemma et al. 1989).  
82 Experimental studies of the roles of the dominant foundation species that have long been  
83 hypothesized to build and maintain sand dune plant communities by binding sand and  
84 ameliorating potentially limiting physical conditions such as water and nutrient limitation are  
85 notably absent. Consequently, the critical interactions between biological and physical  
86 processes that have been assumed to generate the organization of sand dune communities  
87 have not been rigorously tested.

88 Descriptive and correlative studies of sand dune communities suggest that substrate  
89 stabilization, water and nutrient limitation, and plant facilitation and competition are the main  
90 drivers of sand dune community structure and organization (Barbour et al. 1985, Ehrenfeld  
91 1990, Lichter 1998, Isermann 2011). Typically, distinct plant zonation occurs in coastal sand

92 dune systems (Hesp 1991, Lortie and Cushman 2007, Acosta 2009). On the seaward border  
93 of sand dunes, the fore dune, a limited number of clonal pioneer plant species with deep roots  
94 trap and bind sand, initiating dune formation. These plants stabilize substrate, trap seeds, and  
95 grow vertically and horizontally as sand accumulates, building the seaward border of sand  
96 dunes (Cowles 1899, Oosting and Billings 1942). At higher elevations in the middle dune,  
97 plant species diversity increases, but unvegetated free space remains common. At these  
98 elevations, substrate stabilization remains important, but interspecific plant interactions,  
99 including facilitation (Franks 2003, Castanho et al. 2015) and competition (Lichter 2000),  
100 and water and nutrient limitation also appear to mediate plant success. In the back dune,  
101 furthest from ocean winds and salt spray, the dominant physical stresses of substrate  
102 instability and low soil nutrients and moisture are less severe, plant cover typically reaches  
103 100%, and numerically dominant woody shrubs or trees, appear to competitively displace  
104 plants that dominate lower dune elevations (Lichter 2000). This descriptive structure of dune  
105 communities is consistent with a hierarchical community organization model and the stress  
106 gradient hypothesis of community assembly.

107 The hierarchical model of community organization (Bruno and Bertness 2001, Ellison et al.  
108 2005, Altieri et al. 2007) hypothesizes that within communities built by biogenic foundation  
109 species, dependent species are only able to persist through positive interactions and feedbacks  
110 initiated by primary foundation species. The stress gradient hypothesis (Bertness and  
111 Callaway 1994, Maestre et al. 2009, He and Bertness 2014) proposes that the biological  
112 processes controlling community development shift from positive, facilitative interactions in  
113 physically and biologically harsh environments to negative, competitive interactions in  
114 benign environments. Many shoreline communities built and maintained by foundation  
115 species, such as salt marshes, coral reefs, mangrove forests, mussel reefs, and seagrass beds,

116 have been hypothesized to be hierarchically organized by the general principles of the stress  
117 gradient hypothesis (Bruno and Bertness 2001).

118 In this paper we examine long-standing assumptions of sand dune plant community ecology.  
119 We hypothesize that sand dunes are hierarchically organized, initially built by facilitation, but  
120 ultimately structured by spatially and temporally predictable shifts from facilitative  
121 interactions to competitive interactions and seedling recruitment across decreasing stress  
122 gradients. Many of these patterns were initially theorized in classic descriptive work (Cowles  
123 1899), but have never been tested experimentally. We take a field experimental approach to  
124 test these underlying assumptions and elucidate the sand dune community assembly by  
125 examining the hypotheses that: 1) foundation species are responsible for stabilizing the  
126 seaward border of the dune from erosion and habitat loss, 2) at intermediate dune elevations,  
127 interspecific plant interactions, plant resource availability, and seedling recruitment dictate  
128 plant abundance and distribution, and 3) at high dune elevations, reduced physical stresses  
129 lead to increased plant abundance, interspecific competitive dominance and displacement.  
130 Our results support a hierarchical model of sand dune community organization and confirm  
131 many, but not all of the assumptions of early work on the organization of these communities.

## 132 **MATERIALS AND METHODS**

133 Our study was carried out on the Badesi dunes (40° 56' 45.571'' N, 8° 49' 41.048'' E) on the  
134 North coast of Sardinia, in the Mediterranean Sea. It is a wide dune system at the mouth of  
135 Coghinas River and has a plant community similar to other dune systems in Sardinia  
136 (Cusseddu personal observations), it is within a Site of Community Importance (SIC) and the  
137 Town of Badesi gave us the field permit to undertake the field experiments (approval  
138 number: 3343 - 23/03/2012). The Coghinas dunes are almost three kilometers long  
139 overlooking the Asinara Gulf, with a width of approximately five hundred meters. Sardinia

140 has a warm temperate Mediterranean climate with hot, dry summers and cooler, wet winters.

141 As in other Mediterranean habitats, most plant growth and reproduction occurs during the

142 winter months (Blondel and Aronson 1999). Previous studies of Sardinian sand dune plant

143 communities reveal that they have high species richness, endemism (Bacchetta et al. 2008,

144 Prisco et al. 2012) and adaption to physical stress (Fenu et al. 2013).  
*Little thing - are communities adapted to stress, or are the species that build them?*

#### 145 *Zonation survey*

146 To quantify the plant distribution across the Badesi dune, we surveyed transects in each

147 distinct plant zone. We defined three major dune plant zones: the fore dune, located on the

148 seaward border of the dune and characterized by a steep lower border of stabilized sand and

149 low plant diversity; the middle dune, characterized by high but patchy plant species diversity

150 and 40-60% bare sand cover; and the back dune, characterized by total woody plant cover

151 (Fig. 2). In addition to these zones we will also refer to the front of the fore dune, or the

152 seaward border of the fore dune where embryo dunes (Cowles 1899) form and transition

153 areas between major vegetation zones. Our objective was to develop a site description of the

154 plant community.  
*So zonation was defined a-priori on the basis of qualitative/semi-quantitative or informal observations? Why not define zonation quantitatively on basis of composition? Would be interesting to see if your quadrats cluster together following your pre-defined zonation system*

155 To assess the plant zonation, we quantified vegetation along 120 m transects parallel to the

156 water in each major dune zone: the embryonic fore dune, the top fore dune on the first ridge

157 of the dune formation, the middle dune with high plant species richness and bare substrate,

158 and the back dune dominated by woody plants. In each zone we ran a transect line, starting

159 from a random point, parallel to the shoreline and every 2 m placed a 0.5x0.5 m sampling

160 quadrat subdivided into a 25 5x5 cm sampling grid to estimate plant species and unvegetated

161 substrate cover. Sixty quadrats were sampled/zone. We characterized species diversity for

162 each zone with the Shannon diversity index (H). All plants, after introduced, will be referred

163 to by genus names.  
*So data are going to be analyzed at the quadrat rather than transect level and there's a single transect per zone? Is that pseudo-replication and does it matter?*

164 In addition to vertical zonation, a conspicuous feature of plants on the fore and middle dunes  
165 were that they generally occurred on elevated sand mounds. Since sand in these zones is  
166 mobile and windblown, we hypothesized that these mounds were created by the presence of  
167 plants rather than plant establishment on transient dune features (Cowles 1899). We used an  
168 auto level and stadia rod to quantify the elevation of plants in each zone (n=20/zone) and bare  
169 sand adjacent to (25-cm away) each plant. In each zone we randomly selected 20 adult  
170 individuals of the most common plant species, measured their elevation and the elevation of  
171 unvegetated sand 10-20 cm away. Plant and adjacent sand elevation differences were  
172 calculated, tested for homogeneity of variances with Cochran's test, transformed as necessary  
173 (Underwood 1997) and analyzed by species with a one-way ANOVA and by a zone x plant  
174 ANOVA for *Armeria*, the only species **in all zones**. Ok but were their other species that were in more than one zone (though not all) where you could examine this interactions

#### 175 *Foundation species removal experiment*

176 To test the hypothesis that foundation dune plants bind sand and build the dune habitat, as  
177 well as to quantify secondary succession, we performed a foundation species removal  
178 experiment. In each of the 3 major dune zones in March 2012, we marked the corners of 24  
179 randomly placed 1x1 m plots each separated by at least 10 m. Each plot was individually  
180 labeled and then randomly assigned in each zone as controls, total species removals, or  
181 procedural controls (n=8/treatment/zone). The 4 corners of each plot were marked with 2 cm  
182 diameter rebar driven to refusal into the sand and cut to initially extend 10-15 cm above the  
183 sand surface. Control plots were otherwise untouched. In plant removal replicates, plots were  
184 perimeter trenched to 30 cm with straight edged shovels and all vegetation in the plots was  
185 sprayed weekly for 3 weeks with a systemic herbicide (Roundup, Monsanto) until all  
186 vegetation was dead. Dead aboveground vegetation was left to simulate natural death.  
187 Roundup is widely used in ecological research, has localized effects if plots are trenched to  
188 avoid translocation outside of the target area, and we have used it successfully in the past in

189 shoreline habitats (Bertness and Hacker 1994). No herbicide effects on plants outside  
190 herbicided plots were observed. Procedural controls were trenched, but not herbicided.  
191 *Why do you expect dead plants to trap sand differently to live plants? Would you expect active erosion/sand loss  
where plants are killed - I'd like to know what your initial hypotheses were for the experiment.*  
191 Surface Elevation Table (SET) posts (Cahoon et al. 2000) modified for experimental  
192 replication were installed in the center of all plots to measure sand erosion/accretion as a  
193 function of the presence/absence of foundation species and dune zone. A 2 cm diameter rebar  
194 rod was driven to refusal in the center of each plot, cut 10-15 cm above the sand surface and  
195 fitted with a 30 cm long horizontal PVC bar with four evenly spaced locations to measure the  
196 height of the sediment (see Brisson et al. 2014). Elevations were taken in October and March  
197 of each year at each SET post for three years. Corner post heights were simultaneously  
198 measured to supplement SET data and assess spatial patterns in sand erosion/accretion.  
199 Sediment height (the sand erosion/deposition balance) data were analyzed with a treatment x  
200 zone ANOVA followed by post-hoc testing (SNK test).

201 In the spring of 2013, we began monitoring temperature after noting apparent summer heat  
202 death of some high middle dune plants during the first year of this experiment. We deployed  
203 24 thermistors (Econorma S.a.s. FT-800/System) to plots of this first experiment (n=8/dune  
204 zone), attaching them under the canopy in control plots and plant removal plots with wire  
205 staples. This allowed us to quantify plant heat exposure during the summer, and quantify  
206 differences between control and removal treatments. Thermistors were left in the field from  
207 the mid-June until the first week of September 2013 measuring temperature hourly. We  
208 *pooled as in averaged?* pooled the data between 01:30 a.m. and 05:30 a.m. and between 13:30 p.m. and 17:30 p.m. to  
209 estimate the lowest and the highest daily temperature, respectively. These temperature ranges  
210 gave us mean minimum (Min) and mean maximum temperatures (Max) for each zone and  
211 treatment. Data were analyzed with a three-way ANOVA, considering zone, temperature  
212 (Min vs Max), and treatment (removal vs control) as orthogonal and fixed. A one-way  
213 ANOVA was used to analyze mean maximum temperature by zone.

214 *Reciprocal species removal experiment (Interspecific plant interactions)*

215 To test the hypothesis that interspecific plant interactions shifted from facilitative to  
216 competitive across the sand dune, being especially important in the middle dune, we  
217 performed reciprocal species removal experiments in all dune zones with dominate species  
218 pairs. On the fore dune, we chose *Armeria pungens* (sea rose) and *Lotus cytisoides*; in the  
219 middle dune we chose *Armeria*, *Lotus*, and *Carpobrotus acinaciformis* (ice plant); and in the  
220 back dune, we chose *Armeria*, *Carpobrotus*, and *Pinus* spp. (*Pinus halepensis* and *Pinus*  
221 *pinea*). For each species pair in each zone, we located 24 **0.5x0.5 m** plots with mixtures of the  
222 two target species. All plots were marked with numbered rebar corner posts driven to refusal  
223 into the sand and labeled with a unique numbered plastic tag. For each zone and species pair  
224 (species a and b), we randomly assigned control plots, “species a” removal plots, and  
225 “species b” removal plots (n=8/treatment/species pair/dune zone). Species assigned for  
226 removal were **pulled manually** with minimal disturbance. Treatments were maintained  
227 monthly as needed for two years. During this time, plots were photographed in the spring and  
228 fall of each year and analyzed for percent plant cover. The height of the corner posts was also  
229 measured to quantify sand deposition/erosion. Plant cover was analyzed by zone with a two-  
230 way ANOVA, only *Carpobrotus* data were Sqrt (X+1) transformed. Separate ANOVAs were  
231 run for each species at 12 and 18 months, to accommodate the loss of plots to sand burial  
232 over time. For the same reason, we also analyzed plant cover and sand deposition on plot  
233 plant cover data pooled by zone with a t test and plant x sediment cover with linear  
234 regression.

235 *Boardwalk shadow effect sampling*

236 During the first year we noticed that in the summer months, temperatures in the middle and  
237 back dune, protected from on shore winds by the fore dune berm, were extremely high and

238 coincided with the death of the ice plant *Carpobrotus* at high dune elevations. To examine  
239 this hypothesis, we quantified the long-term effect of shading on the Badesi dune as a proxy  
240 for high temperature impacts. In February 2015, we quantified shaded and unshaded  
241 vegetation adjacent to boardwalks (1.5 m wide, elevated 50 cm over the substrate)  
242 perpendicular to the shoreline that extended from the fore dune to the highest point of the  
243 back dune, and 4 m on both sides of the boardwalks. We hypothesized that shading by the  
244 boardwalk would decrease solar stress on ice plants. We sampled 2 boardwalks that had been  
245 in place 5 years. At each boardwalk we quantified live and dead ice plant % cover in 0.5x0.5  
246 m quadrats every 2 m from the beginning of the fore dune to the back dune. For analysis we  
247 excluded plots levels without ice plants and pooled the data from adjacent and control plots.  
248 Dead/alive ratio of *Carpobrotus* % cover and dead *Carpobrotus* % cover were transformed to  
249 meet the assumptions of parametric statistics and analyzed with a one-way ANOVA.

#### 250 *Physical stress alleviation experiment*

251 To test the hypothesis that physical stress limits dune plant recovery across the dune, we ran a  
252 fully factorial experiment across all zones manipulating all combinations of nutrient  
253 limitation (with 33 ml of slow release Osmocote NPK pellets spread on them every 6 months  
254 and without nutrient additions), water limitation (with 2 liters of tap water every 2-3 weeks  
255 and without water additions) and substrate stability (with and without substrate stabilizing  
256 fish net attached flush to the surface with wire staples). In each zone we located 72 **0.5x0.5 m**  
257 plots with bare sand substrate. Every combination of nutrient, water, substrate limitations and  
258 controls were marked and labeled with numbered rebar corner posts (n=8/treatment  
259 combination/zone). Replicate treatments were maintained for two years and all plots were  
260 monitored for % plant cover initially and then for <sup>two</sup> 2 years in the spring and fall. Plant cover in  
261 the plots was transformed to meet parametric statistic assumptions and analyzed with a  
262 treatment x dune zone ANOVA.

263

*Seedling recruitment*

264 To examine the distribution of dune plant seeds and test the hypothesis that like sand, seeds  
265 are deposited and trapped under adult plants, we sampled sand under plants and in adjacent  
266 bare sand >25 cm from plants in all dune zones. This was done in October 2013, after the  
267 summer when seed dispersal and germination was most pronounced on the dune (Bakker et  
268 al. 2008). In each zone (fore, middle and back) we sampled sand under and adjacent to the  
269 most common plants in each zone by taking 100 ml surface sand samples (1 cm deep;  
270 n=10/species/habitat/zone). Samples were returned to the laboratory and sorted under a  
271 dissecting microscope. Seed density was analyzed with an experimental treatment (under and  
272 adjacent to adult plants) one-way ANOVA separately by zone and on conspecific seeds of the  
273 target plant and seeds of all other plants combined.

274 To examine seedling survivorship across the dune and test the hypothesis that seedling  
275 survivorship increased with dune elevation and association with adult plants, we marked  
276 natural seedlings in all dune zones that were under adult plants and in bare sand >30 cm from  
277 an adult plant. 450 seedlings were marked and monitored monthly for survivorship over three  
278 seasons. Seedling survivorship was analyzed with a non-parametric log rank test to compare  
279 survival among zones (fore vs middle vs back) and species survival by location (next to adult  
280 vs adjacent bare sand). In both cases the whole follow up period was taken into account  
281 (Bland and Altman 2004) and a  $\chi^2$  test was done on the log rank data of  $\text{Ln}(X+1)$   
282 transformed *Armeria* seedling data.

283 To examine the hypothesis that seed supply is a determinant of the distribution and  
284 abundance of plants across the dune, we performed a seed transplant experiment with the 5  
285 most common Badesi sand dune plants (*Armeria*, *Lotus*, *Carpobrotus*, *Cakile maritima*, and  
286 *Pancratium maritimum*). For each species, we collected dehiscent seed heads and dissected

287 out and separated the seeds of each species. We then sorted them into aliquots of 4-10 seeds  
288 depending on species seed availability and placed them by species into polyester mesh bags  
289 that would retain the seeds, but would allow germination and seedling growth. For each  
290 species we planted 21 seed bags in each zone (fore, middle and back) under conspecific  
291 adults and in unvegetated sand >30 cm from adult vegetation and marked their location with  
292 color-coded wire markers. We monitored seed transplants weekly for germination and  
293 seedling survivorship for 3 months. Germination and seedling survivorship were analyzed  
294 separately by species with non-parametric log rank data, using a  $\chi^2$  test.

295 To test the hypothesis that loose seeds were eroded away on the fore dune, we also  
296 transplanted seeds of *Pancratium* in mesh bags (n=10), loose in the sand (n=10), and loose in  
297 the sand covered on the sand surface with nylon mesh (2 mm mesh, 5x5 cm cover pinned to  
298 the sand surface with garden fabric staples; n=10). We only did this experiment in the fore  
299 dune since the fore dune was the only zone that showed significant erosion. Seed species  
300 were marked and identified by color-coded wires (2 mm). All seeds were planted 3 cm below  
301 the sand surface. We monitored these transplants for germination and survivorship weekly for  
302 the first 3 months and monthly for one year. Germination and seedling survivorship data were  
303 analyzed with a non-parametric log rank data, using a  $\chi^2$  test.

#### 304 *Back dune competitive release experiment*

305 It was not possible to do *Pinus* removal experiments similar to the reciprocal plant species  
306 removal experiments or foundation species removals in other zones because of the size of  
307 *Pinus* trees. Since the Badesi dune is a protected conservation area, removing entire *Pinus*  
308 trees would have been destructive and not permitted. To test the hypothesis that *Pinus*  
309 domination of the terrestrial high dune border is due to competitive dominance, we did a  
310 competitive release experiment by removing large (~2m long) *Pinus* branches and estimated

311 natural plant recruitment by following seed germination and cover in 1.5x1.5 m plots under  
312 *Pinus* canopies (n=10), where *Pinus* shading was alleviated by branch removal (n=10) and in  
313 areas where *Pinus* shading was removed but replaced by a similar level of shading by shade  
314 cloth (n=10), as procedural controls. A central 0.5x0.5m quadrat in each plot was monitored  
315 photographically monthly for a year.

316 To test the hypothesis that allelopathy contributes to the dominance of *Pinus* and ice plant in  
317 the back dune, we also manipulated sediment in the *Pinus* plots described above. Allelopathy  
318 was suggested because in dense *Pinus* and ice plant stands, natural substrate is covered by  
319 *Pinus* needles and ice plant leaves, but seedlings of all species are extremely rare  
320 (Ceccherelli, personal observation). In 100 ml plastic greenhouse seedling pots we planted  
321 seeds of *Armeria*, *Pancreatium*, and *Lotus* (plus no seed controls) with either 1) *Pinus* soil, 2)  
322 middle dune bare soil, 3) middle dune ice plant soil, 4) potting soil mixed with sand, 5)  
323 potting soil with a 2 cm layer of *Pinus* needles and 6) potting soil with a 2 cm layer of ice  
324 plant leaves (n=10/*Pinus* treatment/soil type) and scored them monthly for germination. Seed  
325 germination and survivorship of *Armeria*, and *Lotus* were transformed with  $\ln(X+1)$  and all  
326 were analyzed with *Pinus* treatment x soil type ANOVA.

## 327 **RESULTS**

### 328 *Zonation survey*

329 Elevational zonation of plants across the Badesi dune is striking (Fig. 1). The fore dune has  
330 low plant richness and cover (35%) and 65% unvegetated sand cover. *Armeria* (sea rose),  
331 *Otanthus maritimus* (cotton weed) and *Lotus* (trefoil of the cliffs) are the numerically  
332 dominant plant species on the fore dune and all are clonally spreading, deep-rooted  
333 perennials. The width of the fore dune varies at Badesi from ~20-25 m. The middle dune has  
334 over 28% higher plant cover and 53% higher species richness than the fore dune, but still has

335 considerable bare sand substrate (Fig. 2, 38%). *Armeria*, *Carpobrotus* (ice plant) and  
336 *Ephedra distachya* (joint pine) are the most common middle dune plant species and are all  
337 clonally spreading perennials. The middle dune is ~30-35m wide.

338 The transition from the middle to back dune is more gradual (Fig. 1). The seaward border of  
339 the back dune has the highest plant species richness on the dune, and is dominated by the ice  
340 plant, *Carpobrotus*, a perennial succulent, that can be seen overgrowing other back dune  
341 plants like *Pinus* on the terrestrial border of the dune (33%). At higher elevations of the back  
342 dune, *Pinus* dominates the landscape as a solitary evergreen species that has a prostrate  
343 morphology at lower elevations, an arborescent morphology at higher elevations and an  
344 understory of bare substrate in the dense *Pinus* canopy that dominates high elevations.

345 Substrate topography in relation to plants varied across the dune. In dune zones closest to the  
346 water, plants were found on elevated sand mounds that decreased in elevation with distance  
347 from the water, while in the back dune, furthest from the water, plants were not associated  
348 with sand mounds. On the front dune, *Armeria* and *Otanthus* were found on sand mounds  $53$   
349  $\pm 2.16$  cm (mean  $\pm$  SE) and  $56 \pm 2.51$  cm higher than adjacent substrate, respectively. For the  
350 front dune, the one-way ANOVA did not reveal any significant difference between the two  
351 species ( $F_{1,38}=0.36$   $p>0.05$ ). On the fore dune, *Lotus* and *Armeria* were similarly found on  
352 mounds  $17 \pm 4.64$  and  $24 \pm 1.92$  cm high, respectively, and no significant effect was detected  
353 with the ANOVA ( $F_{1,38}=2.07$   $p>0.05$ ). In contrast, in the middle dune, *Armeria*, *Carpobrotus*,  
354 *Lotus*, *Helicrysum microphyllum* and *Ephedra* were found on smaller sand mounds  $22 \pm 1.47$ ,  
355  $12 \pm 2.06$ ,  $11 \pm 1.06$ ,  $16 \pm 1.27$ , and  $12 \pm 2.48$  cm high, respectively. In this zone the  
356 difference among species was significant ( $F_{4,95}=7.51$   $p<0.0001$ , SNK: *Armeria*>all others).

This is interpretation and so seems to belong in the discussion

357 **These front, fore and middle dune plants occur on elevated sand mounds that appear to be**  
358 **actively trapped by passive deposition of wind-blown sand.** *Armeria*, a robust perennial  
359 shrub, was found on higher sand mounds than all other species. One-way ANOVA on

360 *Armeria* revealed differential *Armeria* sand binding by zone ( $F_{3,76}=111.36$   $p<0.0001$ , SNK:  
 361 front>fore top=middle>back). In the back dune, buffered from winds and sand transport by  
 362 the lower dune zones, *Armeria* =  $9 \pm 1.65$  cm, *Carpobrotus* =  $4 \pm 1.31$  cm, *Pinus* =  $4 \pm 2.76$   
 363 cm, *Acacia cyanophylla* =  $0 \pm 3.8$  cm, and *Juniperus* spp. (*Juniperus macrocarpa* and  
 364 *Juniperus phoenicea*) =  $-2 \pm 4.72$  cm were not found on elevated locations and there were no  
 365 significant species effects ( $F_{4,95}=1.93$   $p>0.05$ ).

#### 366 *Foundation species removal experiment*

367 Removing foundation species had different effects across zones (Fig. 3). We performed a  
 368 two-way ANOVA of zone and treatment, both considered as orthogonal fixed factors. The  
 369 analyses revealed a significant zone x treatment interaction ( $F_{4,63}=2.67$   $p<0.05$ ). In the fore  
 370 dune, foundation species removal led to sand erosion of  $>2$  cm/year, in contrast to control and  
 371 procedural control plots that had annual sand accretion rates of  $>4$  cm/year (Fig. 3,  $p<0.05$ ,  
 372 SNK test fore: removal<procedural control=control). Sand erosion in the fore dune  
 373 foundation species removal plots was dramatic and led to the collapse of the fore dune edge  
 374 in just two years. This was reflected in the erosion of the seaward corner posts in the fore  
 375 dune, where, while the seaward edge corner post of procedural control ( $5.29 \pm 1.3$  cm/year)  
 376 and control plots ( $3.66 \pm 1.77$  cm/year) showed net sand accretion, when foundation species  
 377 were removed, erosion on the seaward edge corner posts increased over 60% leading to an  
 378 amount of sand dispersion of  $-2.8 \pm 1.6$  cm/year (Fig. 3).

Very long sentence and a bit confusing - please rephrase

Not sure what you mean by "sediment variation"

379 In the middle dune, sediment variation resulted in net sand accretion that occurred in all  
 380 treatments (Fig. 3,  $p<0.05$ , SNK test: fore=back<middle), but was nearly twice as high in  
 381 control and procedural control plots with live vegetation to bind and trap sand than in  
 382 removal plots (SNK middle: removal<procedural control=control).

383 In the back dune, annual sediment accretion was more than an order of magnitude less than  
 384 middle dune plots with foundation species (Fig. 3). Sand accretion in the back dune was also  
 385 similar among foundation removal, control and procedural control treatments (Fig. 3,  $p < 0.05$ ,  
 386 SNK back: removal=procedural control=control). In all treatments, annual accretion was  $< 1$   
 387 cm/year and when foundation species were removed there was no sand accretion.

388 Mean minimum temperature (Min) did not differ among treatments or zones (fore  $18.73 \pm$   
 389  $0.45^\circ \text{C}$  and  $18.50 \pm 0.4^\circ \text{C}$ , middle  $19.11 \pm 0.28^\circ \text{C}$  and  $19.12 \pm 0.18^\circ \text{C}$ , back  $16.59 \pm 0.77^\circ$   
 390  $\text{C}$  and  $17.07 \pm 0.87^\circ \text{C}$  for removal and control, respectively;  $F_{2,228}=1.77$   $p > 0.05$  for the

391 interaction zone x temperature range x treatment). In contrast, mean maximum temperature

Perhaps I'm being thick but I don't understand why there are two max temperatures reported for each zone - please explain

392 (Max) differed among zones (fore  $33.73 \pm 1.40^\circ \text{C}$  and  $32.83 \pm 2.46^\circ \text{C}$ , middle  $41.86 \pm 2.74^\circ$

393  $\text{C}$  and  $38.31 \pm 1.34^\circ \text{C}$ , back  $44.89 \pm 3.61^\circ \text{C}$  and  $40.26 \pm 3.45^\circ \text{C}$ ;  $F_{2,114}=39.85$   $p < 0.0001$ ,

394 SNK: fore  $<$  middle = back) peaking in back zone removal treatments ( $F_{1,114}=10.72$   $p < 0.002$ ,

395 SNK: Removal  $>$  Control). Maximum temperatures peaked around  $70^\circ \text{C}$ , and averaged  $45^\circ \text{C}$

This is rather surprising - will be interested to see your explanation

396 in the removal plots,  $5^\circ \text{C}$  lower than when vegetation was present.

397 *Reciprocal species removal experiments (Interspecific plant interactions)*

There's a wee bit of extraneous text in places - can probably reduce it down a bit - e.g.

398 ~~Evaluation of interspecific interactions of common plant species in all dune zones with~~

399 R reciprocal species removal experiments initially revealed significant interspecific interactions

400 (Fig. 4). Over time, however, these interactions were lost due to sand burial and erosion

401 disturbance, particularly in the fore and middle dune zones as evidenced by a decrease in

Report t and p values please

402 plant cover over time in the species interaction plots (Fig. 5, middle  $p < 0.001$ , t test). After 18

403 months, 22% of the middle dune reciprocal species interaction plots had been completely lost

404 due to sand burial, and an additional 10% of the plots were still recognizable but almost

405 totally buried, while no plots were lost in the fore or back dune. To analyze this experiment,

406 we ran separate two-way ANOVAs for each species after 12 months and 18 months of

407 treatments, taking into account species interaction (comparison of each pair in which the  
408 species is involved) and treatment (reciprocal species removal vs control) as orthogonal and  
409 fixed factors. Insignificant interaction p values will always refer to the last sampling date (18  
410 months). In the fore dune after 6, 12, and 18 months, there was no evidence of reciprocal  
411 effects between *Armeria* and *Lotus* (Fig. 4, interaction x treatment  $F_{4,70}=1.96$   $p>0.05$  and  
412  $F_{2,42}=2.27$   $p>0.05$ , respectively).

413 In the middle dune, after one year of treatment, there was evidence of *Armeria* and *Lotus*  
414 competitively depressing *Carpobrotus*, but after two seasons this competitive effect was no  
415 longer apparent (Fig. 4, treatment  $F_{3,56}=12.12$   $p<0.03$ , SNK reciprocal species  
416 removal>control at 12 months, interaction x treatment  $F_{3,56}=1.23$   $p>0.05$  at 18 months). At  
417 the same time, there was no evidence of interactions affecting *Armeria* or *Lotus* (Fig. 4,  
418 interaction x treatment  $F_{4,70}=1.96$   $p>0.05$  and  $F_{2,42}=2.27$   $p>0.05$ , respectively). In all the  
419 interspecific interaction plots in the middle dune there was, over time, a general decrease in  
420 plant cover associated with sand burial disturbance (Fig. 5,  $p<0.001$ , t test).

421 In the back dune sand burial was not prevalent, but a summer die off of *Carpobrotus* was  
422 seen every year (see below). *Carpobrotus* and *Pinus* had a facilitating effect on *Armeria* after  
423 12 months but not at 18 months (Fig. 4, interaction x treatment  $F_{4,70}=3.31$   $p<0.02$ , SNK test  
424 for both Back pairs: reciprocal species removal<control at 12 months,  $F_{4,70}=1.96$   $p>0.05$  at 18  
425 months). While, after one year of removal, the opposite was found for *Carpobrotus*, which  
426 was competitively depressed by both *Armeria* and *Pinus*, but after another two seasons of  
427 observation these interactions were no longer detectable (Fig. 4, treatment  $F_{3,56}=12.12$   
428  $p<0.03$ , SNK reciprocal species removal>control at 12 months, interaction x treatment  
429  $F_{3,56}=1.23$   $p>0.05$  at 18 months). Reciprocal removal of *Pinus* in the back dune did not reveal  
430 significant species interactions (Fig. 4, interaction x treatment  $F_{1,28}=0.18$   $p>0.05$ ). In the back  
431 dune species removal plots, the most conspicuous trend over time was the decrease in the

432 cover of *Carpobrotus* during summer. This left large areas of dead, desiccated *Carpobrotus*  
433 dominating the seaward border of the back dune at the end of the summer (Cusseddu,  
434 personal observation).

#### 435 *Boardwalk shadow effect sampling*

I think this experiment could probably be dropped, not sure it adds much. Other reviewers also felt the paper could probably be reduced somewhat

436 Analysis of *Carpobrotus* cover data (dead/alive ratio) adjacent to and 2 m away from the  
437 shade of boardwalks revealed almost twice as much live ice plant cover under the shade of  
438 the boardwalks ( $46 \pm 3.24\%$ ) than in adjacent unshaded habitats ( $25 \pm 2.84\%$ ;  $F_{1,190}=5.58$   
439  $p<0.02$ ). There was also nearly 10% more dead ice plant in unshaded habitats ( $16 \pm 1.76\%$ )  
440 than under the shade of boardwalks ( $7 \pm 1.10\%$ ,  $F_{1,190}=18.76$   $p<0.0001$ ). Since ice plant death  
441 occurs almost exclusively in summer (Cusseddu, personal observation), ice plant mortality at  
442 high dune elevations appears to be driven by heat and desiccation from direct sun exposure  
443 leaving desiccated ice plant skeletons marking their initial distribution. Interpretation belongs in the discussion

#### 444 *Physical stress alleviation experiment*

Given most results are non-significant report ANOVA results in table and shorten this section?

445 Experimentally manipulating water availability, nutrient availability and substrate stability  
446 across dune zones (fore, middle and back) in a fully factorial 2 year experiment at a **0.5x0.5**  
447 m spatial scale revealed that these factors, long thought to be critical to sand dune plant  
448 communities, had no effect on plant recovery, as evidenced for each zone using ANOVA  
449 with treatment as orthogonal and fixed factor (Fig. 6, fore  $F_{9,70}=1.95$   $p>0.05$ , middle  
450  $F_{9,70}=2.16$   $p<0.04$  but not significant post hoc SNK, back  $F_{9,70}=0.57$   $p>0.05$ ). There were no  
451 significant responses in plant biomass or species identity to treatments within zones, but a  
452 two-way ANOVA (zone and treatment orthogonal and fixed), showed that recovery increased  
453 from the fore to back dune (Fig. 6,  $F_{2,210}=18.30$   $p<0.0001$ , SNK fore<mid<back), although  
454 treatment and the zone x treatment interaction were not significant ( $F_{9,210}=1.70$   $p>0.05$  and  
455  $F_{18,210}=0.87$   $p>0.05$ , respectively). No effect of the environmental manipulations was found

456 at these levels, but this does not mean that other levels would not have an effect, or that water  
457 and nutrient availability are unimportant for the structure of dune communities.

458 *Seedling recruitment: seed and seedling quantification*

459 Seeds of the most common dune plants were most abundant under adult plants independent of  
460 species identity and dune zone (Fig. 7). For each zone, we performed a three-way ANOVA  
461 considering the species, the substrate (under adult vs bare sand) and the seeds category  
462 (conspecific vs other seeds) all as orthogonal and fixed factors. We will present only the  
463 factors and/or the interactions that were significant.

Statistical results should be reported in full, even where results are non-significant. Put these in an Appendix if necessary

464 On the front of the fore dune, seeds of *Armeria* and *Otanthus* were almost exclusively found  
465 under conspecific adults, whereas the seeds of other species were rare and not found  
466 associated with adult plants (Fig. 7, substrate x seeds interaction  $F_{1,72}=0.11$   $p<0.02$ ). On the  
467 top of the fore dune, seeds of *Armeria* were more common under *Armeria* adults than in  
468 nearby bare sand, but for *Lotus* and *Pancratium*, seeds of conspecifics were just as common  
469 in bare sand than under adults (Fig. 7). For *Lotus* and *Pancratium*, conspecific seeds were  
470 equally distributed under and away from adults, but seeds of other species were significantly  
471 more common under *Lotus* and *Pancratium* than in adjacent bare sand (Fig. 7, species x seed  
472 category interaction,  $F_{2,108}=4.43$   $p<0.02$  and species x substrate x seeds category  $F_{2,108}=3.45$   
473  $p<0.04$ , respectively).

474 In the middle dune, *Armeria* seeds were more common under *Armeria* adults than in adjacent  
475 bare sand, but seeds of other species were not (Fig. 7), while for *Carpobrotus*, conspecific  
476 seeds were rare, but seeds of other species were more than an order of magnitude more  
477 abundant under *Carpobrotus* than in bare sand (Fig. 7, species x substrate x seeds interaction,  
478  $F_{1,72}=12.59$   $p=0.0007$ ). In the back dune, *Armeria* seeds were 20 times more common under  
479 conspecifics than in adjacent bare sand, while for *Carpobrotus*, seeds of other species were

480 significantly more abundant under *Carpobrotus* than in adjacent bare substrate (Fig. 7,  
481 species x substrate x seeds interaction  $F_{1,72}=8.34$   $p<0.006$ ).

482 The survivorship of marked seedlings was analyzed with a log rank test comparing the  
483 survival of the seedlings of each species comparing the proximity with adult (next to adult vs  
484 adjacent bare sand) and of the seedlings in general pooled in three groups corresponding to  
485 the three zones (fore vs. middle vs. back seedlings), on the times (weeks) of survival events.  
486 The percent of seedlings survivorship increased dramatically with dune zone elevation but  
487 was not affected by neighboring plants (Fig. 8,  $p<0.05$ ,  $\chi^2$ ). In the fore dune, no *Lotus*  
488 seedlings survived (independent of the proximity to adult neighbors), no *Pancratium*  
489 seedlings survived on bare sand, and less than 5% of *Pancratium* seedlings survived next to  
490 adults, but this result was not significant ( $p>0.5$ ,  $\chi^2$ ). In the middle zone only 5% of *Lotus*  
491 seedlings survived with or without adult neighbors ( $p>0.5$ ,  $\chi^2$ ), while for *Armeria* 25% of  
492 marked seedlings in bare sand survived, nearly three times (10%) the number of seedlings  
493 that survived next to adults ( $p<0.025$ ,  $\chi^2$ ). No *Pancratium* seedlings survived. In the back  
494 dune survivorship of *Armeria* and *Carpobrotus* seedlings was over 80%, far higher than any  
495 other zone, and was not influenced by the presence or absence of neighbors (Fig. 8).

#### 496 *Seedling recruitment: seed transplant experiments*

497 Of the six dune plant species seeds used in transplant studies, three species, *Pancratium*,  
498 *Lotus*, and *Cakile* germinated. Only 2 and 3 *Armeria* and *Otanthus* germinated from back and  
499 fore dune planted seeds respectively, while *Astragalus thermensis* and *Carpobrotus* did not  
500 germinate in any location or treatment. For each of the three species that had sufficient  
501 germination, we compared the germination and survival in each of the three zones. 30-40% of  
502 *Pancratium* seed transplants germinated, but germination was similar among zones ( $p>0.1$ ,  
503  $\chi^2$ ). Survivorship of seedlings from the seed transplant experiment showed that all species had

504 the highest survivorship in the back dune, but this pattern was only significant for  
505 *Pancratium*, which had the highest sample size (Fig. 9,  $p < 0.005$ ,  $\chi^2$ ). Less than 10% of the  
506 transplanted *Lotus* seeds germinated and *Lotus*, found ubiquitously across the dune, had  
507 higher germination in the back dune, and lowest germination in the middle dune (Fig. 9,  
508  $p < 0.025$ ,  $\chi^2$ ), while survivorship did not differ among zones ( $p > 0.5$ ,  $\chi^2$ ). For *Cakile*, a pioneer  
509 species found naturally in the fore and middle dune, 12-18% of transplanted seeds germinated  
510 and among zones had higher germination in the middle than in fore and back dune (Fig. 9,  
511  $p < 0.05$ ,  $\chi^2$ ). Survivorship, however, did not differ among zones ( $p > 0.5$ ,  $\chi^2$ ).

512 In the fore dune seed stabilization experiment with *Panocratium*, germination and survivorship  
513 were analyzed comparing germination and survival among the three treatments (seeds in bags  
514 vs loose seeds vs. loose seeds with net covers). Due to erosion, germination was highest in  
515 the bagged seed treatment, second highest in the seed treatment with stabilized substrate (net  
516 cover), and lowest in the loose seed treatments (Fig. 10,  $p < 0.005$ ,  $\chi^2$ ). The difference in  
517 germination between loose seeds and the secured seed treatments was  $> 10\%$ , suggesting that  
518 sand erosion in the fore dune can lead to seed loss. Seedling survivorship in this experiment  
519 was similar among stabilization treatments ( $p > 0.25$ ,  $\chi^2$ ).

#### 520 *Back dune competitive release experiment*

521 Natural plant recruitment was not observed under *Pinus*, irrespectively of canopy removal  
522 treatments. However, germination of experimentally planted seeds under *Pinus* occurred,  
523 although it was generally lower in control plots, especially for *Armeria* and *Lotus* (Fig. 11).  
524 We ran a two-way ANOVA by species with canopy treatment and soil type as fixed and  
525 orthogonal factors. Under the *Pinus* canopy, *Armeria* seeds attracted small animals as they  
526 were often removed or eaten. *Armeria* germination, however, was significantly higher in the  
527 *Pinus* removal treatment in middle dune soil, and very little germination occurred in any soil

528 type under *Pinus* canopy and in procedural control plots (Fig. 11, canopy treatment x soil  
529 type interaction,  $F_{12,126}=2.54$   $p<0.005$ ). *Pancratium* and *Lotus* germination was not  
530 influenced by the *Pinus* treatment ( $F_{2,126}=2.11$   $p>0.05$  and  $F_{2,126}=0.79$   $p>0.05$ , respectively),  
531 but they were significantly affected by soil type (Fig. 11,  $F_{6,126}=5.02$   $p=0.0001$  and  
532  $F_{6,126}=7.06$   $p<0.0001$ , respectively), even if, for both species, there were no significant post  
533 hoc comparisons. The interaction *Pinus* treatment x soil type was not significant for both  
534 species ( $F_{12,126}=0.96$   $p>0.05$  and  $F_{12,126}=0.84$   $p>0.05$ , respectively).

Spaces needed between numbers and symbols in all stats reporting

## 535 DISCUSSION

536 Our experiments testing the basic assumptions of sand dune community organization  
537 generally support earlier descriptive and correlative studies. ~~This is unusual.~~ Experimental  
538 examination of community assemblages typically has not upheld the findings of earlier  
539 correlative conclusions. For example, rocky intertidal, salt marsh, kelp forest, and coral reef  
540 community dynamics once thought to be driven by physical forces (e.g. Odum 1953, Lewis  
541 1964, Mann 1982), were later shown to be strongly regulated by interactions between  
542 physical and biological factors once community level experiments were carried out (Dayton  
543 1971, Estes and Palmisano 1974, Bertness and Ellison 1987). Our results suggest that fore  
544 dune foundation species are responsible for binding, stabilizing and maintaining sand dune  
545 communities, and that interspecific plant interactions occur across the dune, but are generally  
546 overshadowed by physical stresses, particularly sand burial in the middle dune. Additionally,  
547 they indicate that while physical stresses limit plant distributions across the dune, their  
548 impacts are largely stochastic, except in the back dune where competitively dominant woody  
549 plants competitively displace other sand dune plants.

550 *Biogenic Communities, Foundation species and Hierarchical organization*

551 Like most communities in physically and/or biologically stressful habitats, the Badesi sand  
552 dune plant community is dependent on foundation species that ameliorate stress and facilitate  
553 community development (Angelini et al. 2011). Our foundation plant species removals reveal  
554 that plant species on the fore dune bind and stabilize sand, building the habitat that supports  
555 all the dune plants living at higher elevations, making them foundation species-dependent  
556 (Fig. 3). Without habitat-modifying foundation species that initially colonize potential fore  
557 dune habitats, sand dune plant communities would not develop or be maintained. Biogenic  
558 communities that are dependent on foundation species often display this type of hierarchical  
559 organization (Bruno and Bertness 2001, Angelini et al. 2011) and include salt marshes  
560 (Angelini et al. 2011), terrestrial forests (Ellison et al. 2005), seagrass meadows (Duarte et al.  
561 2000), as well as smaller scale associations within communities (Angelini and Silliman  
562 2014). This common dependency of communities on foundation species habitat modification  
563 needs to be incorporated into ecological theory (Bruno et al. 2003). It is a major organizing  
564 force in community assembly, confirmed by the overwhelming evidence that it is the  
565 template for communities in physically and biologically stressful habitats due to habitat  
566 amelioration and associational defenses, respectively (Bertness and Callaway 1994, Ellison et  
567 al. 2005, Crotty and Bertness 2015).

#### 568 *Competitive dominance*

569 Pairwise quantification of the interaction of the numerically common plants in each dune  
570 zone revealed that interspecific plant competition was common across the dune landscape  
571 (Fig. 4). In the middle dune, however, burial disturbance over the 18-months time course of  
572 our experiments revealed that, while interspecific plant interactions occurred, their  
573 importance was transient and not of long term consequence in generating species distribution  
574 patterns. Rather, sand burial disturbance limited the role of interspecific competition and  
575 competitive displacement, but promoted plant species diversity and coexistence in the middle

576 dune (Fig. 4). Similar results have been found on rocky shores, intertidal boulder fields,  
577 mussel beds, salt marshes, and grasslands (see Dayton 1971, Sousa 1979, Paine and Levin  
578 1981, Bertness and Ellison 1987, and Platt 1975, respectively). In the back dune, where sand  
579 burial is less common, competitive dominance by woody plants emerges as a major factor  
580 leading to competitive dynamics that determine the prevalence of shrub and woody species  
581 like *Pinus* and *Armeria* and exclusion of other dune species. Due to the dense *Pinus* canopy,  
582 germination of other middle dune species is precluded and in some cases soil type prevents  
583 seedling recruitment. Moreover, high summer temperatures in the back dune limit ice plant  
584 competitive dominance, because it suffers drying and summer die-off limiting its dominance,  
585 favoring *Pinus*.

#### 586 *Sand burial disturbance*

587 While our interspecific plant interaction experiments initially revealed significant interactions  
588 (Fig. 4), sand burial, particularly in the middle dune, was ultimately the most pervasive and  
589 powerful driver of plant community patterns at lower dune elevations, rendering competitive  
590 dominance and facilitative interactions inconsequential. Thus, the same physical force that is  
591 responsible for building the dune, sand mobility, is responsible for plant mortality and  
592 diversity, particularly in the middle dune. Burial in sand is recognized as a major aspect  
593 shaping the arrangement and composition of vegetation in coastal sand dune communities  
594 (Ranwell 1958, van der Valk 1974, Maun and Lapierre 1986). Sand deposition has been  
595 renowned as a main selective force in the evolution of seeds, in survivorship of seedlings and  
596 adult plants and, to a larger scale, in zonation and succession of vegetation (Maun 1994 and  
597 1998).

#### 598 *Seedling Recruitment*

599 Sexual recruitment is generally problematic in physically and biologically stressful  
600 communities like salt marshes (Pennings and Callaway 1996) and coral reefs (Hughes and  
601 Jackson 1985), respectively. As a result, asexual reproduction and clonal growth play a  
602 leading role in the community dynamics of communities in physically or biologically  
603 stressful habitats. Sexual recruitment is limited in Sardinian sand dune plant communities  
604 exposed to severe substrate mobility and strong wind and salt spray exposure. Dispersed  
605 seeds of dune plants are trapped near substrate stabilizing adult plants and are uncommon in  
606 unvegetated substrate (Fig. 7). The survivorship of marked seedlings was low, but generally  
607 increased from the fore to the back dune and was higher when seedlings were associated with  
608 adult plants than when on bare sand substrate without neighbors.

609 Field germination experiments with 3 common species had low germination rates and poor  
610 survivorship in all zones except the back dune. Seedlings of back dune grew the best, but  
611 suffered from desiccation, due to high temperature and herbivory (Fig. 9). Like in other  
612 stressful environments, the low success of seed reproduction appears to lead to nurse plant  
613 effects (Franks 2003) and strong reliance of dune plants on clonal reproduction, particularly  
614 at low elevations (Maun 1998). Nurse plant effects have been identified as a strong generator  
615 of pattern in sand dune plant communities in general (Martinez 2003).

## 616 CONCLUSIONS

Generally a "conclusions" section should be a summary of the key points or the take home message. This section is almost the same length as the preceding discussion suggesting the need for some restructuring.

### 617 *Lessons from Sardinian sand dunes*

618 Our results reveal that sand dune plant communities are hierarchically organized and  
619 dependent on the establishment of fore dune foundation plants that bind sand above and  
620 belowground, leading to sand dune initiation, development, and maintenance (Fig. 3).  
621 Without foundation plant species, mechanisms such as sand binding, erosion, mobility, and  
622 burial act as barriers to plant community development (Fig. 3) and are more pronounced than

623 at higher elevations that are less exposed to sand mobility. On the fore dune, removing the  
624 foundation species led to habitat loss, while competitive and facilitative plant species  
625 interactions were not detectable due to sand erosion and burial disturbance (Fig. 4 and 5).  
626 Manipulating physical factors thought to be critical in sand dune communities (i.e. water  
627 additions, nutrient additions, substrate stabilizations) in well replicated plots of all these  
628 factors alone and in combination also did not affect plant colonization at the small 0.25m<sup>2</sup>  
629 spatial scale manipulated. Seed and seedling success were also rare on the fore dune  
630 suggesting that asexual clonal expansion and colonization was more common in the highly  
631 disturbed fore dune habitat. This also suggests that disturbance on the fore dune trumps all  
632 other biological and physical factors. Since all of these physical and biological factors have  
633 been shown to correlatively impact sand dune communities at regional spatial scales, our  
634 results imply that spatial scale is important in understanding process and pattern in sand dune  
635 ecosystems since they are so fundamentally shaped by disturbance processes and their  
636 interaction with foundation plant species that stabilize the substrate.

637 Plant species cover and richness increased from 35% in the fore dune to 63% in the middle  
638 dune (Fig. 1). Like the fore dune, however, recovery from foundation removal was minimal,  
639 being less than 1% in 3 years. Moreover, while the middle dune initially revealed  
640 interspecific plant interactions, it is subjected to heavy sand burial that limited the role of  
641 species interactions, seed germination (Fig. 9), and seedling success (Fig. 8). Therefore,  
642 frequent sand burial disturbances have a large influence over the middle dune zone (Fig. 5).

643 In the back dune we see nearly 100% plant cover and the emergence of competitive  
644 dominants (Fig. 1 and 2c). On the seaward border of the high dune the ice plant is common  
645 and appears to be competitively dominant to middle dune plant species, but, at higher dune  
646 elevations, the evergreen *Pinus* competitively displaces most other dune plants, forming a  
647 back dune *Pinus* monoculture. Seedling germination and survivorship were higher in the back

648 dune than at lower dune elevations (Fig. 9), as was the recovery of bare space (Fig. 6). The  
649 competitive dominance of *Pinus* in the back dune was shown by a competitive release  
650 experiment in which removing *Pinus* canopy in the back dune lead to the success of  
651 important foundation species such as *Armeria*, especially favored by middle dune soil (Fig.  
652 11). In general, however, seeds of plants characteristic of the middle and fore dune planted in  
653 *Pinus* zone showed a quite good capability of germination. This suggests that they are  
654 excluded from the back dune because *Pinus* acts as a physical barrier, having a dense  
655 prostrate morphology (Fig. 11).

656 These results are summarized in a conceptual model of the assembly rules of the Badesi sand  
657 dune plant community (Fig. 12). The gradient of stress in this dune system acts crosswise,  
658 from land to sea and back again, creating an area of aggregation of the various factors in the  
659 middle of the dune, in which the living conditions are particularly difficult. It is for this  
660 reason that facilitation mechanisms are determined among species, however they are transient  
661 in nature due to the high instability of the conditions. Physical stress on the vascular plants of  
662 the dune, including wind exposition, sand scouring, and other stressors of terrestrial origins,  
663 decreases with increasing dune elevation exposure. Conversely, the role of biological factors  
664 in shaping the dune plant community increases with increasing dune elevation. These factors  
665 include interspecific plant competition and facilitation, increasing seedling recruitment and  
666 survival, and increasing herbivory. The Badesi dune plant community is a biogenic  
667 community built and maintained by foundation plant species that stabilize sand on the fore  
668 dune. On the middle dune, sand burial disturbance is the dominant structuring force that  
669 limits the role of sexual recruitment and interspecific competition in structuring the middle  
670 dune zone. In the back dune, ice plant and *Pinus* competitively dominate all other dune  
671 plants, but high summer temperatures limit ice plant dominance in the back dune, resulting in  
672 *Pinus* competitively dominating the back dune terrestrial border.

673 Ecosystems, like sand dunes, where the establishment of foundation species ameliorates  
674 stresses allow community development that would not occur without foundation species.  
675 Coral reefs (Hughes and Jackson 1985), salt marshes (Bruno and Bertness 2001), mangroves  
676 (Ellison and Farnsworth 2001), seagrass (Duarte et al. 2000), and forest ecosystems (Ellison  
677 et al. 2005) have all been explicitly or implicitly described as hierarchically organized  
678 systems. In all of these ecosystems, once foundation species enabled community  
679 establishment, while other biotic factors like competition, recruitment, and trophic dynamics  
680 became important community structuring forces (Bruno and Bertness 2001). These findings  
681 and their implications are important for understanding community organization well enough  
682 to make it a more predictive science and for conservation since they stress that managing,  
683 protecting, and restoring foundation species should often be the first step in many  
684 conservation efforts, rather than focusing on charismatic species.

685

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Figure 1

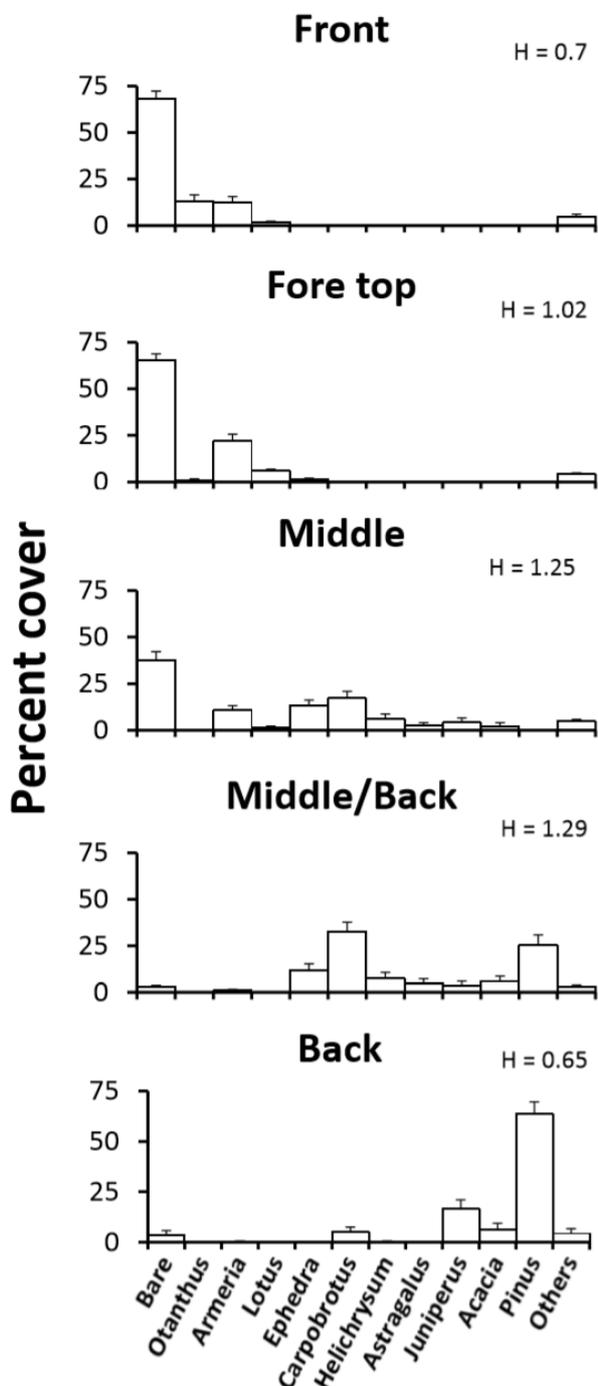


FIG. 1. Plant zonation (mean percent cover + SE) at the Badesi dune. Transects parallel to the shoreline were sampled at 2 m intervals with 0.5x0.5 m quadrats (60/zone) to estimate percent cover. H is the Shannon diversity index.

Figure 2

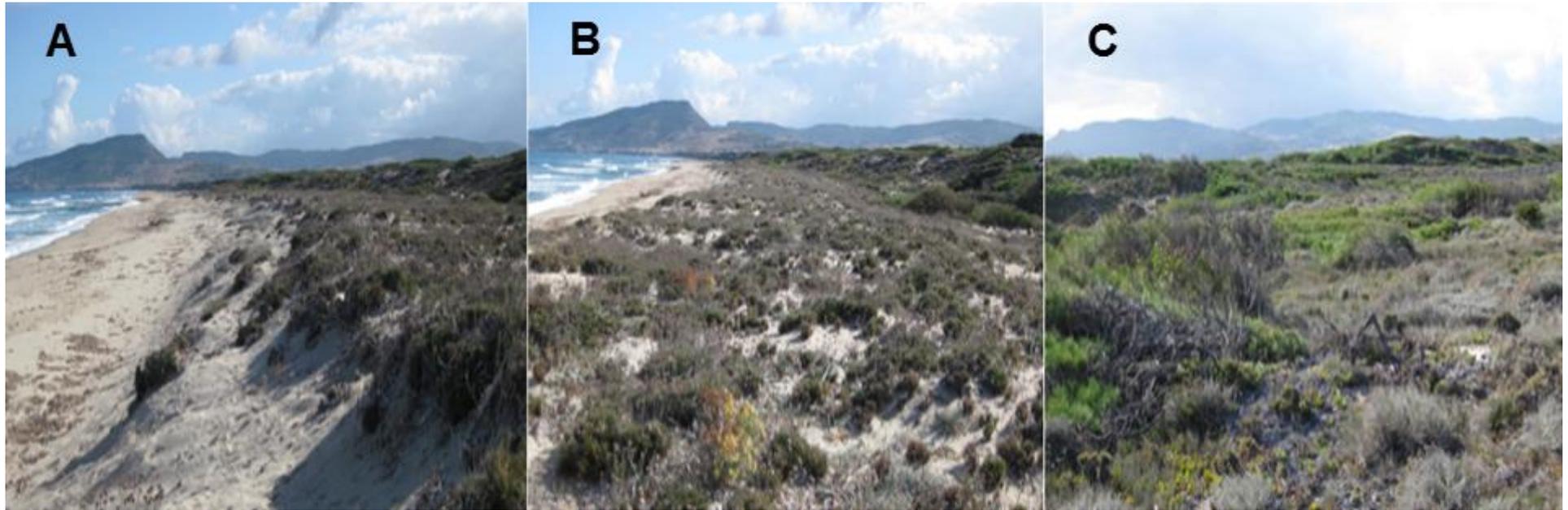


FIG. 2. Photograph of the dune zones at Badesi (Sardinia, Italy). (A) fore dune, (B) middle dune and (C) back dune.

Figure 3

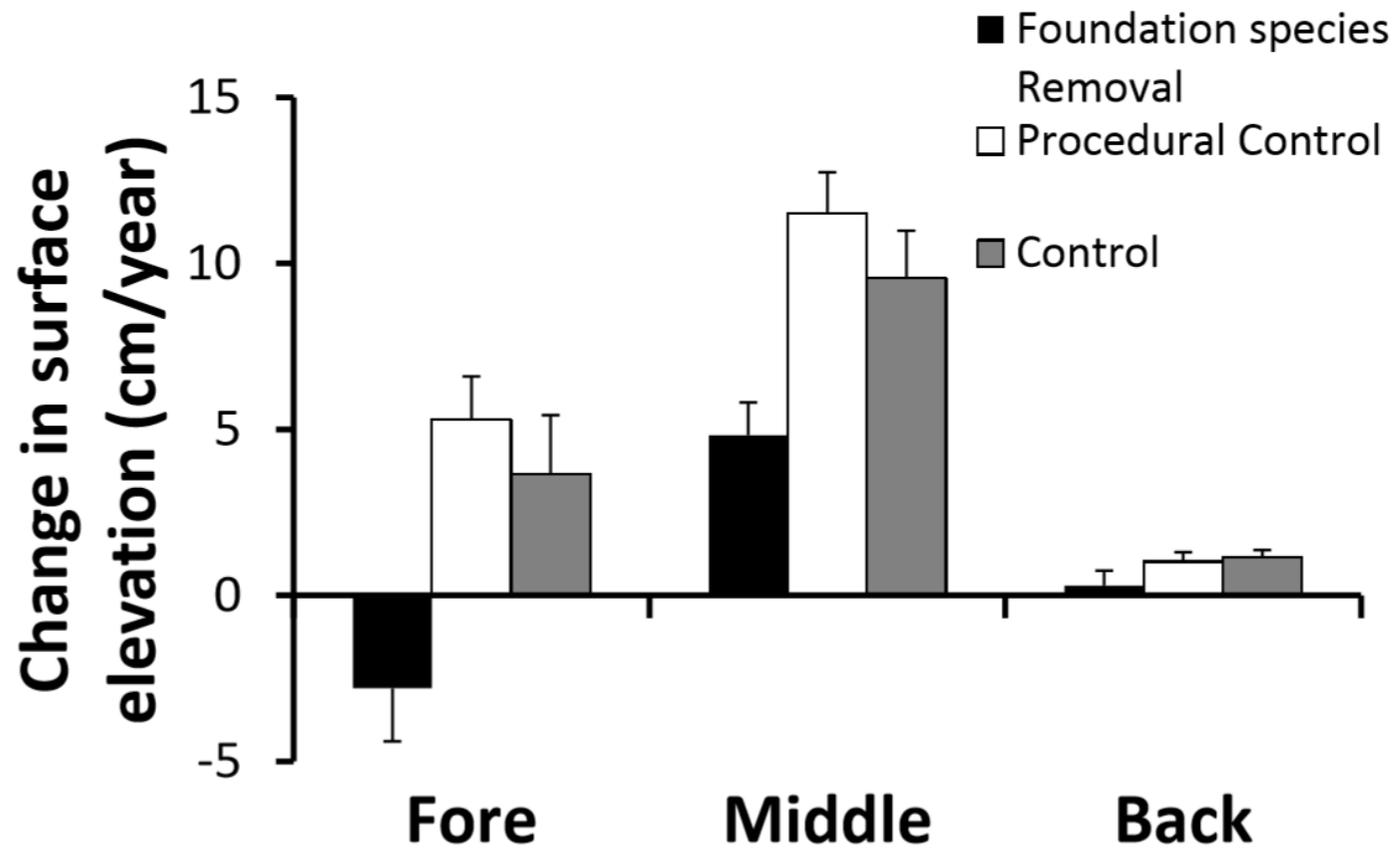


FIG. 3. Surface elevation or sand erosion/deposition balance (mean + SE) of the foundation plant species removal experiment in the three dune zones.

Figure 4

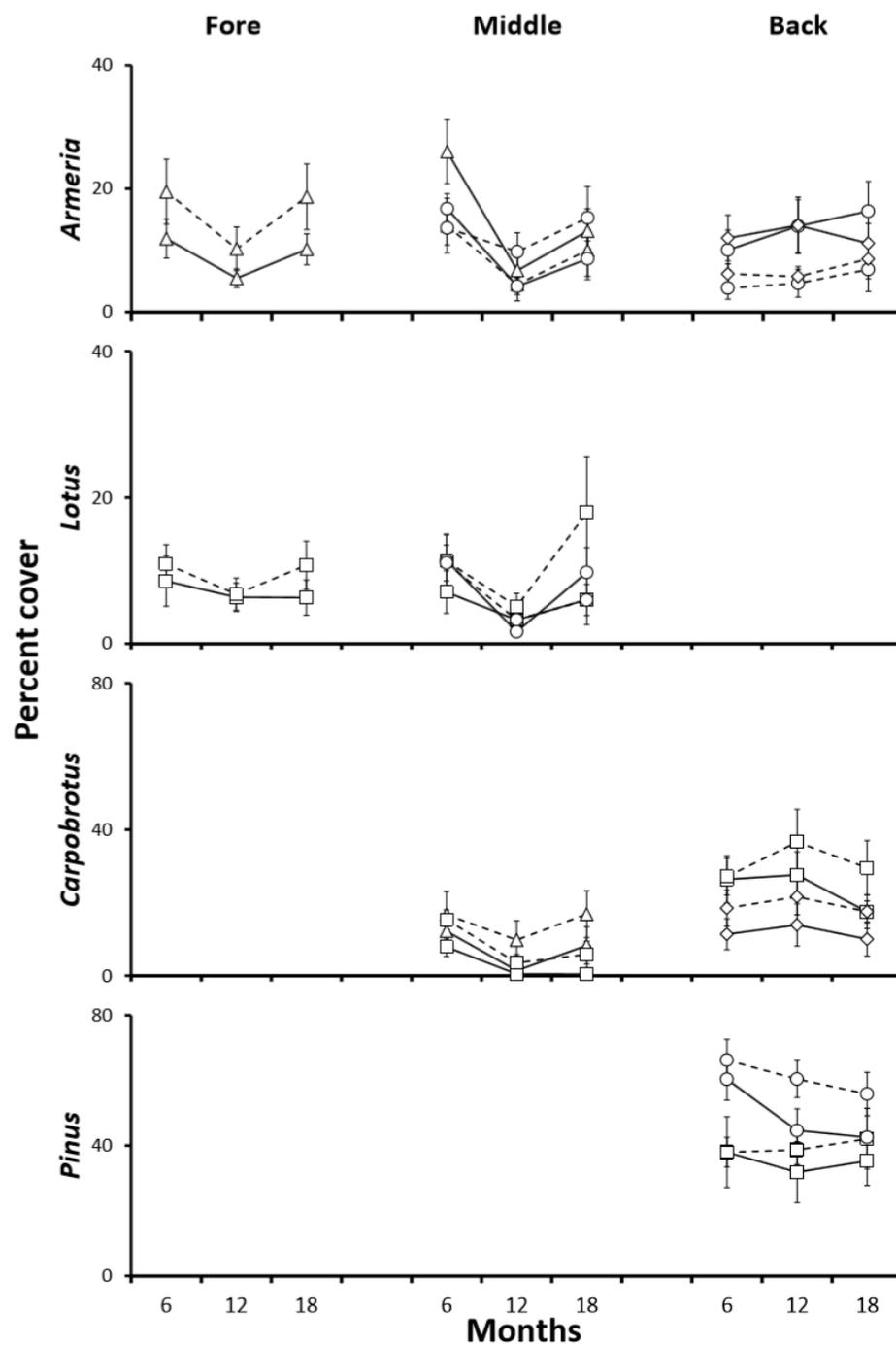
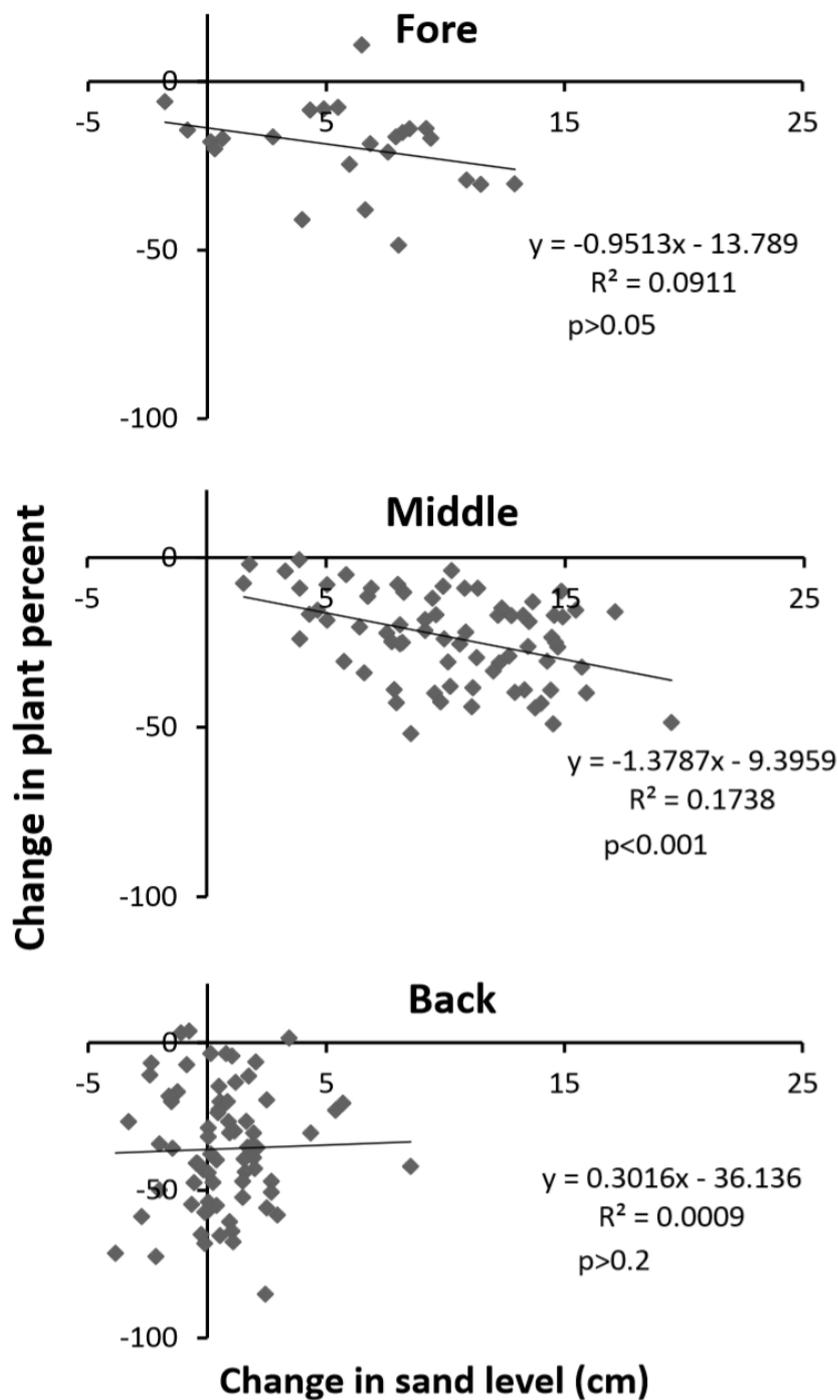


FIG. 4. Reciprocal species removal: *Armeria* ( $\square$ ), *Lotus* ( $\Delta$ ), *Carpobrotus* ( $\circ$ ), *Pinus* ( $\diamond$ ), Species control (—), Reciprocal species removal (- - -). Results of pair-wise reciprocal species removal experiments after 18 months in the fore, middle and back dune.

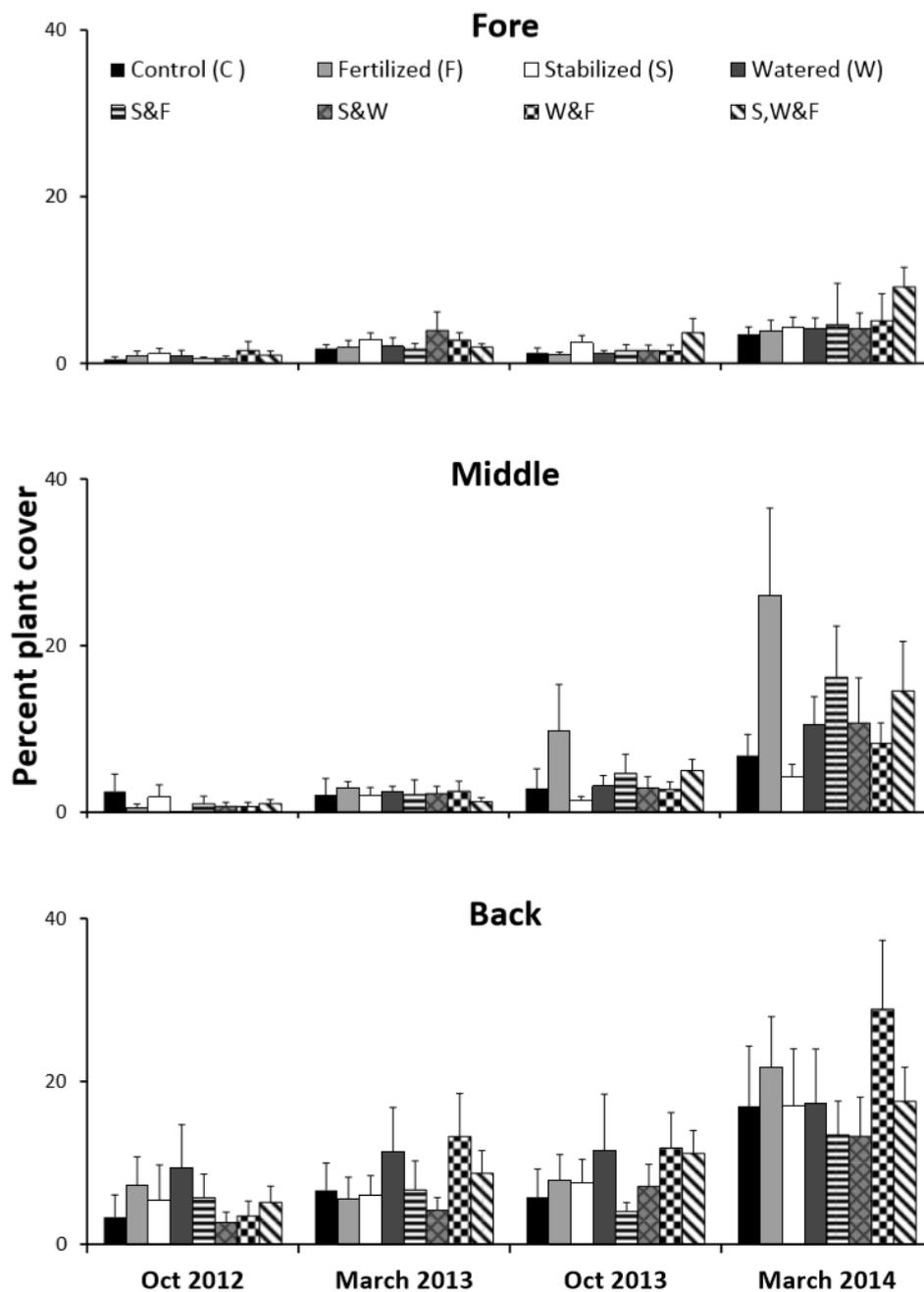
Figure 5



This figure could be presented more neatly, I'm not a fan of the crossing axes. Are the regression analyses described in the methods? I don't recall them being so. The fitted relationship needs to be reported more neatly with a consistent number of decimal places

FIG. 5. Relationship between sand burial and percent plant cover in the pair-wise reciprocal species removal experiments after 12 months in the fore, middle and back dune.

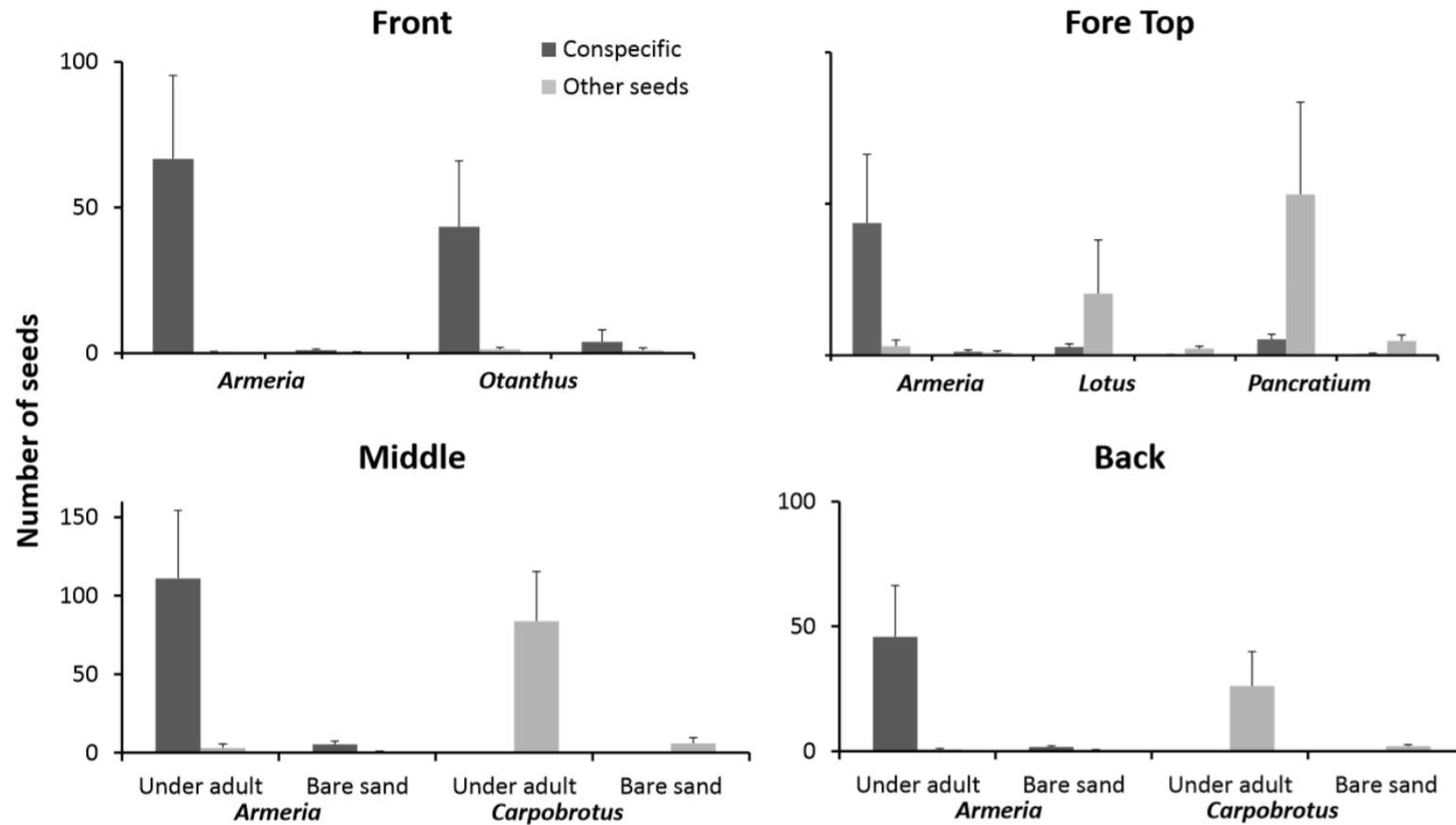
Figure 6



Colour might be preferable to black and white, it's difficult to pick out the different shadings.

FIG. 6. Physical stress alleviation experiment. Percent plant cover (mean + SE) of the fully factorial manipulation of water availability, nutrient availability and substrate stability during 2 years in the fore, middle and back dune. No single or combination of stress alleviation treatments affected plant cover, but higher recovery occurred in back zone.

Figure 7



Error bars should go above and the top of the bar. Boxplots provide more information than bar charts - might be worth thinking about

FIG. 7. Seeds distribution (mean + SE) of common dune plants across zones under adult plants and in adjacent unvegetated sand. Data are given separately for conspecific and non-conspecific seeds.

Figure 8

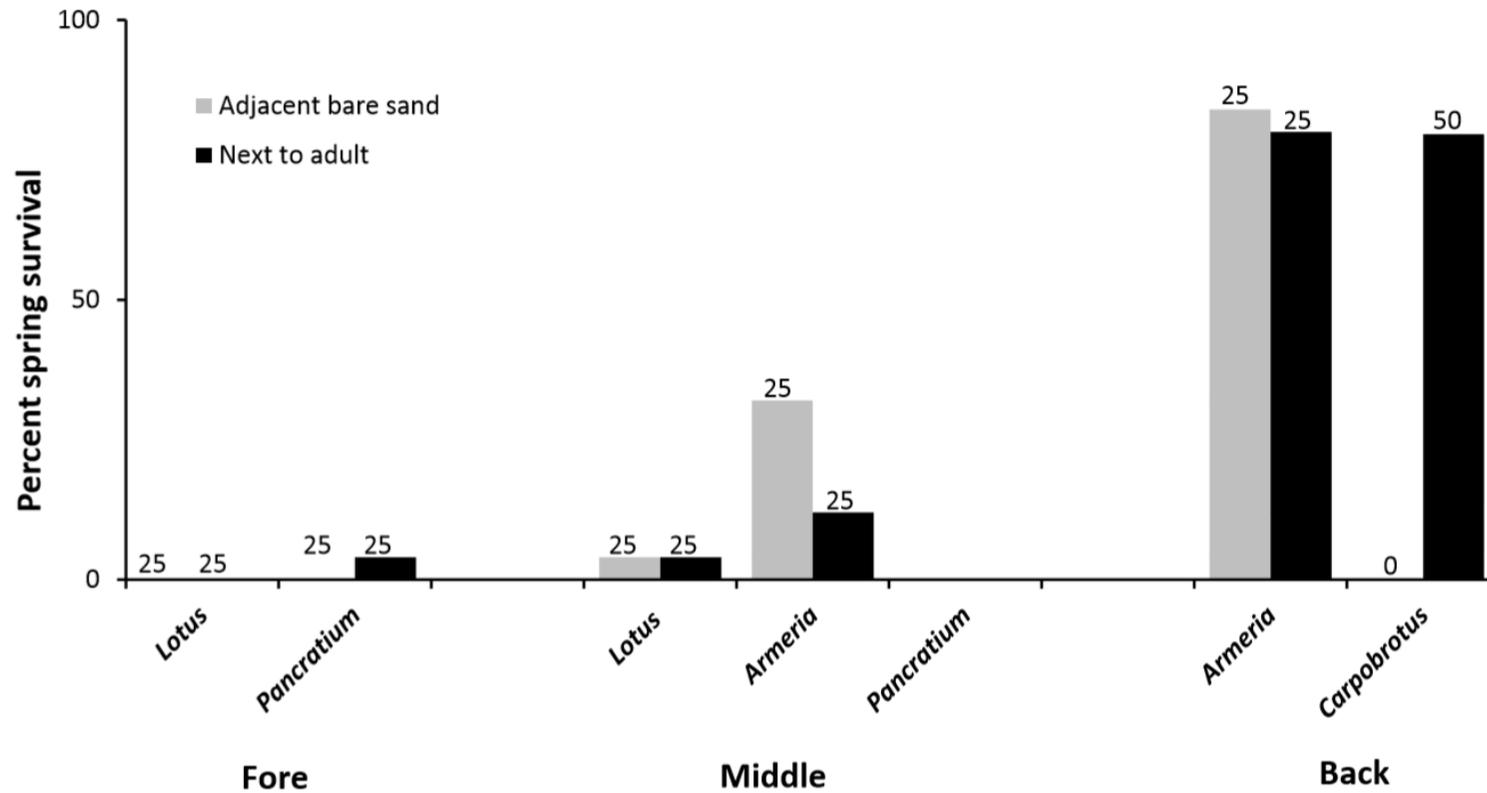


FIG. 8. Survivorship of natural seedlings marked in October 2013. For each zone and species, 25 seedlings were marked associated with conspecific adults and 25 seedlings were marked in bare substrate >30 cm from adult vegetation. Ice plant seedlings were only found under adult ice plants, so all 50 marked ice plant seedlings were with conspecifics. Data are percent of seedlings survived after 3 seasons.

Figure 9

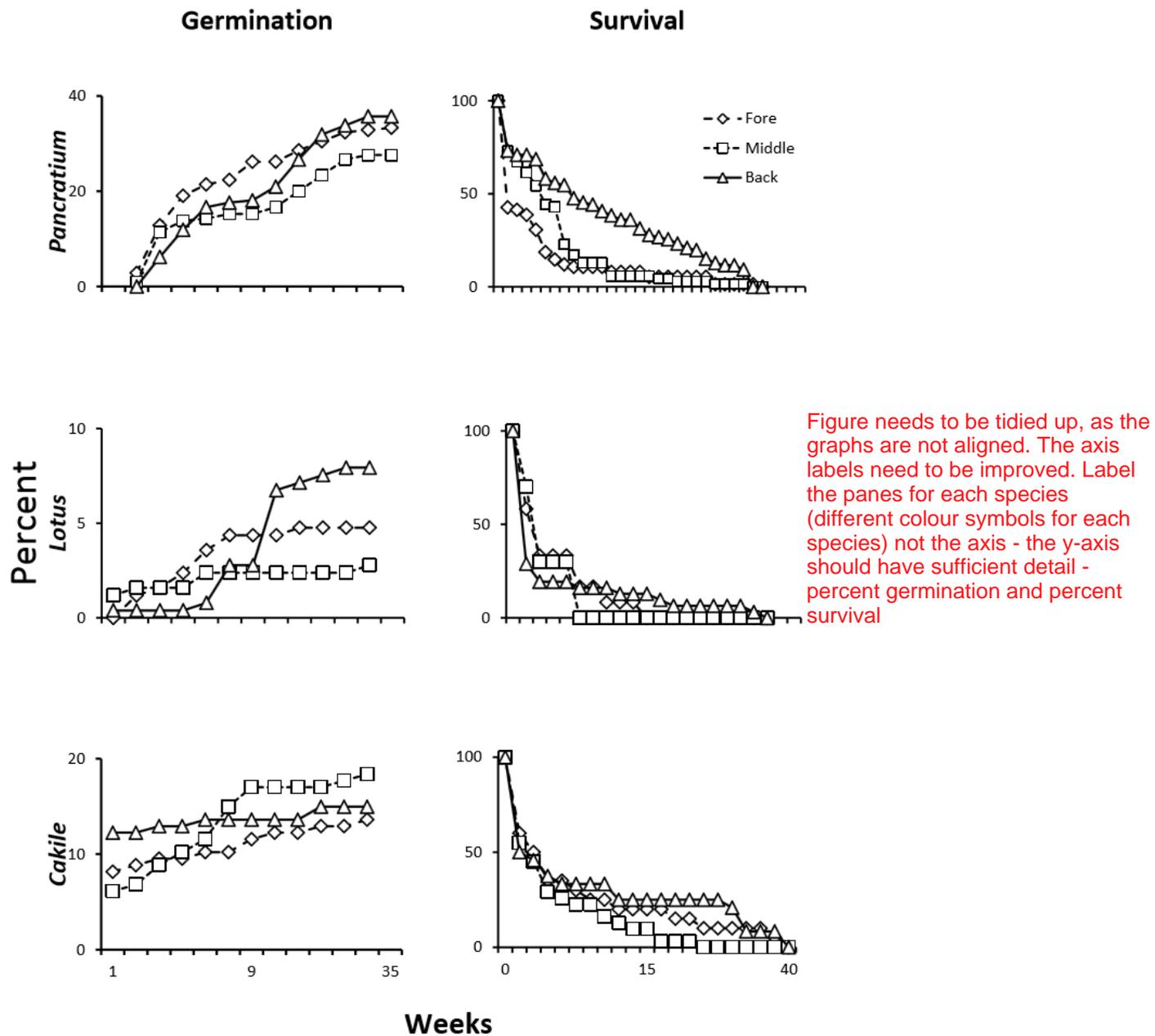


FIG. 9. Results of the seed transplant experiment where germination permeable net bags of locally collected seeds ( $n=21/\text{zone}/\text{species}$ ) from dehiscing seed heads were transplanted to the fore, middle and back dune with and without plant neighbors and scored for germination and seedling survivorship. Data are percent survivorship and germination of the total potential.

Figure 10

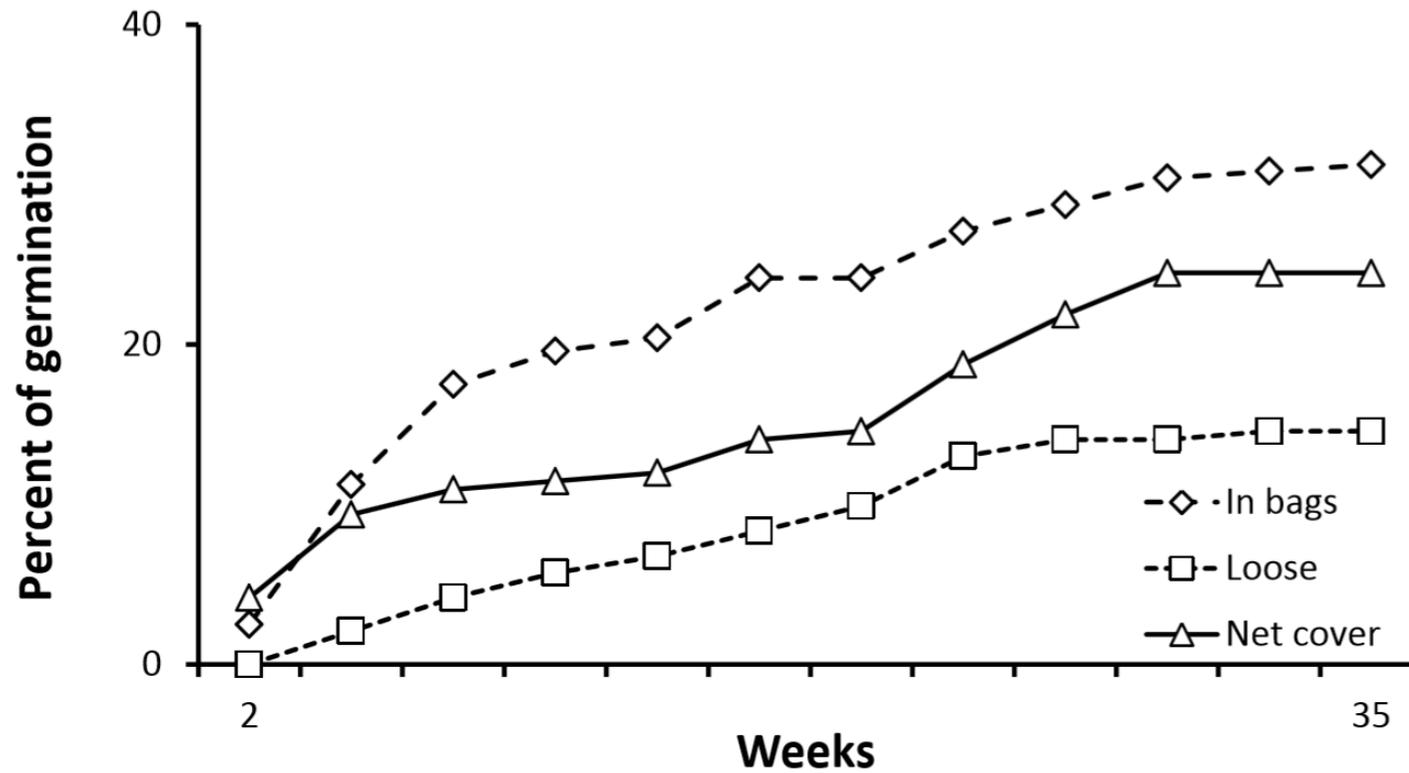


FIG. 10. Seeds erosion experiment. Germination in the fore dune where *Pancratium* seeds were transplanted in germination permeable net bags, loose in the soil and loose in the soil but covered at the surface with nylon mesh to limit erosion (n=8 treatment). Data are percent germination of the total potential.

Figure 11

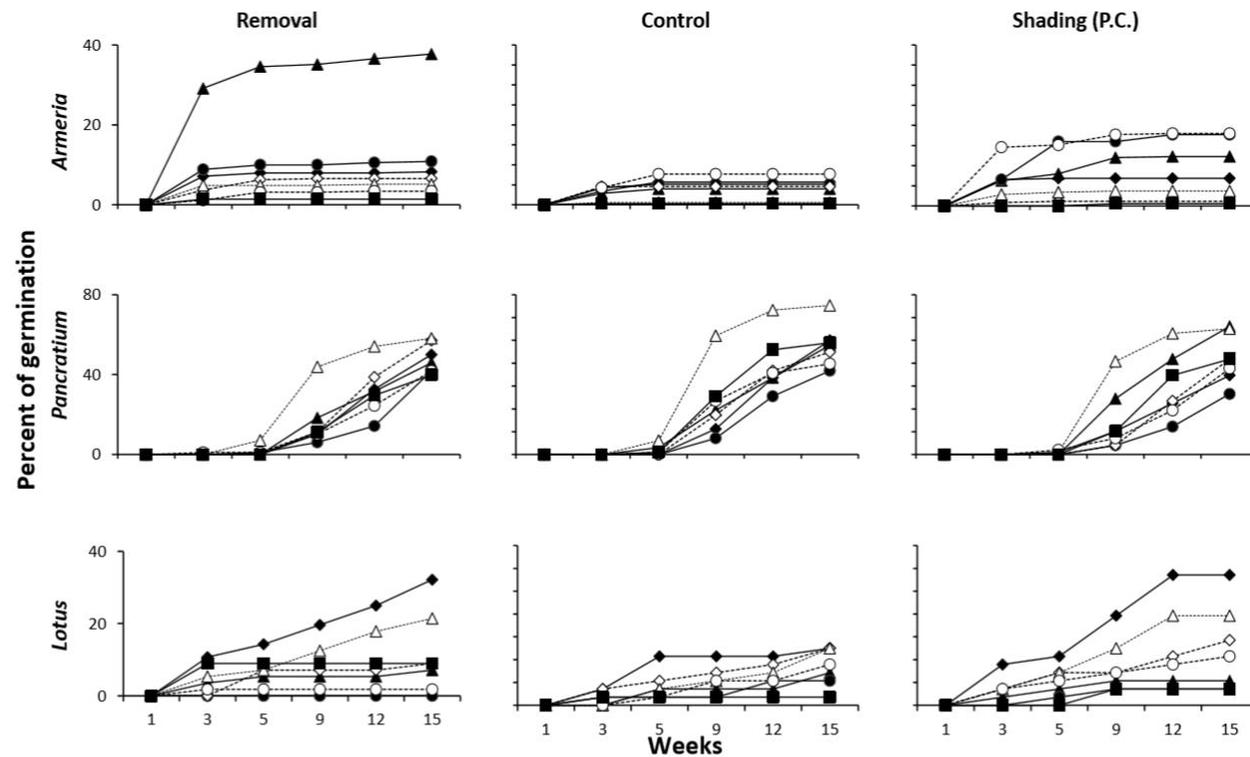


FIG. 11. Back dune competitive release experiment. Germination of *Armeria*, *Pancratium* and *Lotus* seeds sowed in different soils: *Pinus* soil (◆), middle dune soil (▲), *Carpobrotus* soil (●), potting with *Pinus* needles (◇), potting with middle dune soil (△), potting with *Carpobrotus* soil (○) and field (■) (no canopy), Control (under canopy) and Procedural controls (*Pinus* removal with shade cloth to simulate canopy shading, P.C.). N=8/treatment. Data are percent of seeds germinated out of the total potential.

Figure 12

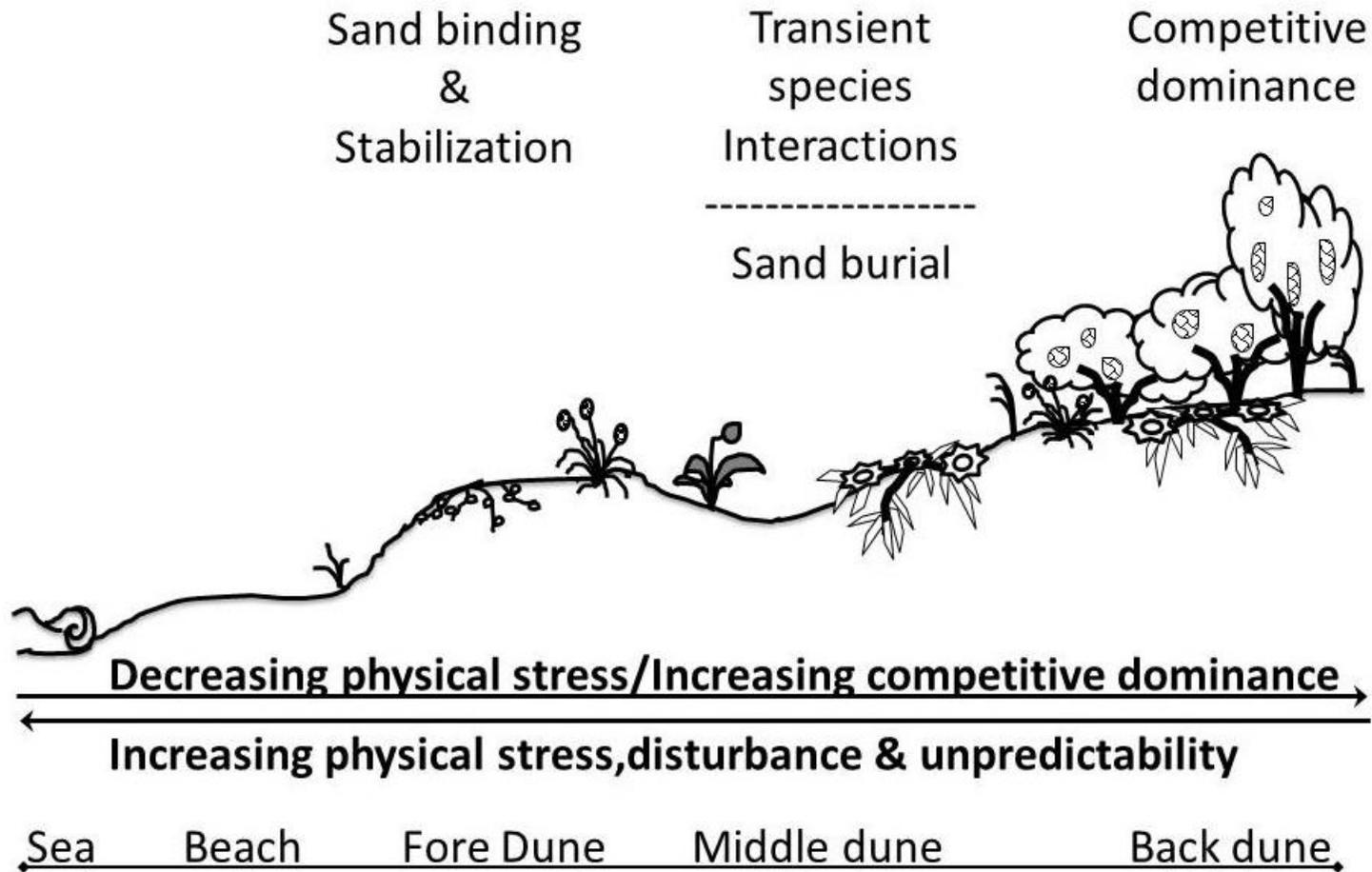


FIG. 12. Conceptual model of the assemble rules of the Badesi sand dune plant community.