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# Arrival order among native plant functional groups does not affect invasibility of constructed dune communities

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# Arrival order among native plant functional groups does not affect invasibility of constructed dune communities

## Abstract

Different arrival order scenarios of native functional groups to a site may influence both resource use during development and final community structure. Arrival order may then indirectly influence community resistance to invasion. We present a mesocosm experiment of constructed coastal dune communities that monitored biotic and abiotic responses to different arrival orders of native functional groups. Constructed communities were compared with unplanted mesocosms. We then simulated a single invasion event by bitou (*Chrysanthemoides monilifera* ssp. *rotundata*), a dominant exotic shrub of coastal communities. We evaluated the hypothesis that plantings with simultaneous representation of grass, herb and shrub functional groups at the beginning of the experiment would more completely sequester resources and limit invasion than staggered plantings. Staggered plantings in turn would offer greater resource use and invasion resistance than unplanted mesocosms. Contrary to our expectations, there were few effects of arrival order on abiotic variables for the duration of the experiment and arrival order was unimportant in final community invasibility. All planted mesocosms supported significantly more invader germinants and significantly less invader abundance than unplanted mesocosms. Native functional group plantings may have a nurse effect during the invader germination and establishment phase and a competitive function during the invader juvenile and adult phase. Arrival order per se did not affect resource use and community invasibility in our mesocosm experiment. While grass, herb and shrub functional group plantings will not prevent invasion success in restored communities, they may limit final invader biomass.

## Keywords

does, not, affect, invasibility, constructed, arrival, dune, order, communities, among, native, plant, functional, groups

## Disciplines

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**Arrival order among native plant functional groups does not affect invasibility of  
constructed dune communities**

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## **Keywords**

Historical contingency, priority effect, exotic, community structure, mesocosm

## **Abstract**

Different arrival order scenarios of native functional groups to a site may influence both resource use during development and final community structure. Arrival order may then indirectly influence community resistance to invasion. We present a mesocosm experiment of constructed coastal dune communities that monitored biotic and abiotic responses to different arrival orders of native functional groups. Constructed communities were compared with unplanted mesocosms. We then simulated a single invasion event by bitou (*Chrysanthemoides monilifera* ssp. *rotundata*), a dominant exotic shrub of coastal communities. We evaluated the hypothesis that plantings with simultaneous representation of grass, herb and shrub functional groups at the beginning of the experiment would more completely sequester resources and limit invasion than staggered plantings. Staggered plantings in turn would offer greater resource use and invasion resistance than unplanted mesocosms.

Contrary to our expectations, there were few effects of arrival order on abiotic variables for the duration of the experiment and arrival order was unimportant in final community invasibility. All planted mesocosms supported significantly more invader germinants and significantly less invader abundance than unplanted mesocosms. Native functional group plantings may have a nurse effect during the invader germination and establishment phase and a competitive function during the invader juvenile and adult phase.

Arrival order *per se* did not affect resource use and community invasibility in our mesocosm experiment. While grass, herb and shrub functional group plantings will not prevent invasion success in restored communities, they may limit final invader biomass.

## **Introduction**

Different arrival orders may result in priority effects where the first species establishes and changes the abiotic environment, in turn influencing site favourability for subsequent immigrating species (Catovsky & Bazzaz 2000; Ladd & Facelli 2008). Prior species may moderate the success of subsequently immigrating species via exploitative competition where precedence allows the prior species to pre-empt resources required by the immigrant (Perry et al. 2003; Grman & Suding 2010). The prior species may also use interference competition to affect growth rates of other species. For example, a prior species may produce soil allelochemicals which interfere with subsequent species germination or establishment (e.g. Wardle et al. 1998). Prior species may also change microbial communities which affect niche availability for subsequent species (Teutsch-Hausmann & Hawkes 2010). Finally, prior species may alter nutrient cycling rates (Maron & Connors 1996).

The potential for different community compositions following different arrival orders has implications for community invasibility. Alternate species arrival orders may build communities with different invasion resistance because one arrival order scenario may more effectively sequester biotic and abiotic resources or express stronger priority effects than an alternate arrival order scenario. Subsequent invaders may have variable success establishing and spreading. Certainly, if native vegetation preempts resources, it is likely that invader germination and establishment will be inhibited or reduced (Baskin & Baskin 1989). An example of priority effects and arrested immigration is in restored floodplain forests of the southcentral United States where replanted tree species (usually *Quercus* spp.) have largely excluded other immigrating species (Allen 1997). In addition, arrival order has been shown to affect experimental plant assembly (Kardol et al. 2012). The observed effect was stronger with greater soil fertility: under

high nutrient conditions, priority species preempted light resources and prevented establishment of deferred species (Kardol et al. 2012).

Practical ecological restoration applies many ecological theories such as succession, competition and niche dynamics (Young et al. 2005), however, few experimental restoration studies have tested the concept of priority (Lulow 2004). If a particular functional group arrival order establishes resistant communities which efficiently sequester resources and exclude or limit subsequent invasion events, this may be a relatively simple and cost-effective restoration procedure to enact.

We devised a mesocosm experiment to investigate arrival order and community invasibility. We manipulated arrival orders of three common coastal dune functional groups – grasses, herbs and shrubs – and compared resultant communities with unplanted mesocosms. We used functional groups based on growth form because size and shape are often good indicators of competitive ability and resource acquisition (Walker et al. 2010). We then simulated an invasion event using bitou (*Chrysanthemoides monilifera* ssp. *rotundata*) seed.

Bitou is a South African shrub which has invaded extensive areas of coastal dune communities on the east coast of Australia. Its dominance has adverse effects on native plant communities (Mason & French 2008) and ecosystem processes (Lindsay & French 2005). Bitou control and dune restoration have been undertaken for decades, but resilient post-control native communities remain elusive. Understanding the effects of arrival order on community invasibility may assist by informing restoration planting protocols.

Our planting regime was constrained as we ensured final representation of all functional groups in the mesocosms (i.e. we did not allow alternate stable states), controlled for species richness and number of individuals and removed volunteer colonizers throughout the experiment. This

approach allowed us to assess the contribution of arrival order alone to biotic and abiotic variables. Many studies which evaluate the role of arrival order in community structure monitor the effects of uncontrolled colonization (e.g. Dean & Hurd 1980; Jenkins & Buikema 1998; Walker et al. 2010). As a result, they are unable to demonstrate that all species or functional groups in the source pool have had a chance to colonise. It is unclear whether a species or functional group is absent in the final community because invasion was unsuccessful and the community was resilient or because invasion simply never occurred and the community was unchallenged (Robinson & Dickerson 1987). Our approach of controlling the introduction of functional groups and the invasion event should remove this uncertainty. Our experimental design allowed us to question: Will the effect of different arrival orders from a pool of functional groups always be the same? We were particularly interested in the response of emergent communities to both an invasion event and abiotic resource availability.

Different arrival orders allowed us to examine the effect of time since full community development on invasion resistance. We predict that simultaneous planting of functional groups at the beginning of the experiment will allow maximal growth and resource use for all planted functional groups prior to introduction of the invader. This establishment and occupation of niche space in turn increases resistance to invasion (Knops et al. 1999; Dukes 2001). In contrast, deferred functional groups in the staggered plantings will have reduced time to establish prior to the invasion event and resource acquisition may be incomplete compared with simultaneous initial plantings (Kardol et al. 2012). For example, if herb and grass species are planted first, they may establish a dense cover at the soil surface and a dense root network in the superficial soil horizon. However, if shrub species are planted first, they may achieve deeper rooting profiles and higher canopy cover. Asynchronous growth of functional groups may increase resource

availability for the invader at the time of introduction and increase invasibility. Finally, we predict that all planted treatments (simultaneous and staggered plantings) will offer greater resource use and invasion resistance than unplanted mesocosms. Invasion resistance effects may be significant throughout the experiment or effects may be evident soon after invasion and then disappear. Specifically, our predictions are: (1) Community invasibility will be lower in planted than unplanted mesocosms; (2) Of the planted treatments, mesocosms where all functional groups were planted together at the beginning of the experiment will be less invaded than mesocosms where functional group plantings were staggered; (3) Abiotic resource use will be highest for the treatment where all functional groups were planted together at the beginning of the experiment, lowest in the unplanted treatment, and intermediate for the planted treatments with variable functional group arrival orders. These arrival effects may carry a legacy throughout the experiment or only be evident in the early stages following invasion.

## **Methods**

### **Mesocosm facility**

The mesocosm experiment was conducted between June 2007 and May 2009 at a fenced outdoor facility (499m x 326m) at the University of Wollongong Shoalhaven Campus on the south coast of New South Wales (34° 53' 23.44" S; 150° 33' 53.66" E). Each mesocosm consisted of a galvanized iron tank with dimensions of 2.1 m diameter and 1.2 m height. These dimensions were chosen to allow for natural variation in species rooting architecture for the duration of the experiment. Each mesocosm was positioned on a timber stand in a grid network and separated from neighbours by at least 1.5m. We lined the base of each tank with drainage aggregate to a depth of 100 mm and then covered the aggregate with geotech fabric to avoid movement of fine material through the base drainage outlet. We then filled each tank with unwashed dune sand to a



depth of 1m. The sand was very fine with low salinity ( $0.037\text{mScm}^{-1}$ ) and was therefore similar to other east coast dune soils (Diggle & Bell 1984; Maze & Whalley 1992). Each mesocosm experienced ambient weather conditions which were measured by a weather station (Davis Wireless Vantage Pro2, California USA) located within the compound.

Dune soil fauna were introduced to each mesocosm using a sample of field soil. In June 2007, we collected soil from the upper 5 cm of the soil profile at seven native foredune sites. The soil was sieved with a 6.5 mm mesh, mixed thoroughly and applied to mesocosms within a week of collection. Each mesocosm received a soil inoculum to a depth of approximately 7 mm applied evenly across the surface of the tank. We also added approximately 250 g of Osmocote Native (NPK controlled release fertilizer with trace elements) to each mesocosm in June 2007 and April 2008. We measured total nitrogen four months into the experiment – this allowed soil chemistry to re-equilibrate after the initial setup disturbance and allowed release of fertilizer. At this early stage, we found that soil ammonia concentrations were low and comparable to those found on foredunes (Lindsay & French 2005).

### **Experimental design**

Twenty mesocosms were randomly distributed within the outdoor facility. Each planted mesocosm consisted of six native foredune species because a pilot study revealed an average of six species in 2 x 2 m quadrats of relatively undisturbed foredune vegetation (Mason unpublished data). Two species were drawn from each of three different functional groups: rhizomatous or stoloniferous grasses, prostrate herbs and shrubs (Table 1).

Species were grown from seed or cuttings collected from coastal sites. Individuals were raised in forestry tubes using a standard native potting mix and were transplanted into mesocosms after at least two months of growth. Rainfall was supplemented with manual watering at commencement

and at dry intervals throughout the experiment. Each mesocosm was watered at the same hose pressure for a set time period. We replaced dead individuals as required for the first 11 months of the experiment. After this time it became difficult to distinguish some grass and herb individuals due to their spreading habit. We subsequently monitored mesocosms for species representation rather than abundance.

The planting scheme involved two species being drawn at random without replacement from the pool of available species within each functional group (Table 1). Four individuals from each species were planted (24 individuals / mesocosm). To minimize confounding effects of neighbourhood structure on invasibility, the location of each individual in the mesocosm was randomly assigned and individuals were positioned approximately equidistantly from each other and the mesocosm boundary. Species richness and diversity along with functional richness were held constant while arrival order varied.

### **Arrival order treatments**

The planting scheme for the three arrival order treatments was staggered over a five month period: initial planting was undertaken in June 2007 and subsequent planting was performed in November 2007. Treatments consisted of grass, herb and shrub individuals planted simultaneously in June 2007 (GHS), grass and herb individuals planted simultaneously in June 2007 followed by shrub individuals in November 2007 (GH-S) and shrub individuals planted in June 2007 followed by grass and herb individuals planted simultaneously in November 2007 (S-GH). We also included an unplanted treatment (unplanted). There were five replicate mesocosms for each treatment.

### **Invasion event**

Seven months after the initial planting (June 2007) and two months after subsequent planting (November 2007), we simulated an invasion event by sowing bitou seed in each mesocosm. We sowed approximately 1250 bitou seeds (by weight) in each mesocosm in January 2008, spreading the seed, which had been mixed with dune sand, over the surface of each tank. We had previously determined the size of bitou seed banks at a variety of foredune bitou invaded, non-invaded and managed sites (French and Mason unpublished). We based our sowing rate on the viable seed bank (mean  $\pm$  SE: 216.54 seed m<sup>-2</sup>  $\pm$  59.26) of fore dune sites which had supported a bitou monoculture, but which were cleared and left fallow for two months to eliminate the first flush of germination. We chose this seed bank classification as it most closely simulated the invasion potential of dune sites which have been prepared for restoration. We collected bitou seed from a number of south coast foredune sites. The seed was air dried, mixed and stored for approximately seven months. Immediately prior to sowing the bitou seed, we conducted a viability test with tetrazolium chloride on a subsample (60% viability) and adjusted the seed count for each mesocosm to achieve the desired viable seed bank density.

We used bitou seed rather than seedlings as the invader propagules to determine in situ establishment fractions (see Prieur-Richard et al. 2000 for related discussion). However, we used native seedlings rather than seed to establish mesocosms because seedlings are often directly planted as part of dune restoration following bitou control efforts, thus the mesocosm experiment mimicked on-ground conditions. Also the research addressed *invasibility* of communities with different arrival orders of functional groups; we therefore sought to establish the community with seedlings prior to introduction of bitou seed. We removed volunteer colonizers (native and exotic) from both planted and unplanted mesocosms throughout the experiment. This was done

to keep functional richness static and to minimise disturbance caused by removing large, well established exotic individuals.

## **Biotic measurements**

### ***Invasion success***

We counted the number of bitou seedlings in each mesocosm at intervals throughout the experiment. Counting was conducted initially at weekly intervals, then fortnightly, then monthly. Counting was more intensive early in the experiment to closely monitor germination and survivorship rates of the invader. We also evaluated bitou abundance by estimating percent foliage cover in each mesocosm. Bitou abundance was measured at intervals once individuals became well established (260 days after sowing of bitou seed). At the conclusion of the experiment, we harvested, bagged and dried the above-ground bitou biomass. All biomass was dried to a constant weight at 60°C and mass was recorded ( $\pm 0.001$ g).

### ***Functional group biomass***

At the conclusion of the experiment, we harvested native above-ground biomass by clipping individuals at soil level. Biomass was sorted to species level, bagged and dried to a constant weight at 60°C and mass was recorded ( $\pm 0.001$ g).

We also sampled the distribution of below-ground biomass for each mesocosm. We used a portable, self-supporting hydraulic vibracorer to extract cores to a depth of 90 cm. The vibracorer consisted of a hydraulic jackhammer driving mechanism, a steel guidetrack and a 4.5 m quadrapod support. We used aluminium cores with a 74 mm internal diameter and extracted three cores per mesocosm. Cores were extracted during February and March 2009. Each core was capped and stored in a cool room until it was processed. Cores were sectioned at the following depths: A: 0-20 cm; B: 20-50 cm; C: 50-75 cm; D: 75-90 cm. Sections reflected likely

root stratification. The extraction process resulted in compaction of the soil in each core which meant that total core lengths were generally less than 90 cm. The core section lengths were therefore proportionately adjusted to account for the compaction factor. Core sections were washed over a 2 mm sieve to remove sand and rock material. Root biomass was then bagged and dried at 60°C until a constant weight was obtained, and the average mass per core section per tank was recorded ( $\pm 0.001$  g). We were unable to attribute root material to particular species.

### **Abiotic measurements**

#### ***Photosynthetically active radiation***

We measured photosynthetically active radiation (PAR) at soil level in each mesocosm. Measurements were taken at monthly intervals from January 2008 to August 2008 except during July 2008 when cloudy weather precluded accurate measurements. Measurements were then taken at two monthly intervals until completion of the experiment. Due to time constraints, we measured PAR in planted rather than unplanted mesocosms in the early stages of the experiment. We used Quantum Sensors (Skye Instruments Ltd. Wales, UK; Li-Cor Environmental, Nebraska, USA) to measure PAR. We took 20 measurements equally partitioned among four quadrants in the mesocosm. Coordinates for each reading were generated randomly for each measurement period and applied to all mesocosms. Measurements were taken between 10am and 2pm on clear sunny days. A further six measurements were taken above the vegetation canopy. We then calculated average percent light penetration to the soil surface for each mesocosm.

#### ***Bare ground cover***

We estimated percentage cover of bare ground in each mesocosm by visualising the foliage cover (i.e. percentage of the mesocosm occupied by the vertical projection of foliage and

branches (Walker & Hopkins 1990)) and then subtracted this number from 100 to give % bare ground cover. Measurements were taken at monthly intervals from February 2008 to January 2009.

### ***Soil moisture***

We obtained profile soil samples at intervals through the experiment: December 2007, June 2008 and December 2008. Samples were taken at 0 cm, 20 cm, 50 cm, 75 cm and 100 cm depths using soil augers. Samples were taken at five random locations stratified in each quadrant of the mesocosm. At each depth, samples were bulked and stored in airtight plastic vials. We used the gravimetric method to determine soil moisture by measuring mass loss after drying 5-10 g soil at 60°C for at least 72 hours.

### ***Soil temperature***

We measured soil temperature for each arrival order treatment by burying five temperature sensors (D21921G-F5 Dallas Thermochron iButton) at a depth of 2 cm in two replicate mesocosms of each treatment. We chose to monitor soil temperature close to the surface as this region is where fluctuations are most apparent (e.g. Auld & Bradstock 1996). Each sensor was placed using random coordinates stratified in each quadrant of the mesocosm and was marked with a flagged peg. The sensors were set to measure temperature hourly for a month. The sensors were then retrieved and the data downloaded. The sensors were reburied the following month. This pattern was followed for the duration of the experiment. Replicate mesocosms were chosen randomly for each measurement cycle. Average monthly minimum and maximum temperatures were extracted from the dataset for analysis.

### ***Soil analyses***

### ***Nutrient analysis of soil leachate***

We measured dissolved soil nutrient leaching losses below the root zone in each mesocosm and assumed that greater nutrient concentrations in leachate related to greater soil nutrient availability for plants (e.g. see Symstad and Tilman 2000). We collected a bulk leachate sample from the base drainage outlet of each mesocosm in December 2007, February 2008, May 2008, September 2008 and December 2008. We were unable to obtain sufficient leachate samples in February 2009 to analyse due to dry conditions.

Leachate samples were collected in 1L polypropylene, acid-washed bottles and stored in a refrigerator until processed. Dissolved concentrations of Ba, Ca, Fe, K, Mg, Mo, Ni and P were determined by inductively coupled argon plasma-atomic emission spectrometry (ICP-AES) (Spectroflame EOP, Spectro Analytical Instruments) (Simpson et al. 2002). We attempted to measure dissolved phosphorus using ICP-AES, ion chromatography and the peroxide-sulfuric acid modified Kjeldahl digestion procedure (Allen 1989). However, phosphorus concentrations were below detection limits ( $\sim 100 \mu\text{g P L}^{-1}$ ) for this procedure.

Soil pH was  $7.53 \pm 0.03$  (mean  $\pm$  SE) and leachate water pH was  $6.74 \pm 0.03$  (mean  $\pm$  SE), both remaining fairly constant throughout the experiment.

### ***Total soil nitrogen***

Five random soil samples were collected at a depth of 20 cm from each mesocosm then bulked and mixed ( $\sim 20$  g). Samples were collected in October 2007 and December 2009. We did not sample nitrogen consistently throughout the experiment because concentrations were initially very low across all treatments and laboratory resources were limited. We measured total nitrogen (N) of dry soil by Kjeldahl analysis with  $\text{SeSO}_4\text{-K}_2\text{SO}_4$  catalyst based on the method of Eaton et

al. (2005) using an ammonia selective electrode (Thermo Orion 9512) and a Thermo Orion meter (Model 720).

### **Statistical analyses**

We analyzed the response of invasion success and abiotic resource availability over time and across functional group arrival order treatments using repeated-measures ANOVA. The effects of Time and the Time x Functional Group Treatment interactions were analyzed with Pillai's Trace multivariate test as it is robust to deviations from normality and equality of variance (Scheiner 1993). Where a significant interaction was observed, the effects of the Functional Group Treatment were compared for each time separately. If the interaction was not significant, the effects of the Functional Group Treatments were compared using average results from all the times. When the analysis indicated a significant main effect, we performed Tukey post hoc tests to identify differences among treatments. In some cases, there were not enough degrees of freedom in the test to include all time periods, so we chose a subset of time periods to include in analyses. In the case of abiotic measurements, we included the time period immediately prior to bitou sowing, and all, or a subset of, post-sowing time periods in analyses (omission of time periods depended on sampling intensity). Where significance was detected, but variances remained unequal despite transformation, we used Welch's Test which is robust to heterogeneity of variance (Welch 1951; Day & Quinn 1989) and examined one-factor ANOVA results using the Dunnetts T3 post hoc test (Day & Quinn 1989) which does not assume equal variances. Where destructive harvesting was required, ANOVAs were conducted for data collected at completion of the experiment. We conducted a two factor ANOVA to determine the effect of planting treatment and core depth on below-ground biomass. We also conducted a two factor nested and crossed ANOVA to determine the effect of planting treatment on the distribution of



final above-ground native biomass among functional groups (each mesocosm was nested within planting treatment and crossed with functional group). The nested structure was necessary to adjust for the fact that biomass of each functional group was not independent in each mesocosm. We performed Tukey post hoc tests to identify differences among biomass of functional groups. Where necessary, data were transformed to meet the assumptions of ANOVA. Data were analysed with SPSS v17 software (SPSS 2008, Chicago). We present data as means  $\pm$  1 standard error throughout.

## **Results**

### **Biotic response variables**

The arrival order of native shrub, herb and grass functional groups in planted treatments did not affect community invasibility by bitou, although planted and unplanted treatments showed significantly different invasibility (Table 2). Post hoc tests revealed that the unplanted treatment had significantly fewer mean bitou individuals over the experimental period than all planted treatments (Figure 1). In contrast, the mean bitou cover was significantly higher in the unplanted treatment than all planted treatments (Figure 2). There were no significant interactions between time and treatment for the number of bitou seedlings or bitou cover (Table 2). Final bitou above-ground biomass reflected time sequence trends: there was a significant difference among treatments ( $F_{3,16} = 28.829$ ;  $P < 0.001$ ) and post hoc tests revealed that the unplanted treatment had significantly higher mean bitou biomass ( $1901.280 \pm 258.585$  g) than all planted treatments. Planted treatments had similarly low mean final bitou biomass (mean  $\pm$  SE: GHS:  $188.471 \pm 99.348$  g; GH-S:  $213.188 \pm 76.361$  g; S-GH:  $163.393 \pm 58.977$  g).

A one-factor ANOVA revealed that above-ground native biomass was similar across all planted treatments ( $F_{2,12} = 0.516$ ;  $P = 0.610$ ). However, a two-factor nested ANOVA indicated that the

distribution of biomass differed across functional groups within planted treatments (Treatment x Functional group:  $F_{4,24} = 5.090$ ;  $P = 0.004$ ). The significant interaction was driven by the priority planted functional groups generally having greater biomass than the deferred planted functional groups (Figure 3). We also conducted a MANOVA, which agreed with our nested ANOVA findings ( $F_{3,11} = 11.964$ ;  $P = 0.001$ ).

For below-ground biomass, the interaction between treatment and depth was non significant ( $F_{9,64} = 0.597$ ;  $P = 0.794$ ), however, the distribution of root biomass differed significantly along the soil profile ( $F_{3,64} = 40.765$ ;  $P < 0.001$ ). Root biomass was highest in the upper soil profile and decreased with depth (post hoc test results:  $0-20 > 20-50 > 50-75, 75-90$  cm). While there was also a significant treatment effect ( $F_{3,64} = 3.292$ ;  $P = 0.026$ ), post hoc tests were unable to identify where the differences lay and we conclude that below-ground biomass did not strongly differ amongst planted and unplanted treatments.

### **Abiotic response variables**

Similarly, the arrival order of native shrub, herb and grass functional groups did not consistently affect most abiotic response variables that we measured. The average monthly maximum soil temperature, surface soil moisture (0 cm) and concentration of Ca, Mo, Ni and K in soil leachate did not show significant interactions between time and treatment nor significant treatment effects among planted and unplanted treatments (Table 2).

Patterns in soil moisture at 20 cm and 50 cm depth were consistent for each treatment across time periods (i.e. the interaction between time and treatment was non-significant); however, there were significant treatment effects at each soil depth (Table 2). We found that the unplanted treatment had significantly higher moisture levels at both 20 cm and 50 cm than the GHS planted treatment. The GH-S and S-GH planted treatments had soil moisture levels which were similar to

each other and both the unplanted and GHS planted treatments. For soil moisture at 75 cm depth, there was a significant interaction between time and treatment (Table 2); however, Welch's test was unable to identify significant differences among treatments at each time period. Soil moisture at 100 cm depth also revealed a significant interaction between time and treatment (Table 2). The interaction was driven by a significant difference between treatments during December 2008 ( $F_{3,13} = 5.879$ ;  $P = 0.009$ ). Post hoc tests revealed that the unplanted treatment had significantly higher soil moisture than the GHS treatment ( $P = 0.008$ ).

The response patterns for average monthly minimum soil temperatures were consistent for all treatments over time (interaction between time and treatment was non significant). However, there was a significant overall treatment effect (Table 2). We found that the unplanted treatment had significantly lower minimums than both the GHS and GH-S treatments.

The response patterns for bare ground cover were consistent for all treatments over time (interaction between time and treatment was non significant), but there was a significant overall treatment effect (Table 2). Post hoc tests indicated that the unplanted treatment had significantly higher bare ground cover than all planted treatments. Of the planted treatments, GH-S had significantly lower bare ground than S–GH, and GHS had intermediate cover (Figure 4). Despite the distinction between planted treatments for bare ground cover, they were indistinguishable in terms of PAR at ground level (Table 2).

There were significant interactions between time and treatment for Ba, Fe and Mg nutrient concentrations in soil leachate (Table 2). While Welch's test indicated that the interactions were driven by significant differences between treatments at particular time periods, Dunnetts T3 tests did not reveal any consistent patterns in the data (Appendix A). As such, the differences appeared unrelated to our treatments and could not be explained in the context of our experiment.

Average total soil nitrogen (mg/g dry soil) was uniformly low across treatments during October 2007 in the first year of the experiment ( $F_{3,16} = 2.085$ ;  $P = 0.143$ ). In December 2008, immediately prior to harvest, there were significant differences in soil nitrogen among treatments ( $F_{3,16} = 54.580$ ;  $P < 0.001$ ). Post hoc analyses revealed that unplanted and grass, herb (GH-S) priority treatments had similarly low total nitrogen concentrations ( $0.005 \pm 0.002$  and  $0.078 \pm 0.029$  mg/g dry soil, respectively). In contrast, shrub priority (S-GH) and grass, herb, shrub priority (GHS) treatments had significantly higher and similar total nitrogen concentrations ( $0.364 \pm 0.033$  and  $0.421 \pm 0.034$  mg/g dry soil, respectively). Consequently, priority planting of shrub species appeared to increase total soil nitrogen.

## **Discussion**

### ***Arrival order does not strongly affect biotic or abiotic variables in mesocosm communities***

Different arrival orders of functional groups resulted in an historical dominance effect in mesocosm communities: the priority planted functional group(s) generally had significantly higher final biomass than the deferred functional group(s). However, this was not reflected in other response variables. Final native above-ground biomass and samples of final total (native + bitou) below-ground biomass were similar amongst planted treatments and they supported similar numbers of bitou germinants and bitou abundance for the duration of the experiment. Invasibility patterns were consistent across all time periods (non significant interaction terms for the number of bitou seedlings and % bitou cover): we did not observe early variation in invasibility for planted treatments which disappeared with time. So our prediction that a staggered planting design would be more invisable than simultaneous initial planting (P2) was not supported at any stage of the experiment.

These invasibility results are perhaps unsurprising given the similarity among planted treatments in abiotic resource availability. Again, our prediction (P3) that abiotic resource use would be higher for simultaneous initial planting than staggered plantings was unsupported. Light availability was similar among planted treatments. Maximum soil temperatures and leached nutrients below the root zone (Ca, Mo, Ni, K, P, Mg) were also similar among the planted treatments. While significant differences in Ba and Fe concentrations in soil leachate were found among planted treatments at particular time periods (December 2007 and December 2008, respectively), the lack of consistency across time periods and our inability to track similar biotic response patterns suggests that differences in nutrient concentrations may simply reflect localised changes in a maturing soil profile (see Weigand et al. (2005) for a related discussion). Confirmation of patterns may require direct analysis of nutrient availability around the root zone. One approach is to measure bioavailability of nutrients around the root zone using cation and anion membrane resin strips (e.g. Forge et al. 2008; Dickson & Foster 2011).

While we detected differences in bare ground cover, PAR at ground level was similar among planted treatments. Possibly there were qualitative differences in cover for the grass, herb priority treatment (GH-S) – where a spreading and chaff-producing ground layer was rapidly established – and the shrub priority treatment (S-GH) – where a more compact overstorey layer developed first. These qualitative differences may have biased bare ground visual estimates. PAR results indicated that quantitatively these two priority treatments were similar.

We did find significantly higher total soil N at the end of the experiment among shrub priority treatments (GHS, S-GH) compared with the herb and grass priority treatment (GH-S). All planted treatments had similar final bitou biomass and followed similar trajectories through time for both bitou cover and number of bitou germinants. Therefore differences in total soil nitrogen

may be attributable to priority native shrub planting. We deliberately avoided known nitrogen fixers (which would have a fertilization effect) when choosing species for the experiment. But previous studies have demonstrated “fertility islands” associated with woody compared with herbaceous vegetation (Schlesinger et al. 1996; Okin et al. 2008) and with increasing time since woody vegetation establishment (Tackett & Craft 2010). Native shrubs planted at the beginning of the experiment may have extracted nutrients from deeper sections of the soil profile and deposited litterfall at greater rates than smaller growth forms (e.g. Keith & Myerscough 1993). This may have contributed to fertilization of the upper soil profile. Despite the potential fertilizing effect of priority shrub planting, it was insufficient to affect invasibility.

Given that different arrival orders were expressed in the biomasses of each native functional group, why were invasibility and abiotic response variables insensitive to these arrival orders? Similar total native above-ground biomass across planted treatments may be the key to answer this question and may indicate that functional identity and historical dominance are unimportant in determining invasibility and resource sequestration in these mesocosm communities. Rather, invasion may be responding only to bulk plant biomass and above-ground net primary productivity. Other studies provide complementary findings: for example, Wilsey (2010) found that weed biomass within mixed grass experimental prairie plots was similar to a number of monoculture grass plots. Emery & Gross (2007) found that experimental communities with an even planting regime (eight species with six individuals each) had similar invasibility (at least initially) as communities planted with one species at high dominance (dominant species with 34 individuals and remaining species with two individuals). However, some studies have found that invasibility is dependent on functional identity and abundance. For example, Fargione et al.

(2003) found that introduced functional groups were less successful when resident members of that functional group were more abundant in experimental grassland plots.

***Planted treatments facilitate bitou germination but suppress bitou biomass***

Contrary to our prediction (P1), invasibility, as measured by germination of bitou seedlings, was significantly higher in planted than unplanted treatments and arrival order was irrelevant. It appears that native functional groups have a nurse effect on bitou seedlings and moderate environmental conditions. Nurse effects of native species on invader germinants have been documented by previous studies which have reported facilitative effects through reducing light and temperature extremes (Lenz & Facelli 2003) and increasing water and nutrient availability (Maron & Connors 1996; Cavieres et al. 2005) under canopies of existing native species compared with uncolonised areas. In our study, bare ground cover was significantly higher in the unplanted than planted treatments. This may have caused higher bitou mortality through desiccation, exposure to extremes of radiation or temperatures or a combination of these factors among newly emerged seedlings in unplanted mesocosms. The mechanism for the nurse effect is unclear. Soil moisture results in the upper profile did not differentiate between planted and unplanted treatments, but measurement intervals may have been too coarse to observe soil moisture differences especially in the first critical weeks of bitou germination. Further, soil temperature did not differ consistently between planted and unplanted treatments. Two planted treatments (GHS and GH-S) had significantly higher average monthly minimum temperatures than the unplanted treatment, but we could not discern a significant difference between the minimum temperatures for the remaining planted treatment (S-GH) and the unplanted treatment. In contrast to results for the number of bitou seedlings, we found that bitou abundance through time, along with final bitou biomass were significantly higher in unplanted than planted

treatments. This result supported our prediction (P1) that invasibility (measured by invader biomass) would be lower in planted than unplanted mesocosms. So, while planted treatments facilitated bitou germination and seedling establishment, they also suppressed bitou biomass and development. It is unlikely that direct resource competition through sequestration of soil moisture or light resources is a mechanism by which native plantings suppress bitou abundance because the unplanted treatment could not be differentiated from all planted treatments based on these response variables. It is possible that native species sequestered physical space as a soil resource. Greater soil volumes have been associated with greater vegetative growth amongst colonizing species independent of nutrient or water resources (McConnaughay & Bazzaz 1991). While we did not find strong patterns in final below-ground biomass across treatments, this does not preclude planted treatments having higher root biomass and lower physical soil space available for bitou invasion in the early- to mid-stages of the experiment (see Ladd & Facelli (2008) for a related discussion). Greater bare ground cover (and hence lower canopy cover) in unplanted compared with planted treatments across all time periods indirectly supports physical space limitations as a mechanism of bitou suppression: canopy biomass is correlated with below-ground biomass and was consistently higher in planted than unplanted treatments. This was particularly evident at the beginning of the experiment where the unplanted treatment had maximal physical space resources available for bitou seedling establishment and growth. Another potential mechanism of bitou suppression is through interference competition via differences in mycorrhizal community composition between planted and unplanted treatments. While an homogenized soil inoculum was applied to all mesocosms at the beginning of the experiment, planted treatments may have subsequently selected mycorrhizal communities by filtering the species pool. The resultant community may then exhibit strong bottom-up control of



plant competition and dominance (see discussion in Teutsch-Hausmann & Hawkes 2010) and restrict bitou growth and development in planted treatments. Confirmation of this possibility would require monitoring of mycorrhizal communities during priority planting and invasion processes.

Finally, competitive interference via allelopathy may be a mechanism of bitou suppression by native plantings. Native species may release compounds via leaf litter or soil exudates which affect the development of bitou individuals. There is some evidence that native species exhibit phytotoxic effects against other native species in coastal dune environments (Ens et al. 2009), and the allelopathic effects of one species used in our experiment (*Cynodon dactylon*) have been reported, specifically in suppressing crop species (e.g. Mahmoodzadeh 2010). However allelopathic effects of the particular native species used in this experiment on bitou are unknown. The planting regime of our constructed mesocosm communities was pre-determined so that the final community functional richness and density were the same amongst all planted treatments. As a consequence, our study solely addressed the importance of arrival order in invasion success and abiotic resource availability. By constraining functional group representation, we did not allow different trajectories of community development. We found that biotic invasibility response variables (bitou seedling and cover abundance) were able to distinguish between planted and unplanted treatments only. However, historical dominance effects among planted treatments (i.e. GHS vs. GH-S vs. S-GH) were indistinguishable in terms of invasibility. This suggests that there is considerable redundancy within and between the functional groups of our planted mesocosms.

Another potential explanation for why invader germination was similar among planted treatments is that invader germinants may be strong competitors and negate any advantage of

primary arrival by native species. Certainly, bitou is a competitive dominant in coastal dune communities (Mason et al. 2012). Resource use by native communities with different arrival orders may be insufficient to affect bitou germination due to plentiful resource availability or lower resource requirements of the invader relative to all native species in the functional group pools. However, the suppressive effect of native plantings on subsequent bitou biomass indicated that invader juvenile and adult stages are adversely affected by native neighbours.

### ***Implications for restoration effort***

Our results indicated that arrival order *per se* among native functional groups does not affect community invasibility or availability of most abiotic resources. Consequently, it is unnecessary to stagger planting of functional groups during coastal dune restoration (but staggered plantings may provide insurance for land managers against failure of mass plantings following drought).

While the order of planting does not affect invasibility, planting of grass, herb and shrub functional groups does suppress invader growth and biomass. The ability of native species to restrict invader productivity has been reported elsewhere (e.g. Corbin & D'Antonio 2004; Chadwell & Engelhardt 2008). However, our study also found that native species failed to inhibit germination and establishment of bitou propagules. We found a facilitative effect of the native plantings on bitou germination. So a disturbance event which removes the moderating effects of native functional groups may also facilitate rapid growth and expansion of juvenile or low-biomass invader individuals in the post-disturbance environment of restored dune communities.

### ***Conclusion***

While we found an historical dominance effect in our constructed communities, where priority planted groups had greater final biomass than deferred groups, we were unable to detect the effect of arrival order on community invasibility or abiotic resource availability. Arrival order of

native plantings did not affect invader establishment or biomass. Resource use may be just as complete irrespective of initial establishment sequence and therefore all planting sequences may suppress the invader similarly.

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Table 1: Species pool used for mesocosm plantings

Functional group	Species *
Rhizomatous / stoloniferous grasses	<i>Zoysia macrantha</i>
	<i>Cynodon dactylon</i>
	<i>Paspalum vaginatum</i>
	<i>Spinifex sericeus</i>
	<i>Sporobolus virginicus var virginicus</i>
	<i>Digitaria didactyla</i>
Prostrate herbs	<i>Carpobrotus glaucescens</i>
	<i>Melanthera biflora</i>
	<i>Tetragonia tetragonoides</i>
	<i>Calystegia soldanella</i>
	<i>Hydrocotyle peduncularis</i>
	<i>Viola hederacea</i>
Shrubs	<i>Leptospermum laevigatum</i>
	<i>Correa alba</i>
	<i>Myoporum boninense</i>
	<i>Breynia oblongifolia</i>
	<i>Westringia fruticosa</i>
	<i>Rhagodia candolleana</i>

\*Nomenclature follows Harden (1992, 1993, 2000, 2002)

Table 2: Results of repeated measures ANOVA for effects of arrival order on bitou invasion success and abiotic resource availability variables. \* Measured for planted treatments only (i.e. excluded the unplanted treatment); n/a = not applicable: One way anova results for each time period are noted in the text

	<b>Pillai's Trace multivariate test (Time x Treatment)</b>	<b>Between Treatment Effects</b>
<b>Biotic response variable</b>		
Number of bitou seedlings	$F_{36,21} = 1.954; P = 0.053$	<b><math>F_{3,16} = 9.360; P = 0.001</math></b>
% bitou cover	$F_{12,45} = 1.604; P = 0.125$	<b><math>F_{3,16} = 17.719; P &lt; 0.001</math></b>
<b>Abiotic response variable</b>		
<b>Soil temperature</b>		
Average monthly minimum	$F_{9,12} = 2.190; P = 0.123$	<b><math>F_{3,4} = 14.007; P = 0.014</math></b>
Average monthly maximum	$F_{9,12} = 1.206; P = 0.397$	$F_{3,4} = 2.857; P = 0.168$
<b>Soil moisture</b>		
0 cm	$F_{6,26} = 2.080; P = 0.091$	$F_{3,13} = 0.355; P = 0.787$
20 cm	$F_{6,26} = 1.420; P = 0.245$	<b><math>F_{3,13} = 4.578; P = 0.021</math></b>
50 cm	$F_{6,26} = 1.684; P = 0.165$	<b><math>F_{3,13} = 4.501; P = 0.022</math></b>
75 cm	<b><math>F_{6,26} = 3.595; P = 0.010</math></b>	n/a
100 cm	<b><math>F_{6,26} = 3.060; P = 0.021</math></b>	n/a
<b>Photosynthetically active radiation at ground level *</b>		
	$F_{16,12} = 1.124; P = 0.426$	$F_{2,12} = 2.444; P = 0.129$

**Bare ground cover (%)** $F_{33,24} = 1.229; P = 0.303$  $F_{3,16} = 72.363; P < 0.001$ **Nutrient concentration in soil leachate**

Barium	<b><math>F_{9,33} = 3.066; P = 0.009</math></b>	n/a
Calcium	$F_{9,21} = 1.417; P = 0.243$	$F_{3,7} = 0.718; P = 0.572$
Iron	<b><math>F_{9,39} = 3.551; P = 0.003</math></b>	n/a
Magnesium	<b><math>F_{9,39} = 2.281; P = 0.036</math></b>	n/a
Molybdenum	$F_{9,33} = 2.087; P = 0.060$	$F_{3,11} = 1.442; P = 0.283$
Nickel	$F_{9,33} = 1.834; P = 0.099$	$F_{3,11} = 2.022; P = 0.172$
Potassium	$F_{9,21} = 1.092; P = 0.409$	$F_{3,7} = 1.924; P = 0.214$

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## Figure legends

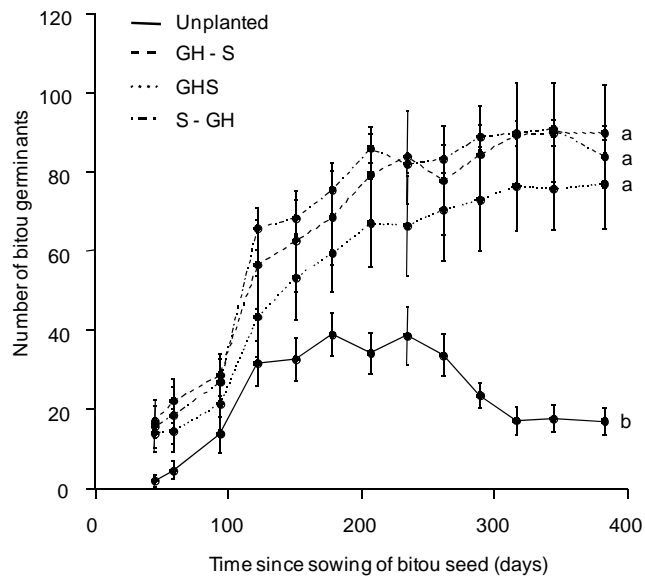
Fig. 1 Number of bitou individuals (mean  $\pm$  SE;  $n = 5$ ) across treatments over the sampling period. GH-S = grass and herb individuals planted simultaneously followed by shrub individuals; GHS = grass, herb and shrub individuals planted simultaneously; S-GH = shrub individuals planted first followed by grass and herb individuals; Unplanted = unplanted control. See methods for detailed description of treatments. Letters indicate treatments that are significantly different averaged over all time periods ( $P < 0.05$ )

Fig. 2 Percent of cover of bitou (mean  $\pm$  SE;  $n = 5$ ) across treatments over the sampling period. Letters indicate treatments that are significantly different averaged over all time periods ( $P < 0.001$ )

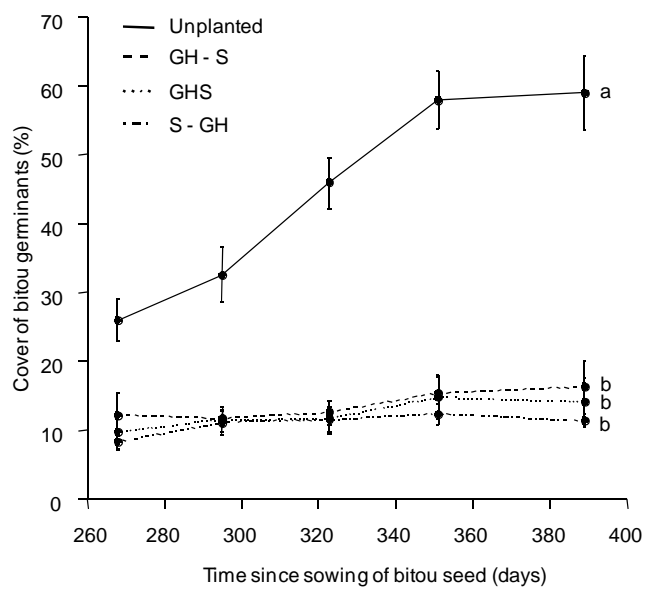
Fig. 3 Final above ground biomass (g) (mean  $\pm$  SE;  $n = 5$ ) for different functional groups across treatments. Letters indicate significantly different values within each planted treatment (Tukey post-hoc test results)

Fig. 4 Percent bare ground cover (mean  $\pm$  SE;  $n = 5$ ) across treatments over the sampling period. Letters indicate significant differences among treatments over all time periods ( $P < 0.01$ )

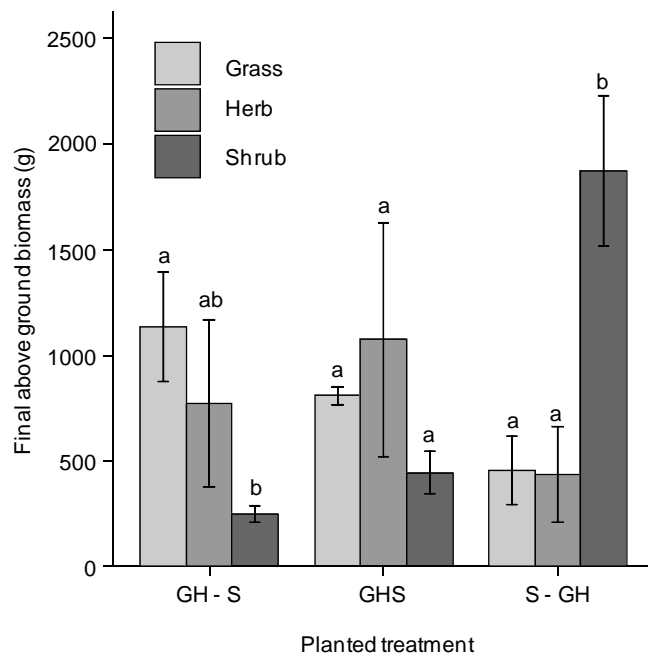
## Figures



**Fig 1**

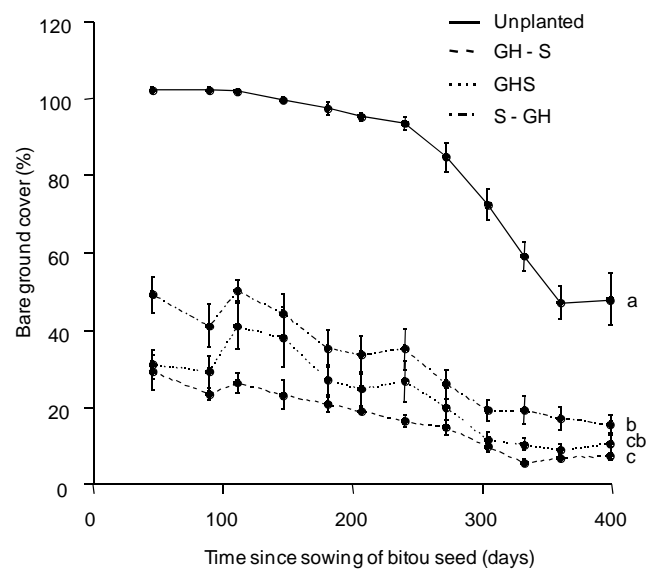


**Fig 2**



**Fig 3**





**Fig 4**

**Appendix 1:** Single month ANOVA results for the effects of arrival order on soil nutrient availability

Nutrient	Time period	Welch test	Dunnett's T3*
Ba	<b>Dec 2007</b>	<b><math>F_{3,6.8} = 374.190</math>; <math>P &lt; 0.001</math></b>	S-GH < GHS, Unplanted, GH-S
	Feb 2008	$F_{3,8.5} = 0.731$ ; $P = 0.570$	
	Sept 2008	$F_{3,7.1} = 1.369$ ; $P = 0.327$	
	<b>Dec 2008</b>	<b><math>F_{3,4.6} = 11.235</math>; <math>P = 0.015</math></b>	Unplanted < GHS
Fe	Dec 2007	$F_{3,8.6} = 0.258$ ; $P = 0.853$	
	Feb 2008	$F_{3,7.4} = 0.319$ ; $P = 0.812$	
	May 2008	$F_{3,7.5} = 3.375$ ; $P = 0.079$	
	<b>Dec 2008</b>	<b><math>F_{3,5.6} = 8.641</math>; <math>P = 0.015</math></b>	GHS, unplanted < GH-S
Mg	<b>Dec 2007</b>	<b><math>F_{3,8.3} = 4.185</math>; <math>P = 0.045</math></b>	Unplanted <GHS
	Feb 2008	$F_{3,8.7} = 1.162$ ; $P = 0.379$	
	<b>May 2008</b>	<b><math>F_{3,7.4} = 8.787</math>; <math>P = 0.008</math></b>	Unplanted <GH-S, S-GH, GHS
	<b>Dec 2008</b>	<b><math>F_{3,4.9} = 12.901</math>; <math>P = 0.009</math></b>	$P > 0.05$ for all comparisons

\* significant comparisons are indicated at  $P < 0.05$ .