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## Do Per-capita Impact or Abundance Dominate the Impact of an Invader? Interactions Among Neighboring Species in Context-dependent Competition

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DO PER-CAPITA IMPACT OR ABUNDANCE DOMINATE THE IMPACT OF AN INVADER?  
INTERACTIONS AMONG NEIGHBORING SPECIES IN CONTEXT-DEPENDENT  
COMPETITION

by

HAOYU LI

B. S. Sun Yat-sen University, China. 2015

A thesis submitted in partial fulfillment of the requirements  
for the degree of Master of Science  
in the Department of Biology  
in the College of Sciences  
at the University of Central Florida  
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Major Professor: Pedro F. Quintana-Ascencio

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## ABSTRACT

Evaluating relative species competitive strength is a central question in community ecology, with strong implications for invasion ecology. Models assessing invader success consider three components: distribution, abundance and per-capita impact. However, relative strength and interactions among these factors remain unclear when applying to specific invasion scenarios. We hypothesized that performance of native and non-native species will vary as a function of direct and indirect effects at different abundances and scales. We conducted a replacement experiment between two dominant grasses in subtropical grasslands (the native *Axonopus fissifolius* and the non-native *Paspalum notatum*) in central Florida, USA. Thirty fenced plots (1 m x 3 m each) representing a gradient (15 levels) of increasing non-native groundcover and decreasing native groundcover were set up in November 2017. We transplanted individuals of these two species in subplots (12 subplots and 36 transplants per plot; 1080 plants in total) in a 2\*2 factorial design (mixed /single focal species \* 2/4 transplants per subplot). Leaf length/number and plant biomass were evaluated at the beginning and end of the experiment along with plot species composition and soil nutrients. Over 92% of transplants of each grass species survived until harvest (11 months). There were significant differences in leaf length, leaf number and plant biomass between conspecific/allospecific subplots. Both *P. notatum* and *A. fissifolius* performed better when transplanted in non-native *P. notatum* subplots. There were also interactions between conspecific/allospecific subplot treatment (direct effects) and the gradient of increasing *Paspalum notatum* /decreasing *Axonopus fissifolius* groundcover (indirect effects) treatments. Increasing *P. notatum* in the whole plot made environments more favorable for both grass species. Effects were consistent for leaf length/number and biomass of

the two focal species. More comprehensive evaluation on indirect effects need to be considered when examining competition between non-native species and native species.

## **ACKNOWLEDGMENTS**

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## CHAPTER ONE: INTRODUCTION

Understanding the dynamics and consequences of interactions among organisms has been a central goal in invasion ecology for decades, as they shape ecological processes which affect population dynamics and community structure (Thompson, 1988; Silander & Antonovics, 1982; Abrams, 2001). Recent analyses reveal that invasive species impacts are strongly context-dependent on both biotic and abiotic factors (Chamberlain, Bronstein, & Rudgers, 2014; Weigelt, Steinlein, & Beyschlag, 2002; Antonovics & Levin, 1980), and may vary in both magnitude and direction (Pyšek *et al.*, 2012; Van der Putten, Macel, & Visser 2010; Thomsen, Wernberg, Olden, Griffin, & Silliman 2011; Boughton, Quintana-Ascencio, Bohlen & Nickerson 2011). Although context-dependent outcomes are common in nature and the research on species interactions has been continued for decades, we still lack enough knowledge about the magnitude and mechanisms of these phenomena on species interactions (Chamberlain, Bronstein, & Rudgers, 2014).

Identifying and properly measuring the ecological impact of invasive species, and applying this knowledge to management of invasive species is critical (Antonio & Meyerson, 2002). Neighboring plant species can change the direction and magnitude of the interaction among plants and between plants and other organisms (Bergvall, Rautio, Kesti, Tuomi, & Leimar, 2006; Orians & Bjorkman, 2009), a process known as associational effects (Underwood, Inouye, & Hambäck, 2014). A better understanding of associational effects may inform management of species invasions since it plays a central role in competition between non-native and native species.

Associational effects can occur through many mechanisms. For instance, physical masking by

neighboring species may hinder herbivory by reducing the chance of locating the focal plant (Hambäck, Inouye, Andersson, & Underwood, 2014; Bergvall, Rautio, Kesti, Tuomi, & Leimar, 2006; Boughton, Quintana-Ascencio, Bohlen & Nickerson 2011). Neighboring plants can also attract more pollinators (Feldman, Morris, & Wilson 2004) resulting in higher demographic rates for the focal species. Conversely, neighboring species can generate higher susceptibility to diseases, leading to more damage to the focal species (Thomas, 1986). Even though associational effects are measured at the individual level, they can contribute to population and community level dynamics (Barbosa *et al.*, 2009) through changes in micro habitat and resource availability. For example, the presence of the non-native species *Lygodium microphyllum*, the old world climbing fern in Florida's pine forest increased fire frequency and fire intensity by introducing fire into canopy (Pemberton & Ferriter, 1998). Invasion of *Prosopis glandulosa*, Honey mesquite patches into Texas's subtropical savanna caused marked increases in soil C and N pool compared to patches dominated by native herbaceous resulting in the shift from grass to shrub domination (Hibbard, Archer, Schimel, & Valentine 2001).

Parker *et al.*, (1999) provided a useful framework to quantify the impact of a species:

$$I = R \times A \times E \quad (1)$$

where overall impact,  $I$ , is defined as the product of the range size  $R$  (in  $\text{m}^2$ ) of a species, its average abundance per unit area across that range  $A$  (in numbers, biomass, or other relevant measure), and  $E$ , the effect per individual or per biomass unit of the invader. The per-capita effect  $E$  refers to the ability of a species to shift and/or modify various ecological level processes and mechanisms, and is expected to be negative for competitive effects, or positive for facilitative effects.

Most basic ecological research on invasion impacts identifies the local effect ( $A * E$ ) as an unspecified combination of per-capita impact and local abundance (Parker *et al.*, 1999). Despite its apparent simplicity, interactions among  $R$ ,  $A$  and  $E$  components may occur and complicate this framework (Barney, Tekiela, Dollete, & Tomasek 2013). Additionally, studies have reported both linear and non-linear relationships between components of this model (Nava-Camberos, Riley, & Harris 2001; Robinson, Smyth, & Whitehead 2005). For example, an invader can have a wide range but exist in low abundance in local communities or an invader can have low abundance with a strong per-capita impact (Hibbard, Archer, Schimel, & Valentine 2001). In contrast, an invader can dominate with overwhelming densities in communities, but may lack novel traits except for higher demographic rates (Pierre, Quintana-Ascencio, Boughton, & Jenkins 2017; Smith, Boughton, & Pierre 2015). Based on Parker *et al.*'s framework, the overall effect of the most noxious invasive species due to per-capita ( $E$ ) and abundance ( $A$ ) effects is whether the impacts are due primarily to aspects of the biology of species affecting their performance during the interactions (Simberloff *et al.*, 2013), or to their sheer numbers or the interaction between these factors.

Understanding  $A * E$  may be difficult because the per-capita impact can co-vary (i.e., successful invaders have high abundance because they have high per-capita impact). The 'abundance' of a competitor could be important at a local or individual neighborhood level through immediate contact, or at a 'landscape' scale through indirect effects. Each level or scale of 'abundance' could have its own effect on per-capita impact  $E$ .

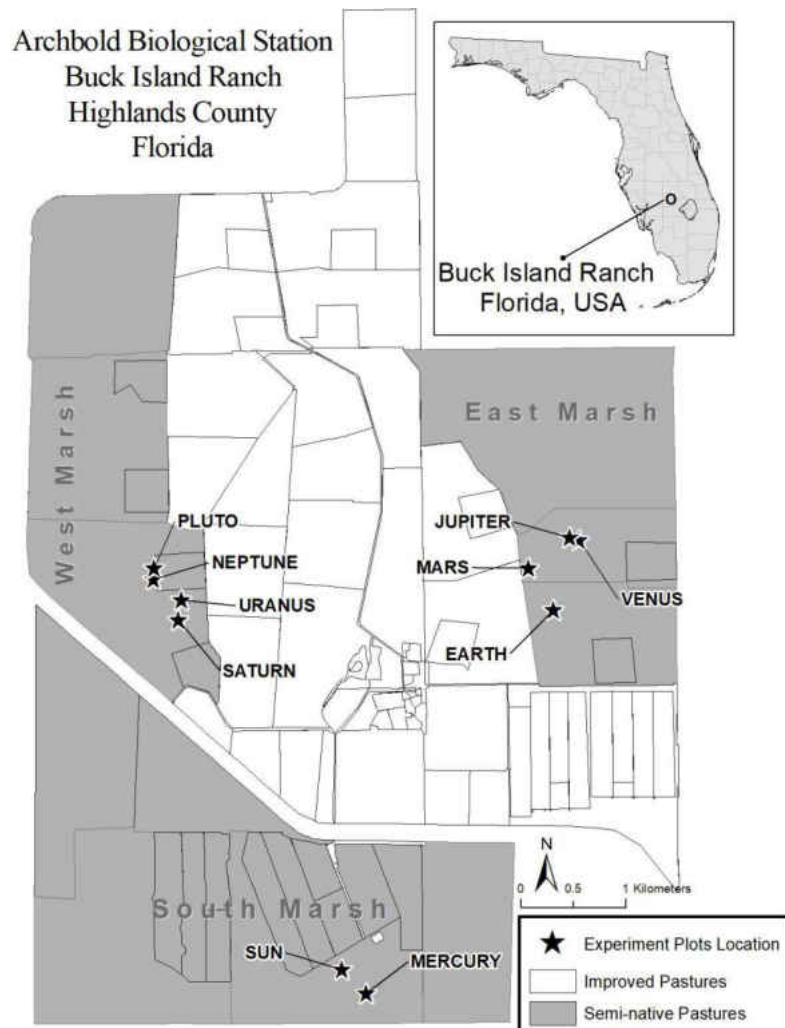
In this study, we examined how the effects of neighbor species at different relative abundance ( $A$ ) affect the competitive interaction between a non-native and native species ( $E$ ) at different ecological

scales. We performed a year-long field competition experiment involving transplanting plants from three different species (non-native invader = *Paspalum notatum*, native species = *Axonopus fissifolius*, and a phytometer = *Phyla nodiflora*). We evaluated the effect of abundance of the invader measured at three different ecological scales, which are ‘individual’, ‘patch’ and ‘plot’ levels respectively. We included a phytometer species to provide an independent evaluation of the competition environment. We hypothesized that (1) plant performance will be affected by the multiple levels of ‘abundance’ with potential different magnitude and direction of the responses at each level; (2) An interactive effect is possible between ‘patch’ and ‘plot’ levels, due to the environmental variations that levels of ‘abundance’ could introduce into the competition; and (3) Soil and canopy effects due to the abundance of the dominant species in different patches could lead to different communities in plots, because *P. notatum* is known to alter soil pH (Tan, Beaty, McCreery, & Jones 1975).

## CHAPTER TWO: MATERIALS AND METHODS

### Study Site

Our experiment was conducted at Buck Island Ranch (BIR), a division of Archbold Expeditions, and a 4170 ha commercial cattle ranch in south-central Florida (27° 09' N, 81° 11' W). BIR has a humid subtropical climate with an annual precipitation of ca. 130 cm, (70% of the annual rainfall happens during the summer rain season; usually from June to October). Two major habitats dominate this ecosystem: semi-native pastures and agriculturally improved pastures. Agriculturally improved pastures were fertilized and planted with Bahia grass (*Paspalum notatum*), an introduced forage grass from South America. The semi-native pastures were never fertilized and are characterized by a more diverse plant community dominated by native grasses (i.e. *Axonopus* spp., *Andropogon* spp. and *Panicum* spp.) with locally abundant *P. notatum*. The experiment was performed in 30 plots distributed in 10 sites within semi-native pastures (Figure 1). At the beginning of the study, all the study sites had continuous (> 95% cover) grass cover by *Axonopus* spp. (*Axonopus fissifolius*, *Axonopus furcatus*).



**Figure 1: Study site and experiment plots location at Buck Island Ranch**

### Species Selection

Non-native Competitor: *Paspalum notatum*, Bahia grass. This is a perennial grass with strong, shallow, horizontal rhizomes, native to South America (Quarin, Burson, & Burton 1984). It adapts best to sandy soil, can tolerate low soil fertility and low pH, and most of its biomass concentrates at the soil surface in the extensive networks of rhizomes.

Native Competitor: *Axonopus fissifolius*, Common Carpet grass, which is a perennial grass with creeping stolons, native to Florida and primarily distributed in subtropical areas. In Southern Florida,



it stays green all year and produce seedheads and stolons during the active growth period (Jun-Oct). It can be found in pine flatwoods, forests with sandy soils, fields and roadsides (USDA Plant Profile). *A. fissifolius* shares similar growth form with *P. notatum*, including strong vegetative propagation, similar heights and growing habit of forming dense patch and canopy.

Phytometer: *Phyla nodiflora*, Turkey Tangle Fogfruit. It is a stoloniferous forb with decumbent stems and scanty roots (root depth c. 15 cm). It is a native to Florida and other southern states in the US. It is well adapted to coarse - fine textured soil and has medium tolerance to drought (USDA Plant Profile).

### **Experimental Design**

The experiment involved a 2\*2 full factorial transplant procedure combined with a replacement gradient (Hamilton, 1994) between the two grasses. We considered the effects of three different “abundance” scales: (1) ‘individual’ level (also a per-capita impact  $E$ ; considered as direct effects of abundance), (2) ‘patch’ level (also a per-capita impact  $E$ ; considered as direct effects of abundance), and (3) ‘plot’ level (considered indirect effects of abundance) (Figure 2). These three scales represented multiple components of the competition effects of abundance.

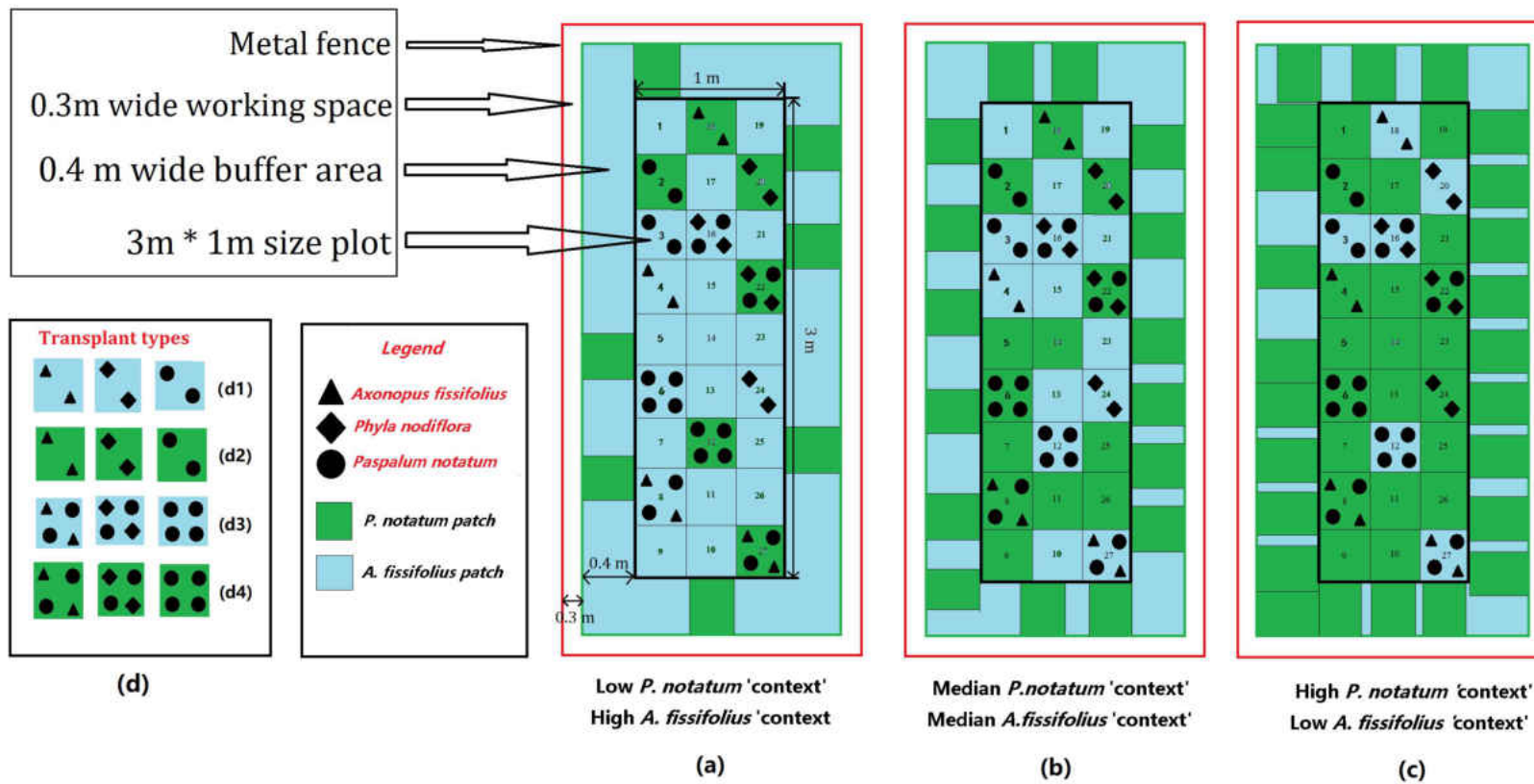


Figure 2: Illustration of experimental design of one typical experiment site. Three levels are presented as example (a-c). The two by two transplant design is illustrated in (d). The additional first column describe the transplant of the phytometer.

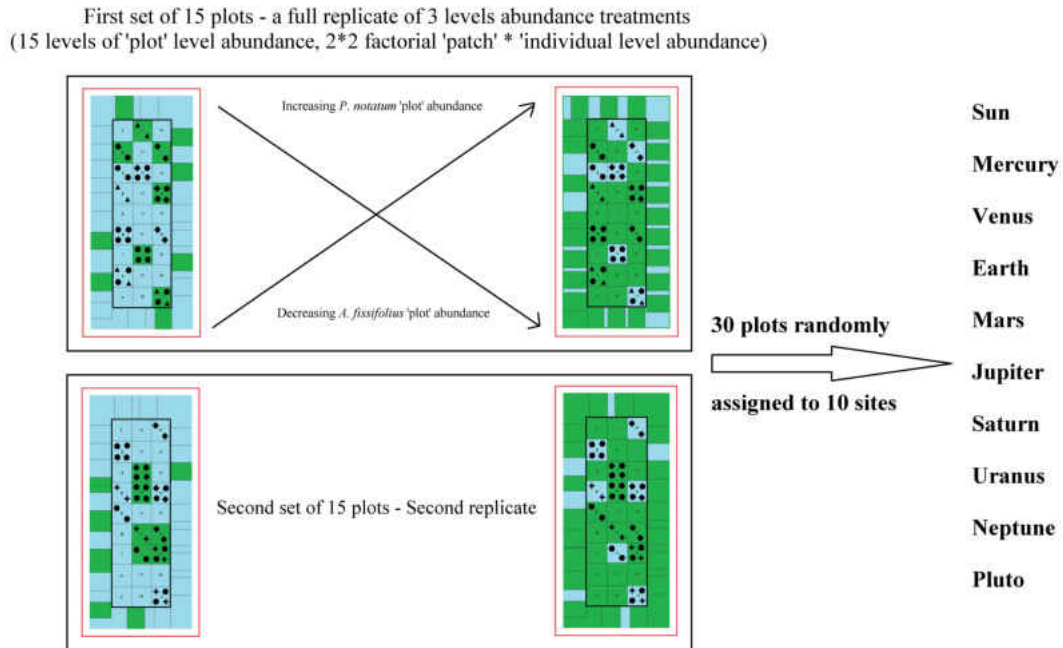
Each of the 10 experiment sites contained three plots which represented a replacement gradient between *P. notatum* and *A. fissifolius* ground cover (examples in Figure 2a, 2b, 2c). Every experimental plot was a 3m \* 1m rectangle divided into 27 patches (3 column \* 9 rows). *P. notatum* ground cover was controlled by removing certain numbers of *A. fissifolius* patches (each 33 x 33 cm) and then replaced by same size *P. notatum* patches. *P. notatum* patches were obtained from improved pastures at BIR using a sod cutting machine (sod size: 40 cm \* 60 cm). Overall there were 15 levels of *P. notatum* abundances at the ‘plot’ level, ranging from 6 (21 for *A. fissifolius*) to 20 patches (7 for *A. fissifolius*) out of the 27 available patches. These plots represented the lowest of 22.2% (77.8 % for *A. fissifolius*) to the highest of 74.1% (25.9 % for *A. fissifolius*) ground cover of *P. notatum* used within our experiment (lowest and highest level of ground cover were limited due to the number of patches that can be transplanted into each plot). Each plot was surrounded by a 0.4 m wide buffer area and fenced to exclude cattle. Additional *A. fissifolius* ground cover in the buffer area was replaced by *P. notatum* sods to keep the relative percentage of each grass ground cover of the buffer area the same as in the core area of each plot.

**Table 1: Number of patches of *P. notatum* and *A. fissifolius* across the 10 experiment sites.**

Pasture	Site name	<i>P. notatum</i> abundance levels of plots (Number of <i>P. notatum</i> patches, out of 27 patches)	<i>A. fissifolius</i> abundance (Number of <i>A. fissifolius</i> patches, out of 27 patches)
South	Sun	6, 11, 15	21, 16, 12
Marsh	Mercury	9, 15, 20	18, 12, 7
	Venus	8, 13, 20	19, 14, 7
West	Earth	12, 16, 19	15, 11, 8
Marsh	Mars	13, 16, 18	14, 11, 9
	Jupiter	6, 9, 17	21, 18, 10
	Saturn	7, 10, 14	20, 17, 13
East	Uranus	8, 11, 17	19, 16, 10
Marsh	Neptune	10, 12, 18	17, 15, 9
	Pluto	7, 14, 19	20, 13, 8

To establish individual and patch level abundance levels, we randomly selected 12 patches in each plot in which we transplanted *P. notatum*, *P. nodiflora* and *A. fissifolius* individuals. Each species had four different transplant types which represents a 2\*2 factorial design for the treatments of individual and patch level competition (Figure 2d). The ‘patch’ level included two treatments: whether the individual was transplanted within a *P. notatum* patch or into *A. fissifolius* patch (Figure 2: (d1) & (d3) compare to (d2) & (d4)). The ‘individual’ level included two treatments: whether the transplanted individuals were accompanied by transplanted *P. notatum* individuals or not (Figure 2: (d1) & (d2) compares to (d3) & (d4)).

The whole experiment had 30 experimental plots, of which 15 plots represented a full replicate of ‘plot’ level abundances, with increasing *P. notatum*/decreasing *A. fissifolius* abundances. Each plot contained a 2\*2 factorial transplanting design of ‘individual’ \* ‘patch’ level abundance treatments. The arrangement of transplanted patches location in the second replicate of the 15 plots was distinctive from the first replicate set (Figure 3). The 30 plots were then randomly assigned to 10 sites (Table 1). They were set up within a week in Mid-November in 2017, four months before the transplant of the individual plants.



**Figure 3. Illustration of the whole picture of experiment design.**

### Plant collection for transplants

Transplants were collected from the field and planted in 10.5 cm diameter pots in November, 2017. For *A. fissifolius* and *P. notatum*, the whole individual was carefully dug out minimizing any damage to the roots and moved to pots. For *P. nodiflora*, establishment was stimulated with the application of rooting powder (0.10% Indole-3-butyric Acid, BONIDE PRODUCT INC). All transplanted individuals were then maintained in a shade house (with free airflow but partial sunlight) to homogenize their growth for 3 months until Feb 2018, when they were randomly transplanted to the field plots.

### Data Collection

We counted total leaf number for all three species and measured cumulative leaf length (cm) for *P.*

*notatum* and *A. fissifolius*, cumulative stem length for *P. nodiflora*) of each transplanted individual in February 2018, immediately after being transferred to the field, and finally in December 2018. Plant survival was recorded in May and September 2018. Biomass was estimated for each alive individual at the beginning and measured at the end of the experiment. To measure biomass, entire individuals were carefully harvested, kept at 80 °C in an oven for 24 h, and weighed. We also surveyed the vegetation of each plot at the beginning and end of the experiment. We recorded the cover of all vascular plant species present in each of the 12 focal patches per plot. In October 2018, we collected three soil cores per focal patch (each core was 3 cm diameter and 15 cm deep). The three cores were mixed and consolidated as one sample. We determined the amount of Ammonia (NH<sub>4</sub><sup>+</sup>), Nitrate (NO<sub>3</sub><sup>-</sup>), Ortho-P (PO<sub>3</sub><sup>-</sup>), pH, and total organic matter in each focal patch using standard protocols. (Sparks, *et al.*, 1996)

### **Statistical Analysis**

To estimate initial biomass of the transplanted individuals, we built an allometric relationship between plant height and plant biomass for each species. To do this, we randomly selected 30 individuals of each species among the same set scheduled to be transplanted ( $r^2 = 0.738$ ;  $0.767$ ;  $0.659$  respectively for *P. notatum*, *A. fissifolius* and *P. nodiflora*) (Appendix).

We used Generalized Linear Mixed Models (GLMM) to evaluate the variation of soil parameters among the two levels of abundance (patch and plot). We used GLMMs to evaluate the effects of treatments (individual, patch and plot) on plant performance, including survival, number of leaf, and proportional size change in cumulative leaf length and biomass (i.e. End/Start). We included 'site' as a

random intercept effect. For the survival model, we used binomial errors distribution and the logit link function. For the model of total number of leaves, we included initial number of leaves as a covariate and used negative binomial distributions and the logarithm link function. Change in leaf length and change in biomass were natural log-transformed and corresponding models used Gaussian error distribution and the identity link function. We used model selection based on AICc to identify the most likely models (Burnham & Anderson, 2002). Effect sizes ( $R^2$ ) of the most plausible models were calculated using methods proposed by Nakagawa and Schielzeth (2013). (Appendix).

We used NMDS with the 'Bray-Curtis' distance to evaluate changes in species composition between plots. We repeated this analysis after removing the focal species (*P. notatum* and *A. fissifolius*).

Analyses were performed using glmmADMB, vegan, piecewiseSEM package in R 3.5.0 program (R Core Team, 2018).

## CHAPTER THREE: RESULTS

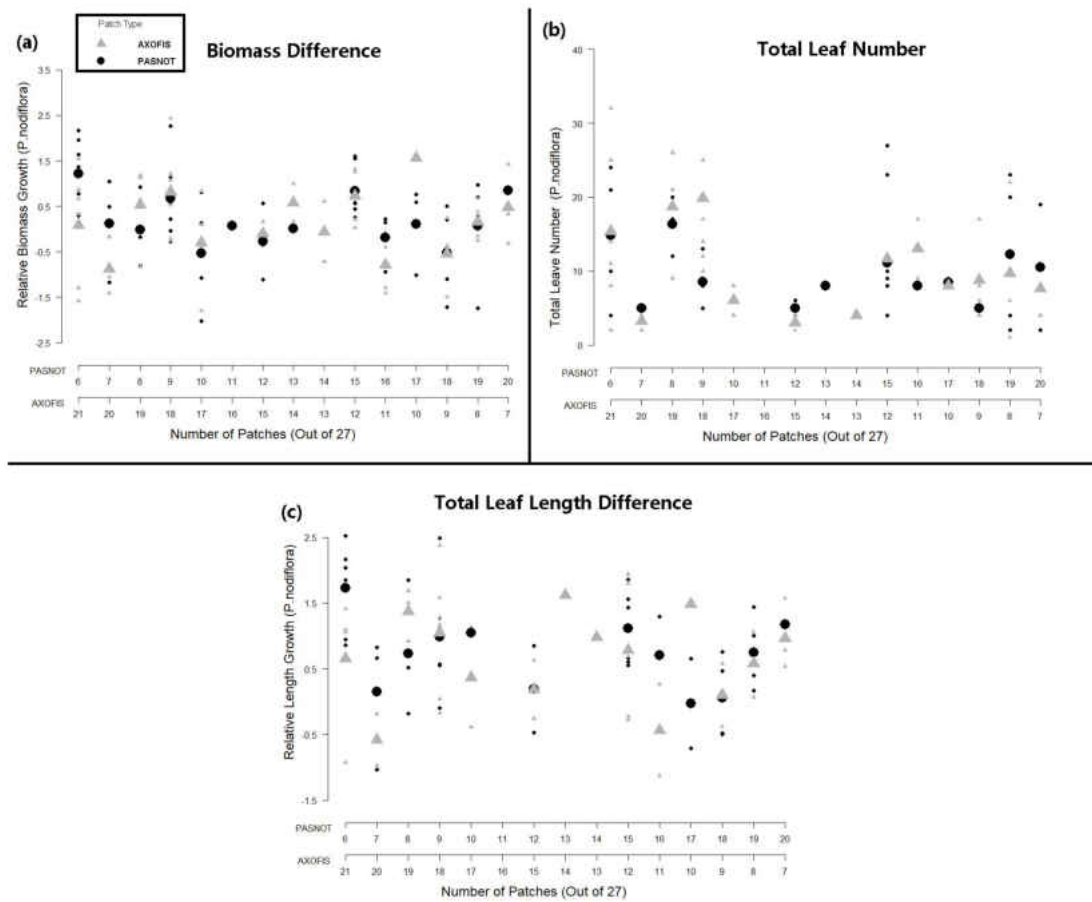
### Effect of Initial Plant Conditions and Plant Survival

We found no significant effect of initial variables on the final condition for any of the three focal species. The average initial total summed leaf number was different among species with 40.77 leaves (SE= 23.09) for *P. nodiflora*, 21.30 leaves (SE= 9.83) for *P. notatum*, and 8.73 (SE= 4.21) for *A. fissifolius*. Initial cumulative leaf (stem) length was 17.51 cm (SE= 11.29) for *P. nodiflora*, 171.56 cm (SE= 85.87) for *P. notatum*, and 57.15 cm (SE= 30.50) for *A. fissifolius*. By the end of the experiment in November, 2018, 92.5% of the focal *A. fissifolius* individuals, 97.5% of *P. notatum* individuals and 40.4% of *P. nodiflora* individuals survived; 94.7% of the *P. notatum* individuals used as competitors at individual level for all three focal species survived.

### Effect of Treatments on Plant Performance

We did not find any significant effects of dominant grass species at patch level or plot level abundance on survival of the two focal grass species. *P. nodiflora* was strongly outcompeted by both grasses. However, we did not observe any significant effect of immediate competitor grass species identity or competitor grass abundance (at patch or plot levels) on the performance of *P. nodiflora* (Figure 4).



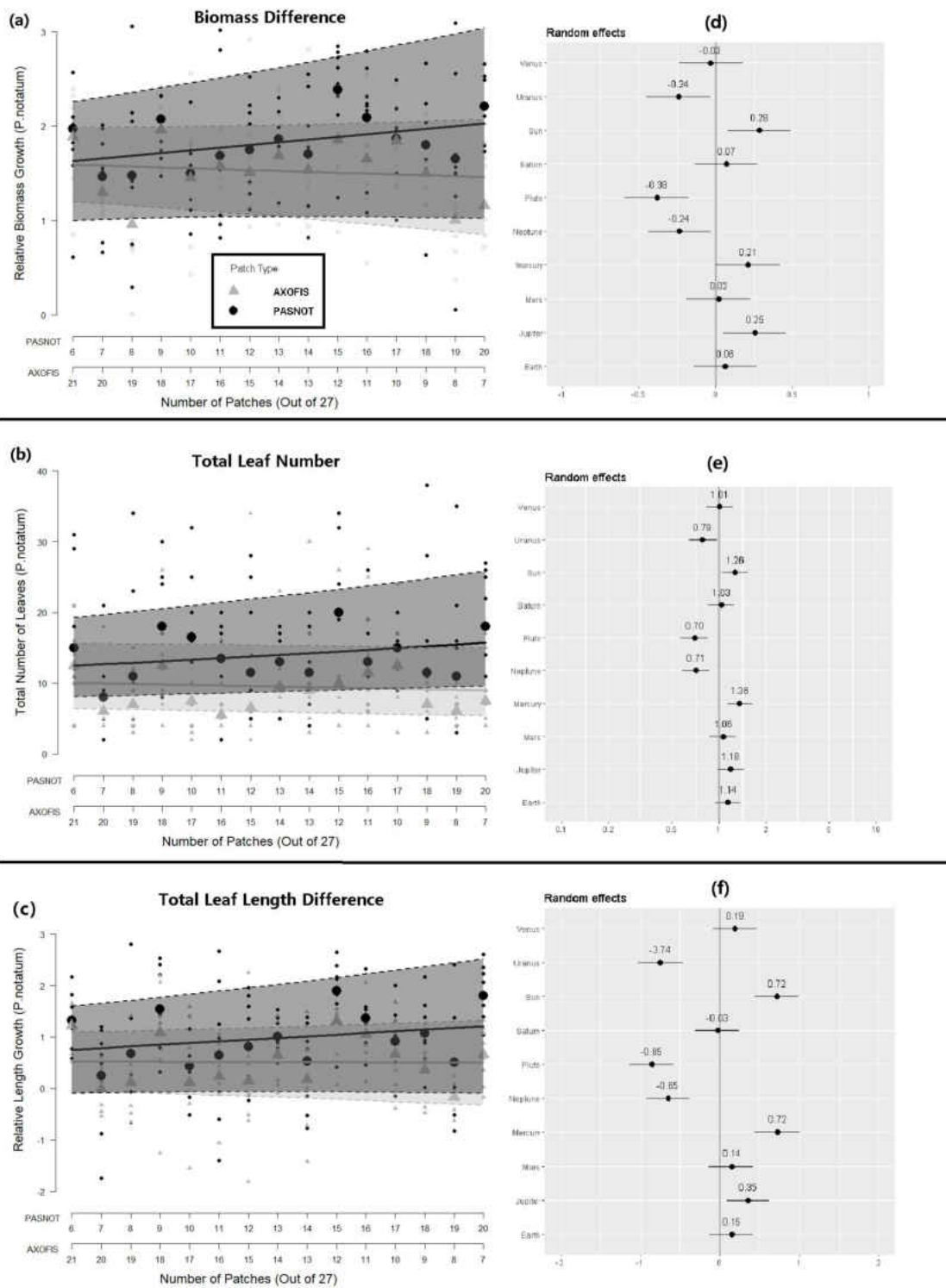


**Figure 4:** *P. nodiflora* performance in two types of patches treatment (*P. notatum* = circles and *A. fissifolius* = triangles) along the 'plot' gradient. Small symbols are all patch observations and large symbols are means by 'plot' level.

**Table 2: Summary of effects of abundance treatments for all three focal species and performance variables.**

Response Variable	Focal Species	Most Plausible Model	dAICc (Weight)	Null model dAICc (Weight)	Coefficients (Intercept + SE)		Effect Size of Top Model	
					Patch* Context	Patch	Marginal R <sup>2</sup>	Conditional R <sup>2</sup>
Biomass	<i>P. not</i>	~ Patch * Plot + Individual + (1 Site)	0.7 (0.293)	18.3 (<0.001)	0.038± 0.017 ( <i>p</i> =0.025)	-0.187± 0.231 ( <i>p</i> =0.418)	0.077	0.229
	<i>A. fis</i>	~ Patch * Plot + (1 Site)	0.0 (0.334)	3.1 (0.071)	0.044± 0.022 ( <i>p</i> =0.041)	-0.364± 0.295 ( <i>p</i> =0.218)	0.038	0.084
	<i>P. nod</i>	-	-	0.0 (0.477)	-	-	-	-
Cumulative leaf length	<i>P. not</i>	~ Patch * Plot + (1 Site)	0.0 (0.307)	22.2 (<0.001)	0.034± 0.021 ( <i>p</i> =0.107)	0.026± 0.291 ( <i>p</i> =0.93)	0.072	0.452
	<i>A. fis</i>	~ Patch + (1 Site)	0.0 (0.382)	0.7 (0.271)	-	0.201± 0.121 ( <i>p</i> =0.095)	0.012	0.044
	<i>P. nod</i>	-	-	0.0 (0.478)	-	-	-	-
Total Leaf Number	<i>P. not</i>	~ Patch * Plot + (1 Site)	1.5 (0.208)	56.4 (<0.001)	0.204± 0.121 ( <i>p</i> =0.091)	0.016± 0.009 ( <i>p</i> =0.066)	0.200	0.331
	<i>A. fis</i>	~ Patch + (1 Site)	0.0 (0.471)	20.3 (<0.001)	-	0.238± 0.085 ( <i>p</i> =0.005)	0.258	0.326
	<i>P. nod</i>	-	-	1.0 (0.2637)	-	-	-	-

The most plausible model for all three performance variables of *P. notatum* included a significant interaction between plot level abundance and patch identity (Figure 5 a, b and c; Table 2). *P. notatum* performance was higher when transplanted in *P. notatum* patches and when plot-level *P. notatum* abundance increased (biomass =  $0.038 \pm 0.017$ ; cumulative leaf length =  $0.034 \pm 0.021$ ; and total leaf number =  $0.024 \pm 0.016$ ; model coefficient  $\pm$  SE used below unless specified). Although random effect (site) was negligible, we identified differences between ranch regions. South marsh plots (Sun, Mercury) being lower than the mean, while West marsh (Uranus, Pluto, Neptune and Saturn) larger than the mean and East marsh (Earth, Mars, Jupiter, Venus) around the mean (Figure 5 d, e and f). Thus *P. notatum* appeared to perform best with conspecifics than with the native grass, consistent with inter-specific effects being greater than intraspecific effects.



**Figure 5:** *P. notatum* performance in two types of patches (*P. notatum* = circles and *A. fissifolius* = triangles) along the plot gradient with random effects by site. Small symbols represents all patches and large symbols are mean by ‘plot’ level. Shaded polygons are 95% CI. In plots d, e and f bars represent 95% CI.

However, *A. fissifolius* performance was not a mirror image of *P. notatum* performance. Instead, *A. fissifolius* performance varied across abundance levels but showed different patterns for different variables (Figure 6 a, b and c; Table 2). Relative biomass growth of *A. fissifolius* was higher in *P. notatum* patches and increased ( $0.044 \pm 0.022$ ) as plot-level *P. notatum* increased. *A. fissifolius* number of leaves ( $0.238 \pm 0.085$ ) and cumulative leaf length ( $0.201 \pm 0.121$ ) were higher in *P. notatum* patches, but we found no evidence that these variables changed significantly with changes in plot-level grass competitor abundance. The overall random effects were negligible for biomass (mean of the variance, 0.019), cumulative leaf length (0.020) and total leave number ( $1.58e-07$ ), and spatial pattern of random effects was minor for *A. fissifolius* (Figure 6 d, e and f).

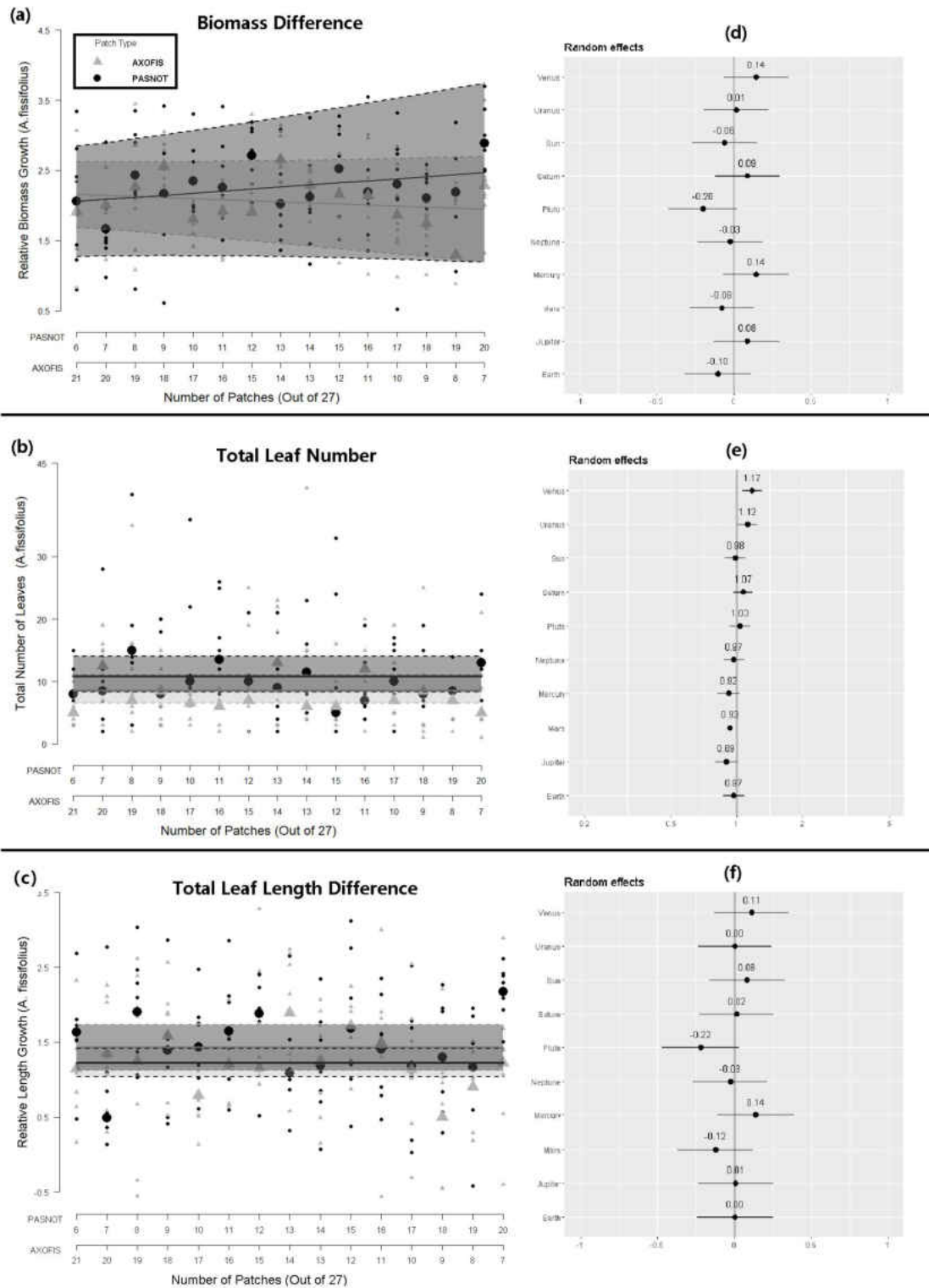


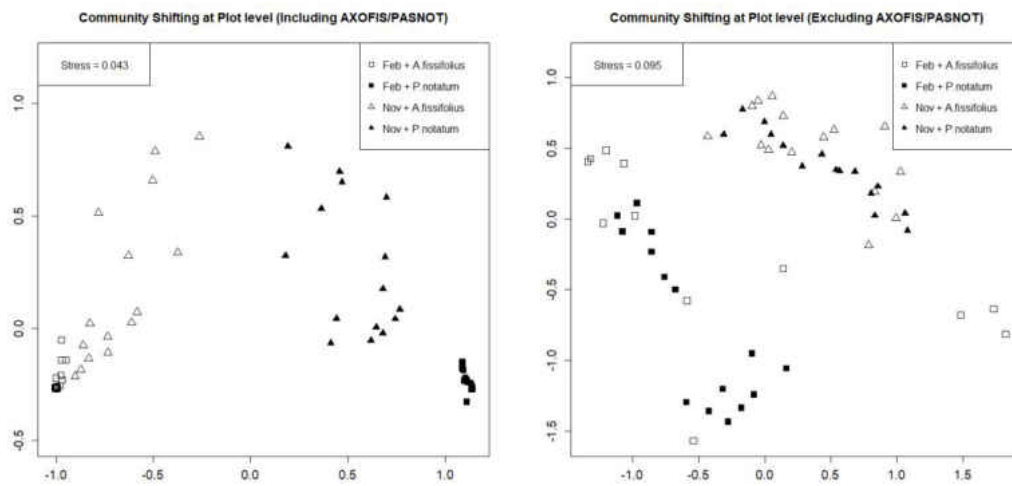
Figure 6: *A. fissifolius* performance in two types of patches (*P. notatum* = circles and *A. fissifolius* = triangles) along the plot gradient with the random effects by site. Small symbols represents all patches and large symbols are mean by 'plot' level. Shaded polygons are 95% CI. In plots d, e and f bars represent 95% CI.

### **Effect of Treatment on Soil Characteristics**

We did not find any significant effects of abundance treatments on the soil variables measured except for pH. Patch pH decreased slightly with increased *P. notatum* and decreased *A. fessifolius* ( $0.010 \pm 0.003$ ,  $p = 0.004$ ) abundance in the plot. We observed a significant interaction between abundance treatment and patch identity (*P. notatum* patch vs. *A. fessifolius* patch) on pH ( $0.0104 \pm 0.005$ ,  $p = 0.026$ ). Due to collinearity, we did not include pH in subsequent plant performance analysis.

### **Multivariate Analysis**

We recorded a total of 68 plant species across the 30 plots. Plant species diversity changed from 31 species during the dry season (February 2018) to 61 species at the end of wet season (November 2018). The ordination analysis indicated evidence of significant differences by season and the dominant grass in the patch, whether or not we included the two dominant grass species (*P. notatum*, *A. fessifolius*) in the analysis (Figure 7). A permutational multivariate analysis of variance (PERMANOVA) confirmed effects of patch type ( $r^2 = 0.75$ ,  $p=0.001$ ) and season ( $r^2 = 0.078$ ,  $p=0.001$ ) when the dominant grasses were included (Figure 7a) and when excluded (Figure 7b)(Patch  $r^2 = 0.038$ ,  $p=0.008$ ; Season  $r^2 = 0.24$ ,  $p=0.001$ )



**Figure 7: Plant species ordinations by patch type and season. In the left plot all species were included while in the right plot the two dominant grasses were excluded.**



## CHAPTER FOUR: DISCUSSION

### Responses of Plants and Environmental Variation

Our study was designed to address the interaction between per-capita impact and abundance for the competition between a non-native plant and a native plant. We performed an experiment that enabled simultaneous evaluation of the effects of abundance levels of three interacting species and per capita impacts on focal species performance. By separating plot and patch effects we were able to measure different components of abundance and per-capita impact  $E$  from; both direct and indirect effects. We found evidence of a direct effect at the patch level, and evidence of indirect effects (apparently mediated by biotic changes in soil pH) at plot level. Contrary to expectations based on competitive effects between native and nonnative species, the magnitude and direction of those effects were relatively consistent between the focal species (*P. notatum* and *A. fissifolius*), where both species performed better when located in nonnative *P. notatum* patches. A positive indirect effect was indicated because both focal species had increased performance when surrounded by more *P. notatum*.

It has been public impressions and an ecological assumption that invasive and non-native species have negative effects on native species and ecosystems (García-Díaz, Cassey, Richardson, Pyšek, & Blackburn 2016; Benjamin & Franck, 2016). We provided evidence that more aspects of interaction between non-native and native species need to be considered. Beyond the variation of direction of interactions, the scales of where effects come from should be paid more attention. Instead of including only relative straight-forward immediate contact direct effect, indirect effect beyond the immediate contact could be substantial or even leading in shaping the interaction effects.

Not all performance variables (biomass, total leaf number, cumulative leaf length) responded similarly

to treatments at patch and plot level, meaning that inferences based on only one variable may miss effects. Models for biomass included more relevant responses to abundance levels, while leaf number and length show relatively weak responses from treatments. Biomass is a more comprehensive variable summarizing energy accumulation and long-term performance, while cumulative leaf length and leaf number are more instantaneous signals of plant performance which can be more heavily influenced by the season. This may explain why no interactive effects between plot and patch level treatment was recognized for *A. fissifolius*.

While areas dominated by *P. notatum* and *A. fissifolius* may be harsh competition environments for other species (e.g, the phytometer here), habitats dominated by *P. notatum* were more benign for both focal grasses than those dominated by *A. fissifolius*. Our evidence on biotic change of soil pH in the plot suggest a possible mechanism contributing to the more benign environment in *P. notatum* patches. It is known that *P. notatum* can decrease soil pH facilitating their own growth by reducing  $\text{Ca}^{2+}$  and  $\text{K}^+$  in the soil (Tan, Beaty, McCreery, & Jones 1975). Since both grasses are well adapted to low pH soil, this may have mediated the facilitation effect from *P. notatum* to both itself and *A. fissifolius*. This effect could be highly context dependent, as at BIR soils are generally sandy with relative low pH (Swain, Boughton, Bohlen, & Lollis 2013). This facilitation effect could be flipped to competitive when soil conditions are different.

There are other mechanisms that could be the causes of these effects, but our experiment was not able to address them. Patch and individual levels effects may due to immediate contact of roots leading to direct competition for macro nutrients and water availability in the soil. Light competition can be another important mechanism, since both *P. notatum* and *A. fissifolius* have a dense canopy. Changes

of microclimate due to different ground cover of *P. notatum* and *A. fissifolius* may result from the last species capturing more humidity during morning fog in dry season and holding back or slowing down evaporation and transpiration after frequent raining in wet season. At the plot level, associational effects of herbivory would be potential important mechanism (Orians & Bjorkman, 2009; Feldman, Morris, & Wilson 2004). Different densities and spatial patterns of plant groups could affect the herbivory intensity due to physical shading and chemical attraction (Bergvall, Rautio, Kesti, Tuomi, & Leimar 2006; Hambäck, Inouye, Andersson, & Underwood 2014). Changes in pollination, predation, herbivory and nutrient competition may lead to significant differences in survival rate at population level (Barbosa *et al.*, 2009). This could be a mechanism lead to community level shifting.

From NMDS analysis, we observed that the 2 most dominant species (*P. notatum* and *A. fissifolius*) were the major factors causing community differences. If those 2 dominant species were excluded from NMDS, then the change of season helped explain community differences. The co-existence of other species may have resulted from the different competition environment created with different types and abundance of patches. This could be a mechanism leading to community level shifting in a long term from neighboring species effects beyond the scope of our year-long experiment

The replacement of the abundance of the two grasses at the plot level across the 30 plots provided a more unbiased and comprehensive understanding on the relationships between *P. notatum* and *A. fissifolius*. However, this design had also drawbacks. The embedded individuals within the patch creates a lack of independence among these factors that inflated the confidence intervals of some our model coefficients. The individual level effect could not be completely separated from patch effect, due to the focal species individuals are always nested in the patch, which overwhelms any effect of

the transplanted individuals.

Wlocated in *P. notatum* patch. Also both focal species experienced an interactive effect of increased performance when there were more *P. notatum* patches in one plot. Performance variables (biomass, leaf number, leaf length) were not consistent in showing the significance of the treatment effects at patch and plot level. Models for biomass included more relevant responses to abundance levels, while leaf number and length show relatively more dim responses from treatments. Biomass is a more comprehensive variable summarizing energy accumulation and long-term performance, while cumulative leaf length and leaf number are more instantaneous signals of plant performance which can be more heavily influenced by the season. This may explain why no interactive effects between plot and patch level treatment was recognized for *A. fissifolius*.

## **Application**

With lots of literature addressing ecological impacts of non-native species, most of them are compared under a ‘worst-case’ scenario (e.g., invaded vs un-invaded), few studies address the change of impacts along abundance gradients (Jackson, Ruiz-Navarro,& Britton 2015). The direction of invaders’ effects at multiple scales may vary and the magnitude of these effects may change in non-linear fashions (Yokomizo, Possingham, Thomas, & Buckley 2009; Jackson, Ruiz-Navarro & Britton 2015). Depending on the shape of the non-linear relationships, different management priorities and strategies could be deployed to maximize their efficiency (Brown, Huth, Banks, & Singleton 2007; Nava-Camberos, Riley, & Harris 2001). Preventing arrival and establishment of non-native species with low-threshold curves (i.e., species that show remarkable impacts even at relatively low

abundance) should be a priority of management. While optimal investment at relative low abundance is justified for high-threshold species (i.e., species that show remarkable impacts only when reached relatively high abundance) (Yokomizo, Possingham, Thomas, & Buckley 2009).

### **Future Directions**

Successful observation of indirect effects depends on proper selection of study scales (Underwood, Inouye, & Hambäck 2014). In our experiment, there were two important scales, the patch level (direct effects) and plot level (indirect effects). We determined these scales based on observation of focal species' biological characteristics (e.g, depth and length of roots, length of leaf, density of shoots, canopy shading) and working experience with the focal species. Based on the study species, ecosystems and response variables, the relevant scales could vary from a grass sod, to meter size plots, to the whole community and landscape (Underwood, Inouye, & Hambäck 2014). Expanding temporal and spatial scale of studies on indirect effects would be also helpful for identifying more significant variables for population and community processes. The evidence and information on responses of species' survival, reproduction rates and dispersal at multiple scales could better enable us to evaluate another dimension from Parker's model of " $I = R*A*E$ ", the distribution (R), instead of only addressing  $A*E$  interaction in this study.

## **APPENDIX A: INITIAL BIOMASS ESTIMATION MODELS**

Appendix A: Linear regression models summary for initial biomass estimation

Public models tested for each species	Species	Best model	Estimation formula	Multiple R <sup>2</sup>
Model 1 (Aboveground Biomass ~ Total Leaf Length + Average Leaf Length + Total Leaf Number)	<i>A. fissifolius</i>	Model 4	0.00395*(Total Leaf Length) + 0.0432	0.738
Model 2 (Aboveground Biomass ~ Total Leaf Length + Total Leaf Number)	<i>P. notatum</i>	Model 2	0.00347*(Total Leaf Number) + 0.00986*(Total Leaf Length) + (-0.018913)	0.767
Model 3 (Aboveground Biomass ~ Average Leaf Length + Total Leaf Number)	<i>P. nodiflora</i>	Model 4	0.00241*(Total Leaf Length) + 0.139	0.659
Model 4 (Aboveground Biomass ~ Total Leaf Length)				

## **APPENDIX B: TREATMENT EFFECTS ON SOIL PARAMETERS**

### **MODELS**



**Appendix B: Model selection summary of treatment effects on soil parameters**

Public models tested for each variable	Soil variable	Transformation	Best model dAICc (Weight)	Null model dAICc (Weight)	Significance of treatments
Model 1 ~ Individual + (1 Site)	Total Organic Matter	log	Model 1 0.0 (0.276)	0.5 (0.212)	No evidence
Model 2 ~ Plot + (1 Site)	Total Mineral Content (NH <sub>4</sub> <sup>+</sup> NO <sub>3</sub> <sup>-</sup> )	log (x+1)	Null model 0.0(0.34)	-	-
Model 3 ~ Patch * Plot + (1 Site)	Ortho-P (PO <sub>3</sub> <sup>-</sup> )	log	Model 3 0.0 (0.414)	1.3 (0.212)	No evidence
Model 4 ~ Patch * Plot + Individual + (1 Site)	pH	inverse	Model 4 0.0 (0.892)	13.6 (0.001)	Patch * Plot ( <i>p</i> =0.0414)

**APPENDIX C: MODELS SELECTION ON PLANT PERFORMANCE  
RESPONSE**

### Appendix C: Model selection summary of treatment effects on plant performance

Public models tested for each species and variable	Response Variable	Transformation	Error family	Link	Focal Species	Best model by AICc	Most plausible model used in paper	Note
Model 1 ~ Individual + (1 Site)	Response ratio of Biomass	Log (Nov/Feb)	Gaussian	Identity	<i>P. not</i>	Model 5 (0.0, 0.426)	Model 4 (0.7, 0.293)	95% CI inflated by model 5
Model 2 ~ Patch + (1 Site)					<i>A. fis</i>	Model 3 (0.0, 0.334)	Model 3 (0.0, 0.334)	
					<i>P. Nod</i>	Null model (0.0, 0.477)	-	
Model 3 ~ Patch * Plot + (1 Site)	Response ratio of Total Leaf Length	Log (Nov/Feb)	Gaussian	Identity	<i>P. not</i>	Model 3 (0.0, 0.307)	Model 3 (0.0, 0.307)	
Model 4 ~ Patch * Plot + Individual + (1 Site)					<i>A. fis</i>	Model 2 (0.0, 0.382)	Model 2 (0.0, 0.382)	
					<i>P. nod</i>	Null model (0.0, 0.478)	-	
Model 5 ~ Patch * Plot + Patch * (Plot^2) + (1 Site)	Total Leaf Number (November)	-	Negative binomial	Logarithm	<i>P.not</i>	Model 2 (0.0, 0.449)	Model 3 (1.5, 0.208)	Interaction observed in data pattern
					<i>B. fis</i>	Model 2 (0.0, 0.471)	Model 2 (0.0, 0.471)	
Model 6 ~ Patch * Plot + (Plot^2) + (1 Site)					<i>P. nod</i>	Model 1 (0.0, 0.708)	-	
Model 7 ~ Patch * Plot + Individual + (1+ Patch Site)	Survival (November)	-	Binomial	Logit	<i>P.not</i>	Model 1 (0.0, 0.437)	Null model (0.9, 0.275)	No difference from null model
					<i>C. fis</i>	Null model (0.0, 0.473)	-	
					<i>P. nod</i>	Null model (0.0, 0.403)	-	

Note: In models evaluating Total Leaf number, the total leaf number in February was added as a co-variable in the model

## REFERENCES

- Abrams, P. A. (2001). Describing and quantifying interspecific interactions: a commentary on recent approaches. *Oikos*, 94(2), 209-218.
- Antonovics, J., & Levin, D. A. (1980). The ecological and genetic consequences of density-dependent regulation in plants. *Annual Review of Ecology and Systematics*, 11(1), 411-452.
- Antonio, C. D. & Meyerson, L. A. (2002). Exotic Plant Species as Problems and Solutions in Ecological Restoration : A Synthesis. *Restoration Ecology*, 10, 703-713.
- Barbosa P., Hines J., Kaplan I., Martinson H., Szczepaniec A., Szendrei Z. (2009). Associational resistance and associational susceptibility: having right or wrong neighbors. *Annual Review of Ecology, Evolution, and Systematics*, 40,1-20.
- Barney, J. N., Tekiela, D. R., Dollete, E. S., & Tomasek, B. J. (2013). What is the “real” impact of invasive plant species?. *Frontiers in Ecology and the Environment*, 11(6), 322-329.
- Benjamin D. Hoffmann, Franck Courchamp. (2016). Biological invasions and natural colonisations: are they that different? *NeoBiota*, 29, 1-14.
- Bergvall, U. A., Rautio, P., Kesti, K., Tuomi, J., & Leimar, O. (2006). Associational effects of plant defences in relation to within-and between-patch food choice by a mammalian herbivore: neighbour contrast susceptibility and defence. *Oecologia*, 147(2), 253-260.
- Boughton, E. H., Quintana-Ascencio, P. F., Bohlen, P. J., & Nickerson, D. (2011). Differential facilitative and competitive effects of a dominant macrophyte in grazed subtropical wetlands. *Journal of ecology*, 99(5), 1263-1271.
- Brown, P. R., Huth, N. I., Banks, P. B., & Singleton, G. R. (2007). Relationship between abundance of

- rodents and damage to agricultural crops. *Agriculture, Ecosystems & Environment*, 120(24), 405-415.
- Burnham, K.P. & Anderson, D.R. (2002). *Model Selection and Inference: A Practical Information-Theoretic Approach*. Springer, New York.
- Chamberlain, S. A., Bronstein, J. L., & Rudgers, J. A. (2014). How context dependent are species interactions? *Ecology letters*, 17(7), 881-890.
- Feldman T. S., Morris W. F., Wilson W. G. (2004). When can two plant species facilitate each other's pollination? *Oikos*, 105, 197–207.
- García-Díaz, P., Cassey, P., Richardson, D. M., Pyšek, P., & Blackburn, T. M. (2016). Biological invasions and natural colonisations are different—the need for invasion science. *NeoBiota*, 31, 87-98.
- Hambäck, P. A., Inouye, B. D., Andersson, P., & Underwood, N. (2014). Effects of plant neighborhoods on plant–herbivore interactions: resource dilution and associational effects. *Ecology*, 95(5), 1370-1383.
- Hamilton, N. S. (1994). Replacement and additive designs for plant competition studies. *Journal of Applied Ecology*, 31 (4), 599-603.
- Hibbard, K. A., Archer, S., Schimel, D. S., & Valentine, D. W. (2001). Biogeochemical changes accompanying woody plant encroachment in a subtropical savanna. *Ecology*, 82(7), 1999-2011.
- Nava-Camberos, U., D. G. Riley, & M. K. Harris. (2001). Density-yield relationships and economic injury levels for *Belmesia argentifolia* (Homoptera: Aleyrodidae) in cantaloupe in Texas. *Journal of Economic Entomology*, 94, 180-189.
- Nakagawa, S., & Schielzeth, H. (2013). A general and simple method for obtaining R<sup>2</sup> from

- generalized linear mixed-effects models. *Methods in Ecology and Evolution*, 4(2), 133-142.
- Orians, C. M., & Björkman, C. (2009). Associational resistance to a tropical leaf-miner: does neighbour identity matter?. *Journal of Tropical Ecology*, 25(5), 551-554.
- Parker, I. M., Simberloff, D., Lonsdale, W. M., Goodell, K., Wonham, M., Kareiva, P. M., *et al.* (1999). Impact: toward a framework for understanding the ecological effects of invaders. *Biological Invasions*, 1(1), 3-19.
- Pemberton, R. W., & Ferriter, A. P. (1998). Old World climbing fern (*Lygodium microphyllum*), a dangerous invasive weed in Florida. *American Fern Journal*, 165-175.
- Pierre, S. M., Quintana-Ascencio, P. F., Boughton, E. H., & Jenkins, D. G. (2017). Dispersal and local environment affect the spread of an invasive apple snail (*Pomacea maculata*) in Florida, USA. *Biological Invasions*, 19(9), 2647-2661.
- Pyšek, P., Jarošík, V., Hulme, P. E., Pergl, J., Hejda, M., Schaffner, U., & Vilà, M. (2012). A global assessment of invasive plant impacts on resident species, communities and ecosystems: the interaction of impact measures, invading species' traits and environment. *Global Change Biology*, 18(5), 1725-1737.
- Quarin, C. L., Burson, B. L., & Burton, G. W. (1984). Cytology of intra-and interspecific hybrids between two cytotypes of *Paspalum notatum* and *P. cromyorrhizon*. *Botanical Gazette*, 145(3), 420-426.
- Robinson, C. J., Smyth, D., & Whitehead, P. J. (2005). Bush tucker, bush pets, and bush threats: cooperative management of feral animals in Australia's Kakadu National Park. *Conservation Biology*, 19(5), 1385-1391.
- R Core Team. (2018). R: A language and environment for statistical computing. R Foundation for

Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.

- Smith, C., Boughton, E. H., & Pierre, S. (2015). *Pomacea maculata* (Island Apple Snail) invasion in seasonal wetlands on Florida ranchland: association with plant-community structure and aquatic-predator abundance. *Southeastern naturalist*, 14(3), 561-576.
- S Feldman, T., F Morris, W., & G Wilson, W. (2004). When can two plant species facilitate each other's pollination?. *Oikos*, 105(1), 197-207.
- Silander, J. A., & Antonovics, J. (1982). Analysis of interspecific interactions in a coastal plant community - a perturbation approach. *Nature*, 298(5874), 557.
- Simberloff, D., Martin, J. L., Genovesi, P., Maris, V., Wardle, D. A., Aronson, J., *et al.* (2013). Impacts of biological invasions: what's what and the way forward. *Trends in ecology & evolution*, 28(1), 58-66.
- Sparks, D. L., et al. (1996). "Methods of soil analysis—soil science society of America book series." ASA and SSA, Madison, WI, USA.
- Swain, H. M., Boughton, E. H., Bohlen, P. J., & Lollis, L. O. G. (2013). Trade-offs among ecosystem services and disservices on a Florida ranch. *Rangelands*, 35(5), 75-87.
- Tan, K. H., Beaty, E. R., McCreery, R. A., & Jones, J. B. (1975). Differential Effect of Bermuda and Bahiagrasses on Soil Chemical Characteristics 1. *Agronomy Journal*, 67(3), 407-411.
- Thomas, C. D. (1986). Butterfly larvae reduce host plant survival in vicinity of alternative host species. *Oecologia*, 70(1), 113-117.
- Thomsen, M. S., Wernberg, T., Olden, J. D., Griffin, J. N., & Silliman, B. R. (2011). A framework to study the context-dependent impacts of marine invasions. *Journal of Experimental Marine Biology and Ecology*, 400(12), 322-327.

- Thompson, J. N. (1988). Variation in interspecific interactions. *Annual review of ecology and systematics*, 19(1), 65-87.
- Underwood, N., Inouye, B. D., & Hambäck, P. A. (2014). A conceptual framework for associational effects: when do neighbors matter and how would we know? *The Quarterly review of biology*, 89(1), 1-19.
- USDA plant Profile. <https://plants.usda.gov/java/charProfile?symbol=PHNO2> [Accessed 06/14/2018].
- Van der Putten, W. H., Macel, M., & Visser, M. E. (2010). Predicting species distribution and abundance responses to climate change: why it is essential to include biotic interactions across trophic levels. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1549), 2025-2034.
- Weigelt, A., Steinlein, T., & Beyschlag, W. (2002). Does plant competition intensity rather depend on biomass or on species identity?. *Basic and Applied Ecology*, 3(1), 85-94.
- Yokomizo, H., Possingham, H. P., Thomas, M. B., & Buckley, Y. M. (2009). Managing the impact of invasive species: the value of knowing the density–impact curve. *Ecological Applications*, 19(2), 376-378.