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Population structure and growth of a non-native invasive clonal plant on coastal dunes in Southern Brazil

Estrutura populacional e crescimento de uma planta exótica invasora clonal em dunas costeiras no sul do Brasil

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Abstract

Furcraea foetida (L.) Haw. (Asparagaceae) is a non-native invasive plant in Brazilian coastal ecosystems. This study focused on characterizing its population structure in coastal dune vegetation in southern Brazil. We also assessed which community structure characteristics were associated with its invasion and verified whether its growth negatively affected richness, diversity, and cover of local plant communities. We registered 67 individuals of *F. foetida*, most of them large and potentially reproductive. The species was positively associated with greater cover and height of native plant species which seems to promote the establishment of *F. foetida* by reducing extreme temperatures at the ground level. Overall, *F. foetida* plants growth did not result in changes in cover, richness or diversity of the studied plant communities. However, changes in cover of dominant native species might be a consequence of growth of *F. foetida* plants. These changes could result in changes in the structure of local plant communities which must be assessed in long-term studies. From a preventive perspective, immediate control actions, public awareness campaigns and legal regulations are essential to minimize *F. foetida* impacts to local biodiversity.

Keywords: diversity, dominant species, *Furcraea foetida*, richness, potential impact, vegetation cover.

Resumo

Furcraea foetida (L.) Haw. (Asparagaceae) é uma planta exótica invasora em ecossistemas costeiros brasileiros. O objetivo deste estudo foi caracterizar a estrutura populacional dessa espécie na vegetação de dunas costeiras no sul do Brasil, avaliando quais características estruturais das comunidades vegetais estão associadas à invasão pela espécie e verificando se seu crescimento interferiu negativamente na riqueza, diversidade e cobertura das comunidades vegetais. Foram registrados 67 indivíduos de *F. foetida*, a maioria deles de grande porte e potencialmente reprodutivos. A espécie mostrou-se positivamente associada com maior cobertura e altura de espécies de plantas nativas, o que parece promover o estabelecimento de *F. Foetida*, devido à redução de temperaturas extremas na superfície do solo. De maneira geral, o crescimento de plantas de *F. foetida* não resultou em mudanças em cobertura, riqueza e diversidade das comunidades vegetais estudadas. Entretanto, alterações na cobertura de espécies nativas dominantes podem ser uma consequência do crescimento de indivíduos de *F. foetida*. Essas alterações podem resultar em mudanças na estrutura das comunidades vegetais locais, o que poderia ser avaliado em estudo de longa duração. Em uma perspectiva preventiva, ações imediatas de controle, campanhas de sensibilização da população e instrumentos legais são essenciais para se minimizarem os impactos potenciais de *F. foetida* sobre a biodiversidade local.

Palavras-chave: diversidade, espécies dominantes, *Furcraea foetida*, riqueza, impacto potencial, cobertura vegetal.

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Introduction

Many plant communities are becoming seriously dominated by non-native invasive plant species as a consequence of human-mediated transport and introduction (Rejmánek *et al.*, 2013). In coastal dune systems, different microhabitats may be distinctly susceptible to invasion by non-native species as a consequence of resource availability and stress level (Carboni *et al*., 2010; Santoro *et al*., 2012). In coastal ecosystems, a strong environmental gradient along the sea-inland is mainly due to salinity, wind action, temperature, drought and sand instability (Kolb *et al*., 2002; Lortie and Cushman, 2007; Santoro *et al*., 2012). Kolb *et al.* (2002) showed that coastal grasslands which occur in milder conditions (with higher levels of nitrogen and soil moisture) are more susceptible to invasion by non-native plants than those subjected to harsher conditions (lower levels of nitrogen and soil moisture). On the other hand, Lortie and Cushman (2007) suggested that more severe conditions favored invasion in a coastal dune ecosystem. In a later study, Carboni *et al.* (2011) related the spread of non-native alien species to intermediate stress conditions on dunes along the coast of Italy. Although evidence can be controversial, most empirical studies show facilitative effects by resident species in severe environments, in the sense that they can buffer neighboring plants from abiotic stressors (He *et al*., 2013).

The introductions of non-native plants in coastal dune ecosystems result from direct human interventions, mainly for dune stabilization or ornamental purposes (Carboni *et al*., 2010; Carboni *et al*., 2011). Introductions may also develop from accidental propagule arrivals from plants cultivated nearby (Kim, 2005). Propagules may also arrive on coastal dunes from the ocean especially with high tides (Aptekar and Rejmánek, 2000). Non-native invasive species impacts on costal dune ecosystems include native species displacement, decreasing soil stabilization functions (Kim, 2005), competition for resources (Santoro *et al*., 2012), and native species richness or diversity decline (Badano and Pugnaire, 2004; Carboni *et al*., 2010).

Furcraea foetida (L.) Haw. (Asparagaceae) is an invasive species native to Central and northern South America (García-Mendonza, 2001). In Brazil, populations of *F. foetida* are currently distributed along the eastern part of the country, invading mainly coastal ecosystems of the Atlantic Forest biome, such as coastal dunes and rocky shores. Records of the species in Brazil date back to the early 19th century, when it was cultivated for fiber (García-Mendoza, 2001). *Furcraea foetida* is invasive in several countries, such as South Africa and overseas departments of France (*e.g.* Reunión Island) (Baret *et al*., 2006; Crouch and Smith, 2011). Its invasiveness is highly associated with reproduction by thousands of bulbils per plant (Crouch and Smith, 2011). It displaces and competes with surrounding vegetation, and is controlled for conservation purposes in New Zealand, Hawaii, South Africa, Florida and Brazil (Motooka *et al*., 2002; Wilcox, 2005; Howell, 2008; Crouch and Smith, 2011; Randall, 2012; Dechoum and Ziller, 2013).

This study aimed to characterize the population structure of *F. foetida* and habitat conditions, in which it occurs, as well as to assess its potential impacts on plant communities at the Praia Mole, Florianopolis, Brazil. Previous studies showed that plants of *Agave desertii* and *A. macroacantha,* species morphologically similar to *F. foetida*, were found only in sheltered microhabitats in desert environment due to the lower survival rates of seedlings and bulbils in exposed areas where temperature may exceed 70°C in summer (Franco and Nobel, 1988; Arizaga and Ezcurra, 2002). Considering that soil temperature may also exceed 70°C on bare sand during mid-summer in coastal dune ecosystems (Scarano, 2002), we hypothesized that *F. foetida* is associated with sites with milder habitat conditions generated by greater vegetation cover and height in coastal dune vegetation (hereafter *restinga*). Based on the impacts caused by introduced plants in coastal dune ecosystems, we also hypothesized that individual plant growth of *F. foetida* decreases native species richness, diversity, and cover. Taking into account that coastal dune ecosystems are one of the most invaded ecosystems in Brazil (Ziller and Dechoum, 2013), anticipating sites that are most susceptible to invasion by non-native species is key information for designing more effective control and eradication strategies.

Methods

The study system

The study was carried out between 2009 and 2010 at Praia Mole (27°36' - 27°36' S and 48°26' - 48°25' W), along the eastern coast of Florianopolis. The regional climate is humid mesothermal (Cfa) according to Köppen–Geiger. The study area consisted of a 48 m wide transect on the front dune, 760 m along the ocean line. The vegetation is dominated by herbs but sub shrubs such as *Sophora tomentosa* L. and *Scaevola plumieri* (L.) Vahl may occur (Falkenberg, 1999), usually being irregularly distributed or aggregated in groups. The vegetation is not higher than one meter, and sometimes it can be very sparse or even absent in some sites (Falkenberg, 1999).

Furcraea foetida forms a leaf rosette up to 4 m in diameter and more than 2 m in height. It produces a floral woody peduncle up to 10 m in height in the rosette center. This monocarpic plant can live 5-20 years depending on growing conditions (Francis, 2004). It produces pseudovivipary vegetative propagules (bulbils or plantlets) in large numbers (Hueck, 1953; Elmqvist and Cox, 1996), a rare clonal mechanism that consists in producing vegetative propagules on sexual organs, such as in inflorescences. Adjacent to the study area, three reproductive plants were observed 40, 50, and 130 m away from the front dune.

Data collection

Two transects were set up 10 and 30 m away from the beginning of the vegetation on the front dune. The *F. foetida* population was surveyed in 180, 16 m^2 plots (4 m x 4 m), 90 per transect. Distance between plots was 2 m, while plots were 2 m away from transect lines, alternatively set on the right and left of the lines. We registered the number of *F. foetida* plants in each plot as well as rosette diameters and height. We classified the plants in five stages of development based on rosette diameter: bulbils (rosette not formed), small (> 100 cm) and large juveniles (≥ 100 cm and < 250 cm), potentially reproductive adults (≥ 250 cm), and reproductive adults (bearing floral stalks).

A subplot of 1.4 x 1.4 m was defined in the center of each 16 m^2 plot for vegetation structure data. In each subplot the cover percentage of each species, bare soil percentage, and vegetation height were recorded. Cover percentage was visually estimated for each species according to the methodology by Assumpção and Nascimento (2000), as follows: class 1: >0 to 5%; class 2: >5 to 15%; class 3: >15 to 25%; class 4: >25 to 50%; class 5: >50 to 75%; and class 6: >75 to 100%. Mean value of classes was used for statistical analyses. Vegetation height was estimated from the mean of five measurements, 4 taken at plot corners and 1 in the center of each 140 x 140 cm plot.

We sampled 16 young, isolated *F. foetida* plants and set up 1.96 m^2 plots (1.4 m x 1.4 m) around each plant, centralized within the larger plot. Control plots (without *F. foetida*) were randomly set at 0.5 m of each *F. foetida* plant, in order to ensure sampling in a similar microhabitat. We estimated *F. foetida* and all the other species cover percentage in each plot, and measured *F. foetida* height, diameter, and number of rosette leaves in October 2009 and October 2010.

Data analysis

The population structure of *F. foetida* was characterized by plant density descriptions in the 180 plots, frequency at each development stage, and spatial distribution patterns using the Morisita dispersion index (Id) and the χ^2 test for significance of getting far away from randomness. We calculated the importance value index (IV) for *F. foetida* and of sampled plant species.

We conducted a principal component analysis (PCA) using Canoco software, version 4.5 (Ter Braak, 1995) and developed a correlation matrix to assess whether plots with *F. foetida* were correlated to structural *restinga* parameters. Variables used in this analysis were bare soil percentage, Σ absolute cover of all species, average vegetation height, richness, and diversity (H' Shannon-Wiener, with Log_{10}). *Furcraea foetida* was excluded from the estimates of the vegetation parameters.

Plant height and diameter of *F. foetida* were correlated (Spearman $r = 0.75$, $p < 0.0001$), so only diameter, number of leaves and cover were used to check whether these parameters varied between 2009 and 2010. Generalized linear mixed models (GLMM) were fitted assuming the Poisson distribution for number of leaves and the Gamma distribution for diameter and cover. Year was considered a fixed effect while each plant ID was considered a repeated measured replicate, therefore a random effect.

GLMM were also used to check whether the growth of *F. foetida* plants has led to changes in native plant communities. In these models, the explanatory variables year (2009 and 2010) and condition (plots with or without *F. foetida*, called treatment and control, respectively), as well as the interactions between year and condition were considered fixed effects. Plots were considered a random effect. Furthermore, the sum of absolute cover of the five species with highest IV (*Smilax campestris*, *Rumohra adiantiformis*, *Diodella radula*, *Remirea maritima*, and *Sophora tomentosa*, respectively; Table 1) were compared fitting zero-inflated GLMM assuming the negative binomial distribution for the response variable. Year and condition as well as their interaction were considered fixed effects, while plots were considered a random effect. All GLMM analyses and figures were produced with R software (version 3.2.2) (R Core Team, 2015) using the “glmmADMB” and the “sciplot” packages.

Results

We registered 67 plants of *F. foetida* distributed in 19 (10.5%) of the 180 plots, resulting a density of 0.37 plants/16 m^2. Plant distribution patterns showed a tendency for aggregation (Id = 18.4), differing from random distribution ($\chi^2 = 1{,}327.33$, $p < 0.05$, df = 179). Large plants were more abundant (51%), then small juveniles (30%), plants with bulbils (7%), and potential reproductive adults (12%). No reproductive plants were found. We registered 123 plant species (or morphospecies) distributed into 45 botanical families. *Furcraea foetida* was the 33rd species in IV (2.27%), the 50th in relative frequency (0.49%), and the 19th in relative cover (1.78%) (Table 1).

Axis 1 in the PCA explained 47.2% of the variation with bare soil (0.59), Σ absolute cover of all species (-0.56), and vegetation height (-0.53) as the most important variables (Figure 1). The most important variables on axis 2 were richness (-0.66) and diversity (-0.69), explaining 38.5% of variation (Figure 1). Axis 1 separated most of the plots with *F. foetida* on the negative side with higher values of vegetation cover and height.

Table 1. Floristic list and importance value (IV) of species sampled in restinga vegetation at Praia Mole, Florianopolis, southern Brazil. Ac: absolute cover (%), Af: absolute frequency (%), Rc: relative cover (%), Rf: relative frequency (%), and IV: importance value of species = Rc + Rf. *non-native species.

Family	Species	Af	Rf	Ac	Rc
Smilacaceae	*Smilax campestris* Griseb.	81. 67	6.56	11. 43	6.69
Dryopteridaceae	*Rumohra adiantiformis* (G. Forst.) Ching	36. 67	2.95	13. 32	7.8
Rubiaceae	*Diodella radula* (Willd.) Deprete	38. 33	3.08	11. 21	6.56
Cyperaceae	*Remirea maritima* Aubl.	50	4.02	7.68	4.5
Fabaceae	*Sophora tomentosa* L.	24. 44	1.96	11. 12	6.51
Nyctaginaceae	*Guapira opposita* (Vell.) Reitz	28. 33	2.28	9.4	5.5
Poaceae	*Paspalum vaginatum* Sw.	45.56	3.66	6.79	3.98
Piperaceae	*Peperomia glabella* (Sw.) A. Dietr.	37.22	2.99	6.79	3.98
Poaceae	*Stenotaphrum secundatum* (Walter) Kuntze	46.67	3.75	3.69	2.16
Boraginaceae	*Cordia curassavica* (Jacq.) Roem. & Schult.	24.44	1.96	6.41	3.75
Fabaceae	*Crotalaria* cf. *pallida* Aiton	40.56	3.26	3.32	1.94
Araliaceae	*Hydrocotyle bonariensis* Lam.	43.33	3.48	1.47	0.86
Poaceae	*Sporobolus virginicus* (L.) Kunth	28.89	2.32	3.26	1.91
Myrtaceae	*Eugenia catharinae* O. Berg	15.56	1.25	4.99	2.92
Goodeniaceae	*Scaevola plumieri* (L.) Vahl	14.44	1.16	5.12	3
Fabaceae	*Canavalia rosea* (Sw.) DC.	25	2.01	2.92	1.71
Polypodiaceae	*Microgramma* sp.	21.11	1.7	3.11	1.82
Rubiaceae	*Chiococca alba* (L.) Hitchc.	25	2.01	2.41	1.41
Araceae	*Anthurium* sp.	23.33	1.87	2.43	1.42
Lamiaceae	*Vitex megapotamica* (Spreng.) Moldenke	20.56	1.65	2.72	1.59
Amaranthaceae	*Alternanthera ramosissima* (Mart.) Chodat	31.11	2.5	1.24	0.73
Bromeliaceae	*Aechmea lindenii* (E. Morren) Baker	13.89	1.12	3.59	2.1
Anacardiaceae	*Schinus terebinthifolia* Raddi	10	0.8	3.74	2.19
Amaranthaceae	*Alternanthera maritima* (Mart.) A. St.-Hil.	28.89	2.32	1.1	0.64
Fabaceae	*Dalbergia ecastaphyllum* (L.) Taub.	11.67	0.94	3.34	1.96
Asteraceae	*Noticastrum malmei* Zardini	20.56	1.65	1.97	1.15
Cactaceae	*Opuntia monacantha* Haw.	20.56	1.65	1.96	1.15
Convolvulaceae	*Ipomoea imperati* (Vahl) Griseb.	23.89	1.92	1.28	0.75
Asteraceae	*Mikania involucrata* Hook. & Arn.	18.33	1.47	1.92	1.12
Apocynaceae	*Oxypetalum tomentosum* Wight ex Hook. & Arn.	24.44	1.96	0.89	0.52
Sapotaceae	*Bumelia obtusifolia* Humb. ex Roem. & Schult.	10.56	0.85	2.64	1.55
Apiaceae	*Centella asiatica* (L.) Urb.*	20	1.61	1.23	0.72
Asparagaceae	*Furcraea foetida* (L.) Haw.*	6.11	0.49	3.04	1.78
Euphorbiaceae	*Sebastiania corniculata* (Vahl) Müll. Arg.	20	1.61	0.89	0.52
Poaceae	*Panicum racemosum* (P. Beauv.) Spreng.	17.78	1.43	0.86	0.5
Orchidaceae	*Epidendrum fulgens* Brongn.	13.89	1.12	0.97	0.57
Polygalaceae	*Polygala cyparissias* A. St.-Hil. & Moq.	16.11	1.29	0.6	0.35
Polypodiaceae	*Polypodium lepidopteris* (Langsd. & Fisch.) Kunze	13.89	1.12	0.71	0.41
Solanaceae	*Solanum* sp. 1	11.11	0.89	1.04	0.61
	Non identified 1	15.56	1.25	0.22	0.13
Sapindaceae	*Dodonaea viscosa* Jacq.	6.67	0.54	1.43	0.84
Apocynaceae	*Oxypetalum* sp.	11.11	0.89	0.58	0.34
Commelinaceae	*Commelina* sp. 1	12.22	0.98	0.41	0.24
Euphorbiaceae	*Dalechampia micromeria* Baill.	11.11	0.89	0.53	0.31
Asparagaceae	*Asparagus* sp.	6.11	0.49	1.02	0.6
Bromeliaceae	*Vriesea friburgensis* Mez	8.33	0.67	0.61	0.36
Malpighiaceae	*Peixotoa* sp.	9.44	0.76	0.32	0.19
Asteraceae	*Conyza* sp.	8.33	0.67	0.42	0.25
Myrtaceae	*Myrcia palustris* DC.	3.33	0.27	1.07	0.63
Verbenaceae	*Lantana camara* L.	6.11	0.49	0.53	0.31
Plantaginaceae	*Plantago tomentosa* Lam.	5.56	0.45	0.56	0.33
Asteraceae	*Senecio crassiflorus* (Poir.) DC.	7.22	0.58	0.29	0.17

Table 1. Continuation.

Family	Species	Af	Rf	Ac	Rc
Passifloraceae	*Passiflora foetida* L.	6.67	0.54	0.33	0.2
Orchidaceae	*Orchidaceae* 1	7.22	0.58	0.22	0.13
Convolvulaceae	*Merremia* sp.	6.11	0.49	0.3	0.18
Asteraceae	*Eupatorium* sp.	4.44	0.36	0.42	0.25
Blechnaceae	*Blechnum* sp.	6.11	0.49	0.18	0.11
Onagraceae	*Oenothera mollissima* L.	6.11	0.49	0.18	0.11
Dioscoreaceae	*Dioscorea* cf. *scabra* Humb. & Bonpl. ex Willd.	5.56	0.45	0.24	0.14
Orchidaceae	*Vanilla* sp.	5	0.4	0.31	0.18
Poaceae	*Ischaemum minus* J. Presl	3.33	0.27	0.52	0.31
Dioscoreaceae	*Dioscorea subhastata* Vell.	5	0.4	0.28	0.17
Fabaceae	*Abarema langsdorfii* Barneby & J.W. Grimes	1.67	0.13	0.71	0.42
	Non identified 2	2.78	0.22	0.45	0.26
Anacardiaceae	*Lithraea brasiliensis* Marchand	1.11	0.09	0.6	0.35
Asteraceae	*Vernonia* sp. 2	4.44	0.36	0.13	0.08
Fabaceae	*Vigna luteola* (Jacq.) Benth.	3.33	0.27	0.23	0.14
Poaceae	*Paspalum* sp.	2.22	0.18	0.36	0.21
Poaceae	*Melinis minutiflora* P. Beauv.*	2.78	0.22	0.27	0.16
Amaranthaceae	*Chenopodium retusum* (Moq.) Moq.	2.78	0.22	0.26	0.15
Sapotaceae	*Labramia bojeri* A. DC.*	0.56	0.04	0.49	0.29
Poaceae	*Cenchrus incertus* M.A. Curtis	1.11	0.09	0.37	0.21
Amaryllidaceae	*Zephyranthes robustus* Baker	2.78	0.22	0.12	0.07
Calyceraceae	*Acicarpha spathulata* R. Br.	2.22	0.18	0.18	0.11
Myrtaceae	*Campomanesia littoralis* D. Legrand	1.67	0.13	0.24	0.14
Bignoniaceae	*Pyrostegia venusta* (Ker Gawl.) Miers	2.22	0.18	0.16	0.09
Myrtaceae	*Syzygium cumini* (L.) Skeels*	0.56	0.04	0.35	0.2
Myrtaceae	*Eugenia uniflora* L.	1.11	0.09	0.22	0.13
Dioscoreaceae	*Dioscorea* sp.	2.22	0.18	0.07	0.04
Fabaceae	*Desmodium incanum* DC.	2.22	0.18	0.07	0.04
Solanaceae	*Solanum americanum* Mill.	2.22	0.18	0.07	0.04
	Non identified 3	1.67	0.13	0.11	0.07
Asteraceae	*Vernonia scorpioides* (Lam.) Pers.	1.67	0.13	0.09	0.05
Passifloraceae	*Passiflora edulis* Sims	1.67	0.13	0.09	0.05
Asteraceae	*Baccharis* cf. *ulei* Heering	0.56	0.04	0.21	0.12
Asteraceae	*Porophyllum ruderale* (Jacq.) Cass.	1.67	0.13	0.05	0.03
Euphorbiaceae	*Euphorbia* sp.	1.67	0.13	0.05	0.03
Poaceae	*Spartina ciliata* Brongn.	1.67	0.13	0.05	0.03
Solanaceae	*Solanum pelagicum* Bohs	1.11	0.09	0.11	0.07
Cyperaceae	*Kyllinga brevifolia* Rottb.	1.11	0.09	0.04	0.03
Asteraceae	*Eupatorium casarettoi* (B. L. Rob.) Steyerm.	0.56	0.04	0.11	0.07
Apocynaceae	*Oxypetalum* cf. *banksii* Schult.	1.11	0.09	0.03	0.02
Asteraceae	*Gamochaeta* sp.	1.11	0.09	0.03	0.02
Myrtaceae	*Psidium cattleianum* Sabine	1.11	0.09	0.03	0.02
Poaceae	*Dichanthelium* sp.	1.11	0.09	0.03	0.02
Sapindaceae	*Serjania* sp. 1	1.11	0.09	0.03	0.02
Solanaceae	*Petunia littoralis* L.B. Sm. & Downs	1.11	0.09	0.03	0.02
Asteraceae	*Eupatorium* cf. *pedunculosum* Hook. & Arn.	0.56	0.04	0.06	0.03
Asteraceae	*Vernonia* cf. *chamissonis* Less.	0.56	0.04	0.06	0.03
Cactaceae	*Rhipsalis* sp.	0.56	0.04	0.06	0.03
Erythroxylaceae	*Erythroxylum argentinum* O.E. Schulz	0.56	0.04	0.06	0.03
Fabaceae	*Lonchocarpus* sp.	0.56	0.04	0.06	0.03
Fabaceae	*Mucuna* sp.	0.56	0.04	0.06	0.03
Pinaceae	*Pinus elliottii* Engelm.*	0.56	0.04	0.06	0.03
Solanaceae	*Solanum* sp. 2	0.56	0.04	0.06	0.03

Table 1. Continuation.

Family	Species	Af	Rf	Ac	Rc
Xyridaceae	*Xyris* sp.	0.56	0.04	0.06	0.03
Asparagaceae	*Agave* sp.*	0.56	0.04	0.02	0.01
Apiaceae	*Eryngium* sp.	0.56	0.04	0.02	0.01
Apocynaceae	*Ditassa burchellii* Hook. & Arn.	0.56	0.04	0.02	0.01
Asteraceae	*Achyrocline satureioides* (Lam.) DC.	0.56	0.04	0.02	0.01
Asteraceae	*Mikania* sp.	0.56	0.04	0.02	0.01
Asteraceae	*Vernonia* sp. 1	0.56	0.04	0.02	0.01
Asteraceae	*Vernonia* sp. 3	0.56	0.04	0.02	0.01
Asteraceae	*Tillandsia* sp.	0.56	0.04	0.02	0.01
Cactaceae	*Lepismium cruciforme* (Vell.) Miq.	0.56	0.04	0.02	0.01
Commelinaceae	*Commelina* sp. 2	0.56	0.04	0.02	0.01
Cyperaceae	*Scleria* cf. *melaleuca* Rchb. ex Schltdl. & Cham.	0.56	0.04	0.02	0.01
Erythroxylaceae	*Erytroxylum* sp.	0.56	0.04	0.02	0.01
Primulaceae	*Myrsine* sp.	0.56	0.04	0.02	0.01
Orchidaceae	*Rodriguezia decora* Rchb. f.	0.56	0.04	0.02	0.01
Orchidaceae	Orchidaceae 2	0.56	0.04	0.02	0.01
Poaceae	*Paspalum arenarium* Schrad.	0.56	0.04	0.02	0.01
Sapindaceae	*Serjania* sp. 2	0.56	0.04	0.02	0.01

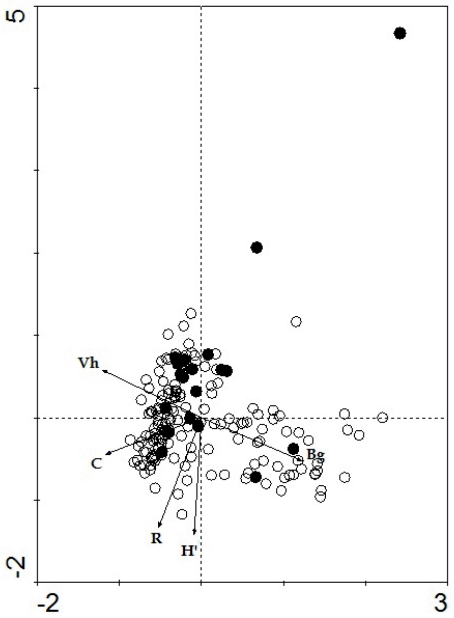

Figure 1. Principal Component Analysis for the structural variables of vegetation at the Praia Mole, Florianopolis, southern Brazil. Bg (%): bare soil; C (%): Σ absolute cover of all species; H': diversity; R: richness; Vh (cm): vegetation height. Filled circles: plots with *F. foetida* (n = 19).

Table 2. Number of leaves, diameter, and cover (mean ± SE) of *F. foetida* plants (n= 16) sampled at Praia Mole, Florianopolis, Brazil. *denotes significant differences between 2009 and 2010 in each of the parameters. Different letters indicate significant differences between years for each of the parameters.

Parameter	2009	2010
Number of leaves	14.2±1.3^{a}	18.9±1.7^{b}
Diameter (cm)	70.6±29.4^{a}	83.1±31^{a}
Cover (%)	23.9±4.7^{a}	24.2±4.9^{b}

Considering leaf number and cover percentage, *F. foetida* plants significantly increased in size between 2009 and 2010 (Tables 2 and 3). There was a significant increase in species richness from 2009 to 2010, but it did not differ between treatments (Table 4). On the other hand, native species cover decreased between 2009 and 2010, but also did not vary between treatments (Table 4). Species diversity did not vary between years or between treatments (Table 4).

The assessment of cover percentage for the five species with highest IV values shows that *D. radula*, *R. maritima*, and *S. campestris* increased in treatment plots and decreased in control plots between 2009 and 2010 (Figure 2, Table 5). Conversely, *R. adiantiformis* cover decreased in treatment plots and increased in control plots. *Sophora tomentosa* cover did not differ between conditions or years (Figure 2, Table 5).

Discussion

Our first hypothesis was corroborated considering that *F. foetida* was positively associated with milder environmental conditions, more specifically with greater native plant cover and vegetation height. Conversely, regarding our second hypothesis, although *F. foetida* plants showed

Table 3. Generalized linear mixed model results for *Furcraea foetida* (N=16) leaves, diameter, and plant cover measured in 2009 and 2010 in restinga vegetation at Praia Mole, Florianopolis, southern Brazil. Fixed effect: year, random effect: plant ID. Significant p values in bold.

Response variables	Fixed effects	Estimate	SE	Z value	p	AIC
Leaves	Intercept	-562.077	176.31	-3.19	**0.001**	203.4
	Year	0.2811	0.0877	3.20	**0.001**	
Diameter	Intercept	-332.975	254.61	-1.31	0.19	313.3
	Year	0.168	0.127	1.32	0.19	
Cover	Intercept	-468.945	200.27	-2.34	**0.02**	-42.3
	Year	0.2326	0.0997	2.33	**0.02**	

Table 4. Generalized linear mixed model results for all species richness, diversity and Σ of absolute cover in plots with and without *Furcraea foetida* in restinga vegetation at Praia Mole, Florianopolis, southern Brazil. Fixed effects: year and condition (with and without *F. foetida*); random effect: plots. Significant p values in bold.

Response variables	Fixed effects	Estimate	SE	Z value	p	AIC
Richness	Intercept	-436.9389	201.15	-2.17	0.03	331.5
	Year	0.2187	0.1001	2.18	**0.03**	
	Condition	175.1891	285.36	0.61	0.54	
	Year:condition	-0.0872	0.1420	-0.61	0.54	
Diversity	Intercept	-119.751	93.753	-1.28	0.2	-57.5
	Year	0.0595	0.0467	1.28	0.2	
	Condition	94.9119	132.7	0.72	0.47	
	Year:condition	-0.0472	0.066	-0.71	0.47	
Σ cover of all native species	Intercept	310.4176	138.64	2.24	**0.02**	53.4
	Year	-0.1544	0.069	-2.24	**0.02**	
	Condition	96.1828	196.02	0.49	0.62	
	Year:condition	-0.0478	0.0975	-0.49	0.62	

Table 5. Generalized linear mixed model results for the five species with highest importance value of species (IV) in plots (N = 180): Σ absolute cover with and without *Furcraea foetida* in restinga vegetation at Praia Mole, Florianopolis, southern Brazil. Significant p values in bold; IV: Rc + Rf.

Response variables	Fixed effects	Estimate	SE	Z value	P	AIC
Smilax campestris	Intercept	1,990	512	3.88	**<0.001**	325.7
	Year	0.99	0.255	-3.88	**<0.001**	
	Condition	-10,200	1,510	-6.73	**<0.001**	
	Year:condition	5.06	0.752	6.73	**<0.001**	
Rumohra adiantiformis	Intercept	-498.266	1,796.4	-0.28	0.781	268.9
	Year	0.247	0.894	0.28	0.783	
	Condition	6,290.82	2,857.9	2.2	**0.03**	
	Year:condition	-3.128	1.422	-2.2	**0.03**	
Diodia radula	Intercept	3,550	797	4.45	**<0.001**	211.1
	Year	-1.76	0.397	-4.45	**<0.001**	
	Condition	-13,100	823	-15.87	**<0.001**	
	Year:condition	6.5	0.41	15.87	**<0.001**	
Remirea maritima	Intercept	236.772	797.48	0.30	0.767	412.8
	Year	-0.117	0.397	-0.29	0.767	
	Condition	-4,903.7	1,449.3	-3.38	**<0.001**	
	Year:condition	2.44	0.721	3.38	**<0.001**	
Sophora tomentosa	Intercept	139.0226	1,422	0.1	0.92	247.5
	Year	-0.0673	0.7076	-0.1	0.92	
	Condition	-86.4430	2,019.4	-0.04	0.97	
	Year:condition	0.0427	1.0049	0.04	0.97	

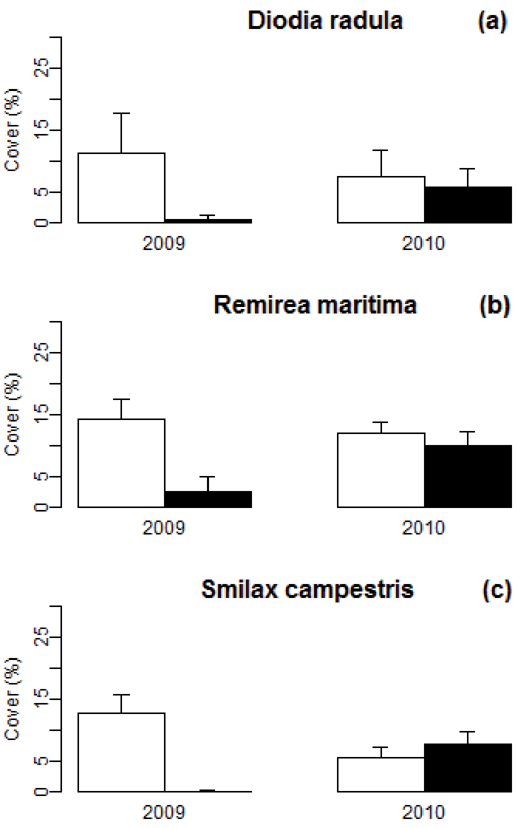

Figure 2. Cover (%; mean + SE) of three of the five native species with highest importance value (IV) in the sampled plots at the Praia Mole, Florianopolis, southern Brazil. The three species represented are those whose cover significantly changed between 2009 and 2010. White bars = Control (plots without *F. foetida*); black bars = Treatment (plots with *F. foetida*).

significant increase in cover and number of leaves over the one-year period of the study no difference was found for native species richness, diversity, and cover between invaded and uninvaded plots. Other authors have showed that species richness remained stable in invaded and uninvaded plots by different invasive plant species although some of them only displaced the dominant native species and had no effects on non-dominant species (Sax, 2002; Mason and French, 2008; Powell *et al*., 2013; Dong *et al*., 2015). Hejda *et al*. (2009) found that decreases in species richness in invaded plots by different invasive plant species significantly interacted with species-specific differences in cover between the invading and native dominant species. In our study, although we cannot be completely certain that changes in cover of dominant species were due to growth of *F. foetida* plants, it is likely that these different species-specific effects of *F. foetida* on dominant native species probably result in changes of local plant communities.

Considering that the assessment of invasion impacts on native species is strongly influenced by space scales (Vilà *et al*., 2011; Pyšek *et al.*, 2012; Powell *et al*., 2011; Powell *et al*., 2013; Ricciardi *et al*., 2013), and change dramatically over time (Flory and Clay, 2010; Dostál *et al*., 2013; Powell *et al*., 2013), long-term studies carried on across the invaded range of *F. foetida* could shed light on which are the main invasion impacts and which biotic and environmental factors are related to these impacts. In addition, experimental studies in which invaded plots could be compared to those from which *F. foetida* has been removed offers a straightforward method to demonstrate that ecological differences between these plots are linked to the effects of alien species (Kumschick *et al*., 2015). However, in order to certify that the outcomes of these experiments are due to the invasive species removal, the confounding effects of disturbance must be minimized (Kumschick *et al*., 2015).

Despite being associated with higher and denser vegetation, *F. foetida* plants had on average higher cover than native dominants and were taller than native plants. Species that can grow vigorously, reaching higher cover/biomass (large and succulent leaves), and are taller than members of invaded resident communities, including dominant species, tend to cause the strongest impacts on these communities (Brabec and Pyšek, 2000; Hedja *et al*., 2009).

The *F. foetida* population studied in the present work consisted predominantly of juvenile not reproductive plants and bulbils in establishment. Some biological traits of *F. foetida* plants such as vegetative reproduction, and very large, succulent leaves may be associated with establishment success. These traits were related to invasiveness across five Mediterranean islands for increasing colonization capacity in disturbed habitats under water depletion (Lloret *et al*., 2005). The current presence of large juveniles, potentially reproductive adults, and adult plants near the study area may result in massive reproduction (García-Mendoza, 2001). If this occurs the invasion will increase significantly, in time potentially generating more impact on local plant communities.

Considering prevention as the cheapest and most effective approach in invasive species management we recommend the removal of *F. foetida* before the studied population becomes able to expand (Ziller and Dechoum, 2013). Management priorities must consider population structure, first controlling reproductive plants in order to refrain bulbil production followed by large juveniles, and then younger plants. Dense *restinga* sites must also be considered a management priority due to establishment success in plots with higher vegetation cover. Public awareness campaigns on non-native invasive species and their impacts on natural ecosystems are important to hinder the species ornamental use in coastal areas. Finally, legal regulations are essential to guide the use of the species and give control and eventual eradication a viable prospect.

To sum up, we consider that *F. foetida* may be an imminent threat to the studied plant communities, considering that mid to long-term changes that may be caused by the current species specific effects of *F. foetida* on the plant community, summed to a likely population growth due to the potential reproduction of large juvenile plants. Furthermore, considering that the ocean is a potential dispersion vector of the species propagules, its arrival in sites susceptible to its establishment may cause impacts on coastal ecosystems in a regional scale. That said, we conclude that immediate control actions, public awareness campaigns and legal regulations are essential to minimize *F. foetida* impacts on local and regional biodiversity.

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