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PHYSIOLOGICAL ECOLOGY – ORIGINAL RESEARCH

Competition for water and rapid exclusion of an island endemic by a pantropical species in a tropical climate

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Abstract

Water availability has major effects on community structure and dynamics globally, yet our understanding of competition for water in the tropics is limited. On the tropical Trindade Island, we explored competition for water in the context of the rapid exclusion of an endemic sedge, *Cyperus atlanticus* (Cyperaceae), by a pantropical, N-fixing shrub, *Guilandina bonduc* (Fabaceae). *Guilandina* patches were generally surrounded by rings of bare soil, and dead *Cyperus* halos commonly surrounded these bare zones. With geo-referenced measurements, we showed that *Guilandina* patches and bare soil zones rapidly expanded and replaced adjacent *Cyperus* populations. We found that soil water potentials were much lower in bare soils than soils under *Guilandina* or *Cyperus*, and that leaf water potentials of *Cyperus* plants were lower when co-occurring with *Guilandina* than when alone. When *Guilandina* was removed experimentally, *Cyperus* populations expanded and largely covered the bare soil zones. Our results indicate that when *Guilandina* establishes, its root systems expand beyond its canopies and these roots pull water from soils beneath *Cyperus* and kill it, creating bare zone halos, and then *Guilandina* expands and repeats the process. This scenario indicates rapid competitive exclusion and displacement of an endemic by a common pantropical species, at least in part through competition for water.

Keywords Competition · Competitive exclusion · Endemic · Root · Tropics · Water

Introduction

Competition affects plant community structure in many biomes (Ascheoug et al. 2016), but maybe more so in the highly productive tropics because the frequency, importance, or intensity of competition generally increases with increasing productivity (Bertness and Callaway 1994; Brooker et al. 2005; He et al. 2013). Theoretically, in any biome or community, the most intense competition should be for the most limiting resources (Tilman 1977; Craine 2009). In the tropics, these limiting resources are likely to be nutrients and light, and there should be less intense competition for more abundant resources, such as water. This follows the general theory that in productive environments plants compete strongly for light, the most limiting resource, whereas in unproductive environments, where light is plentiful, plants compete for limiting resources belowground (Tilman 1988). However, there are remarkably few studies of the specific resources that plants compete for in tropical climates.

Trees in the tropics appear to compete intensely for light (Ewel and Mazzarino 2008; Farrior et al. 2016) and for soil nutrients (Ewel and Mazzarino 2008; Nasto et al. 2017) and the latter can be highly limiting (Haridasan 2008; Bond et al. 2010). There is also some evidence that tropical lianas and trees may compete for water (Alvarez-Cansino et al. 2015). Alvarez-Cansino et al. (2015) removed lianas from large trees in the field and found that estimated transpiration, or sap flow, in trees increased substantially. However, greater light availability after lianas were removed could have also increased sap flow, and other research using stable water isotopes (δ^{18}O and δ^{2}H) suggests that lianas and canopy trees might avoid competition via vertical partition of root systems

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(Deurwaerder et al. 2018; Smith-Martin et al. 2020). Strong competition has been documented among tropical grasses and among grasses and woody species (e.g., D'Antonio and Vitousek 1992, Dohn et al. 2013), but these competitive interactions generally occur where water is strongly limiting during part of the year. To our knowledge, there is little evidence for competition for water in wet tropical systems. To explore the apparent knowledge gap of competition for water in the tropics, we searched the Web of Science using the terms "tropic + water + competition", and this returned no references. In other biomes, there is a substantial literature with experiments showing competition for water (e.g., Fonteyn and Mahall 1978; Ehleringer 1984; Gebauer et al. 2002; Donzelli et al. 2013), but very few studies experimentally connect competition for water to competitive exclusion in any biome (but see Callaway et al. 1996).

Trindade Island, a volcanic Brazilian island in the Atlantic Ocean, has a climate classified as tropical without a true dry season (Koppen Af, Pedroso et al. 2017). The annual average temperature is 25.3 °C and the annual average rainfall is 1476 mm (National Oceanographic Data Bank of the Brazilian Navy). The monthly rainfall pattern is generally uniform (Supplementary material, Fig. S1). However, precipitation and soil moisture are higher at the highest elevations (Alves et al. 1998; Clemente et al. 2009), creating a gradient of soil water availability–lower at low elevations and higher at high elevations.

The island formerly had more forest, but due to intense logging and the introduction of exotic animals in 1770, including goats, the island lost a great deal of vegetation and experienced intense soil erosion. The Brazilian government removed all livestock from 1994 to 2005. Since then, much of the native flora has regenerated and many creeks have reappeared (Martins and Alves 2007; Alves et al. 2011; Silva and Alves 2011). Currently, trees occupy only 5% of the island and are concentrated at higher elevations. Lower altitudes are covered by herbaceous vegetation dominated by the endemic sedges *Cyperus atlanticus* Hemsl (Cyperaceae) (henceforth *Cyperus*) and *Bulbostilis nesiotis* Hemsl. However, the island vegetation is experiencing dynamic changes as the shrub *Guilandina bonduc* L (Fabaceae). (Gagnon et al. 2016) is rapidly expanding in many places. *Guilandina bonduc* (henceforth *Guilandina*) is a pantropical species, with seeds that disperse across the ocean (Lewis et al. 2005). We do not know when and how *Guilandina* arrived in Trindade, but its occurrence was first registered by Lobo in 1916 as *Caesalpinia bonducella* (L.) Fleming (Alves 1988).

In several areas of the island, observations suggested that populations of *Guilandina* form dense, rapidly expanding patches that are replacing herbaceous vegetation, in particular that dominated by the endemic *Cyperus* (Carvalho-Silva et al. 2013). Goats were thought to control *Guilandina* (Alves 1998), and elimination of goats corresponds with the spread of *Guilandina* across the island. There are multi-year observations of its spread into, and replacement of *Cyperus* stands (Carvalho-Silva et al 2013). Also, rings of dead *Cyperus* and bare ground are common around patches of *Guilandina* (Fig. 1). The mechanism for this apparent competitive exclusion is unknown, but our field observations found that large roots extend for many meters beyond the edges of *Guilandina* patches into the bare soils and rings of dead *Cyperus* (Fig. S2), suggesting that these plants could be competing for soil resources. Others hypothesized that *Cyperus* displacement could be driven by allelopathy (Carvalho-Silva et al 2013). In this scenario, *Guilandina* might deliver compounds via roots extending beyond the canopies which could inhibit the growth of other species, including *Cyperus*. However, this has not been experimentally addressed.

Because dying *Cyperus* show visual signs of apparent water stress, and because dead *Cyperus* near *Guilandina* is much less common at wetter, higher altitudes (see below),

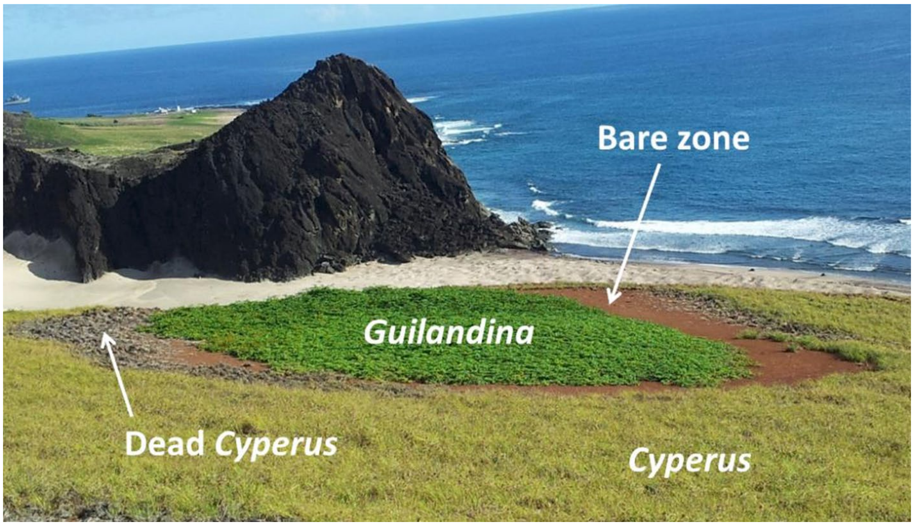


Fig. 1 Expanding *Guilandina bonduc* patch and surrounding halos at 160 m (Site 2) altitude on Trindade Island, Brazil. *Guilandina* patches, bare soil (including dead individuals of *Cyperus atlanticus*) and living *C. atlanticus* constituted the three zones from which samples and measurements were taken

we explored the potential for competition for water to be the major mechanism driving the exclusion of *Cyperus* by *Guilandina*. We organized our study with three approaches. First, we quantified spatiotemporal changes in plant growth and area covered by *Guilandina*, *Cyperus* and bare soils. Second, we experimented with allelopathy and measured soil nutrients as possible mechanisms for the interaction between *Cyperus* and *Guilandina*. Third, we measured spatiotemporal changes in soil and leaf water potentials to consider competition for water as a possible mechanism for the exclusion of *Cyperus* by *Guilandina*.

Materials and methods

Study area and species

The study was conducted on Trindade Island (20°29’32 “S, 29°17’21” W), which is 1,140 km off the shore of the Espírito Santo state in Brazil. Trindade Island has a total area of 9.28 km^2, and its highest peak reaches 620 m a.s.l. *Cyperus atlanticus* (Cyperaceae) is endemic to Trindade and the Martin-Vaz archipelago and is the most common species on the island. It is an herbaceous perennial with dense terminal inflorescences. It is a C4 rhizomatous sedge (Alves 1998) and appears to reproduce primarily by seeds (A. Gomes, *personal observation*). *Guilandina bonduc* (Fabaceae) is a shrubby species with a pantropical distribution (Gagnon et al. 2016) including all South Atlantic islands. This species has bipinnate leaves and spiny fruits usually bearing only one seed, and adult individuals average 1.5 m in height.

Experimental design

Field surveys and experiments were conducted from June 2013 to February 2016, during 10 expeditions to the island. We collected data from four sites along an elevational gradient to incorporate variation in the interactions among *Guilandina* and *Cyperus* (Fig. 2). There were different patterns of *Cyperus* and *G. bonduc* at our four sites, but in general, patches of *Guilandina* were surrounded by bare soil halos, which were in turn surrounded by dead *Cyperus* zones, and then living *Cyperus* zones (Fig. 1). We focused on three zones at the three lower elevation sites—*Guilandina*, bare soil (which often included dead *Cyperus*), and living *Cyperus*. At the one high-elevation site (Site 1), *Guilandina* and *Cyperus* grew intermixed with each other, with very few dead *Cyperus*, little bare soil, and without the clear zonation that was so obvious at the lower-elevation sites (Fig. S3).

On slopes at lower altitudes, *Guilandina* typically formed monospecific clusters. Of the three sites on lower slopes, one site (Site 2) had isolated clusters of *Guilandina* that were usually surrounded by an inner ring of bare soil and an outer ring of dead individuals of *Cyperus*, forming halos, beyond which was a dense matrix of living individuals of *Cyperus*. At the second site (Site 3), such bare and dead-*Cyperus* halos were larger and often contacted each other,

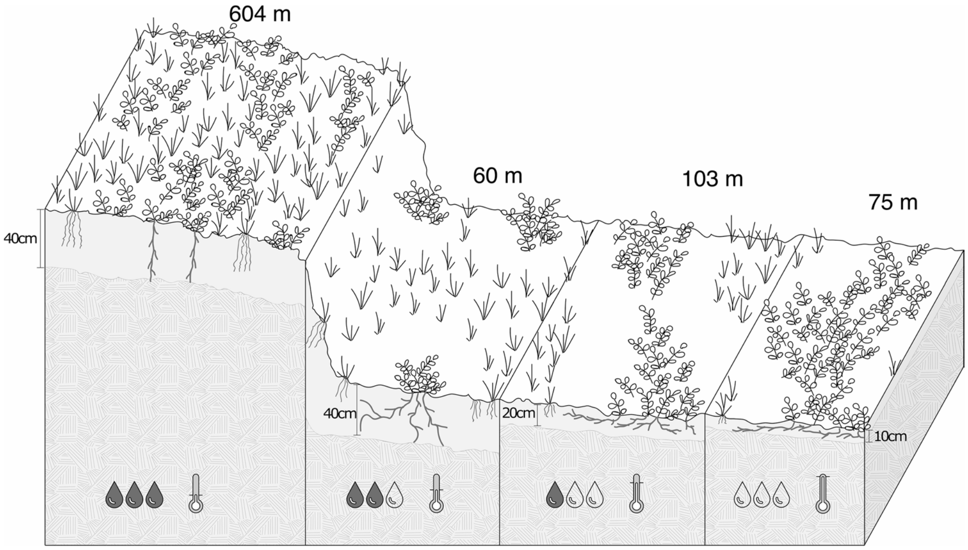


Fig. 2 The schematic illustrates our estimates of soil and rooting depths from permutational multivariate modeling, as explained in the Methods, and observations of precipitation and temperature at the four sites on Trindade Island, Brazil. Site 1 (~604 m) consisted of integrated patches of *Guilandina bonduc* with limited mortality of *Cyperus atlanticus*. Site 2 (~160 m) consisted of isolated patches of *G. bonduc* surrounded by halos of bare soil and dead *C. atlanticus*. Site 3 (~103 m) consisted of many connected patches of *G. bonduc* surrounded by halos of bare soil and dead *C. atlanticus*. Site 4 (~75 m) consisted of more coalesced patches of *G. bonduc*, more coalesced bare soil zones, and few, scattered living *C. atlanticus*

as they apparently displaced *Cyperus*. The third site (Site 4) consisted of patches of *Guilandina* individuals, large areas of bare soil, and only a few living, scattered individuals of *Cyperus* (Fig. 2). We chose these sites because they represented the range of different patterns of *Guilandina* and *Cyperus* on the island, based on our observations, and thus provided reasonably unbiased scenarios in which to explore their interaction. In these four areas, representative halos were selected (see below) and sampled for dynamic changes in the areas occupied by *Guilandina*, bare soil and *Cyperus* zones, root biomass in soils beneath the zones, soil texture and nutrient content, and soil and plant water potentials.

Dynamics of zones and plant growth

We quantified the expansion and retraction rates of *Guilandina*, bare soil and *Cyperus* zones at the three lower elevation sites (Sites 2, 3 and 4, Fig. 2) using ten representative patches. Four patches were selected at Site 2, and three each at Sites 3 and 4. Georeferenced points were recorded every two meters along the border between each *Guilandina* patch and bare soil, and the border between bare soil and *Cyperus* zones. Points were recorded with a 60CSx Garmin® UTM format. Measurements were taken in July 2013, April 2014, October 2014, June 2015, and December 2015. We estimated changes in the patch and zone borders with EasyGps® software. By comparing these measurements among time point, we were able to calculate changes in the areas occupied by *Guilandina*, bare soil and *Cyperus* zones, and also which zone replaced the other. We measured root distribution of *Guilandina* and of *Cyperus* at each of the four sites. At each site, we selected one halo and collected four soil samples in each zone—under monospecific populations of *Guilandina*, in adjacent bare soil zones, and under populations of *Cyperus* surrounding the halos. A cylindrical metal tube (40 cm length and 10 cm diameter) was driven into the soil, then the core was removed and subdivided into 10 cm long sub-samples. Each sub-sample was sieved, and roots of *Guilandina* and *Cyperus* with a diameter of 2 mm or less were removed, dried at 50 °C for 72 h and then weighed. We also followed and excavated dozens of large (3–5 cm circumference) roots of *Guilandina* extending beyond the patches to determine if they extended into the bare soil zones and *Cyperus* zones.

To explore whether *Guilandina* removal increased the abundance of *Cyperus*, we removed *Guilandina* from two patches (different from the ten patches selected for patch dynamics) at each of Sites 2, 3 and 4 in November 2014. We removed all aboveground parts of *Guilandina* at each patch using pruning shears and shovels. We made measurements along the border of each *Guilandina* patch and the border between bare soil and *Cyperus* zones before removal and we re-measured 6 and 12 months after the removal of *Guilandina*. Before the removal, the sizes of the six *Guilandina* patches ranged from 30 to 355 m^2. With these measurements, we determined the area of revegetation of *Cyperus*, regrowth of *Guilandina* and the dynamics of bare soil zones.

Allelopathy and soil nutrients

We collected soil samples from four patches (taken at random within patches used for spatial dynamics and the removal experiment) at Sites 2, 3 and 4. For each patch, we collected ten soil samples in each of the three zones. Samples from a zone for an individual patch were mixed. Soil was collected in September and stored at 8 ± 2 ºC, sieved before planting, and experiments were initiated in October 2013. *Cyperus* seeds were germinated at 25 °C in growth chambers and seedlings were planted with the field-collected soil in 200 mL plastic pots. Seedlings were grown in a greenhouse with a natural photoperiod 12 h ± 1 and a temperature of 23 ºC ± 2 SE. Plants were watered daily to field capacity. After 45 days, seedlings were harvested, dried for 24 h at 50 °C, and shoot and root mass were weighed.

We sampled soil at three zones at each of all four sites for physical and chemical soil analysis. At each site, we placed four transects running from the center of the *Guilandina* zone to the *Cyperus* zone, which were oriented north, south, east, and west. We collected a 1–10 cm deep soil sample at the center of each of the three zones along each transect. The four samples for each zone in a patch were mixed so that there was a single composite sample for each zone at each of the four sites. The proportion of clay, silt and sand from each site was also measured. The pH in water (1:2.5 soil/water) was checked with a pH meter, and the organic matter was determined with colorimetric techniques using potassium dichromate (Fontana and Campos 2017). Cation exchange capacity – CEC ($cmol_c/dm^3$) was calculated by S + H + Al (H + Al extracted by calcium acetate, 0.5 mol/L at pH 7.0). Nutrient analysis followed Mehlich (1953) with modifications; The element P was estimated by a molybdite – ascorbic acid reaction followed by spectrometry (Teixeira et al. 2017a); The elements K, Zn, Fe, Mn, Na and Cu were estimated by a modified Mehlich methodology followed by atomic spectrometry (Teixeira et al. 2017b). Total N was estimated by an adapted Kjeldahl procedure for tropical soils (Balieiro and Alves 2017). Total Sulphur (S) measurements followed the mono-calcium-phosphate methodology (Sinclair 1973), and Boron (B) was extracted using hot water. All analyses were conducted by *Campo Análises* Ltda (Paracatu-MG, Brazil).

Soil and leaf water potential

Soil water potentials (ψ_{wS}) were taken at all four sites over 32 days in the field between December 2015 and February 2016. Soil samples were collected in soils under *Guilandina*, *Cyperus*, and in bare soil zones from four patches each randomly selected at Sites 2, 3 and 4, the lower elevation sites. There were ten soil samples per zone per patch. At Site 1, the high elevation site, because of the absence of zonation, soil samples were collected at random under pure stands of *Guilandina*, *Cyperus* and for bare soils. Sampling was conducted eight times at each of the four sites. For each day, we took measurements at 9:00 am, 12:00 pm, 2:30 pm and 12:00 am, at depths of 4–5 cm and 9–10 cm. Each soil sample was stored in a hermetically sealed capsule and transported to the laboratory at the Trindade Island Scientific Station, where soil water potentials (ψ_{wS}) were recorded with a Water Potential Meter WP4C (Decagon devices), within 12 h of soil collection. The dew point sensor inside the WP4C is the measure of water potential and is accurate to 0.05 MPa from 0 to –5 MPa and 1% from –5 to–300 MPa (Scanlon et al. 2002). Leaf water potentials (ψ_{wl}) were measured using mature, fully expanded leaves selected from four *Cyperus* individuals in monodominant populations, and four *Cyperus* individuals growing among *Guilandina* roots at the outer edges of the bare soil zones where living *Cyperus* could be found (see root results). Two leaves per individual *Cyperus* were collected, totaling 8 samples per treatment (either mixed with *Guilandina* or growing without *Guilandina*) for each of the four sites. Sampling was conducted over 16 days between December 2015 and February 2016. Leaves were collected at 12:00 pm and 12:00 am. The leaf samples were stored in hermetically sealed capsules and transported in a thermal box to the laboratory for water potential measurements (WP4C) within 12 h of leaf collection.

Statistical analyses

Dynamics of zones

Rates of expansion or retraction of *Guilandina*, bare soil and *Cyperus* zones (Fig. 1) were followed for 30 months and calculated according to the equations below (in m^2):

$$GuiAcumVariation_t = InnerCircle_t - InnerCircle_0$$

$$\begin{aligned} BareAcumVariation_t = {} & \left(OuterCircle_t - InnerCircle_t\right) \\ & - \left(OuterCircle_0 - InnerCircle_0\right) \end{aligned}$$

$$CypAcumVariation_t = -\left(OuterCircle_t - OuterCircle_0\right)$$

where: $InnerCircle_t$ represents the perimeter of the area occupied by the *Guilandina* zone at time t, $OuterCircle_t$ represents the outer perimeter of the area occupied by the bare soil zone at time t, $GuiAcumVariation_t$ is the accumulated variation of the area occupied by the *Guilandina* zone at time t, $BareAcumVariation_t$ is the accumulated variation of the area occupied by bare soil zone at time t, $CypAcumVariation_t$ is the accumulated variation of the area occupied by the *Cyperus* zone at time t.

We followed expansion and retraction rates of *Guilandina*, bare soil and *Cyperus* zones at Sites 2, 3 and 4 (Fig. 2); as mentioned above, four patches were selected at Site 2, and three each at Sites 3 and 4. Measurements were taken in July 2013, April 2014, October 2014, June 2015, and December 2015. Relationships between changes in the areas occupied by *Guilandina*, bare soil and *Cyperus* zones were examined using correlation analyses (r = Pearson's correlation coefficients). We used simple linear regression to compare the zones by pairs, in which the variation in the areas covered by *Cyperus* and bare soil zones were considered the response variables, and the variation in the areas covered by *Guilandina* as the predictor variable.

Removal experiment

We completely removed the shoots of *Guilandina* from two patches at each of Sites 2, 3 and 4 in November 2014. Six and 12 months after the removal, we calculated the rates of change in the areas covered by bare zones and *Cyperus*, as well as the regrowth of *Guilandina* patches according to the equations below (in m^2):

$$GuiVariation_t = InnerCircle_t - InnerCircle_{t-1}$$

$$\begin{aligned} BareVariation_t = {} & \left(OuterCircle_t - InnerCircle_t\right) \\ & - \left(OuterCircle_{t-1} - InnerCircle_{t-1}\right) \end{aligned}$$

$$CypVariation_t = -\left(OuterCircle_t - OuterCircle_{t-1}\right)$$

where: $GuiVariation_t$ is the net variation of *Guilandina* area at time t, $InnerCircle_t$ represents the perimeter of the area occupied by the *Guilandina* zone at time t, $OuterCircle_t$ represents the outer perimeter of the area occupied by the bare soil zone at time t, $BareVariation_t$ is net variation of the area occupied by bare soil zone at time t, $CypVariation_t$ is the net variation of the area occupied by the *Cyperus* zone at time t.

Generalized linear mixed models (GLMM) were used to analyze variation in the areas covered by *Guilandina, Cyperus* and bare soil zones. Area was a continuous response variable, interactions between zones and time since removal of *Guilandina* patches as predictor variable and sites of occurrence of the halos as a random variable. AIC was used to select the best model from the full model.

Fine root abundance

We measured fine root abundance of *Guilandina* and of *Cyperus* at each of the four sites. At each site, we selected one representative halo and collected four soil samples in each of the three zones. Each 40-cm long sample was subdivided into 10-cm long sub-samples. Many soil samples had no roots, and in many sites the soils were not deep enough for sampling, thus measurements of fine roots did not meet the assumptions for parametric analyses. Therefore, we used permutational multivariate analysis of variance, a semiparametric method that can be used as a univariate ANOVA, where *p*-values are obtained by permutation (Anderson 2017). We ran a model considering zones and the roots of each species (*Guilandina* or *Cyperus*) as fixed independent variables, and another one considering sites and the roots of each species as fixed independent variables using Euclidian distances in both models. Root biomass was the dependent variable, and the roots of each species and zones were the independent variables.

Potential allelopathic interaction

Soil samples were collected from four patches each at Sites 2, 3 and 4. There were ten soil samples collected at random per patch per zone. Samples from a zone for an individual patch were mixed. To analyze the potentially allelopathic effect of soils on the growth of *Cyperus*, we employed a linear mixed-effects model in which the total seedling biomass was the dependent variable, zone was a fixed independent variable, and site was an independent random variable. AIC was used to select the best model from the full model.

Soil nutrients

Soil samples were collected from four patches each at Sites 2, 3 and 4. There were ten soil samples collected at random per patch per zone. At each of the three sites, we placed four transects running from the center of the *Guilandina* zone, passing through the bare zone to the *Cyperus* zone, which were oriented north, south, east, and west. At Site 1, because of the absence of zonation, soil samples were collected at random under pure stands of *Guilandina*, *Cyperus* and at bare soils, which were also mixed per zone as mentioned above. We collected a 1–10 cm deep soil sample at the center of each of the three zones along each transect. The four samples per zone were mixed so that there was a single sample for each zone at each site. To analyze differences of soil nutrients in the three zones, a principal component analysis was conducted on eight soil nutrients (total organic C, P, K, S, Ca, Mg, Al, N), soil pH, organic matter (OM) and cation exchange capacity (CEC). The values were standardized by z-score.

Soil water potential (ψ_{wS})

As mentioned above, soil water potentials were taken systematically in each zone (three), site (four), at two depths and four times per day over 32 days. For each zone-site-depth-time-date combination we collected two replicates and analyzed them separately. As we recorded a lot of zero values for ψ_{wS} (due to the exceptionally wet season), we had to employ zero-inflated models for statistical analysis (Zuur and Ieno 2016). For the analysis, two models were tested—a binomial model and a continuous model (Zuur et al 2009; Zuur and Ieno 2016). The binomial model analyzed the probability of a soil sample being not water saturated. A binomial linear generalized mixed model (GLMM) categorized the response variable (ψ_{wS}) as 0, representing water-saturated soils ($\psi_{wS} = 0$), or 1, representing any value other than zero ($\psi_{wS} < 0$). A continuous model was employed to analyze the intensity of water stress after all samples with zero values were removed. These values of ψ_{wS} were used in linear mixed-effects model with the continuous data $\log^{10}$-transformed. As the measurements of water potential are usually negative, these values were multiplied by -1 before log-transformation). In this model water potential was the dependent variable, zone and soil depth were the fixed independent variables, and days, sites, and sampling time as random independent variables. Model selection was conducted by AIC and means were compared with post hoc Tukey tests.

Leaf water potential (ψ_{wl})

Leaf water potentials were measured from *Cyperus* plants growing under the influence of *Guilandina* roots or not (two levels), considering two leaves (two recordings) per individual at each site (four). Measurements were taken twice a day over 16 days. A linear mixed-effects model was used to analyze leaf water potentials. Leaf water potentials were considered as the continuous dependent variable and populations and sampling times were considered as categorical independent variables. The days when the leaves were collected, and the sites were considered as random variables. AIC was used to select the best model from the full model.

All experimental data were checked for normality by Shapiro–Wilk tests before statistical tests. Those continuous dependent variables which violate the assumption of normality were log10 transformed (the values of soil water potential were multiplied by –1 before the log transformation). All statistics were run with the software Rstudio® version.1.0.136 and were used the packages: car (Fox and Weisberg 2019), lsmeans (Russell 2016), lme4 (Bates et al. 2015), multcomp (Horthon et al. 2008), tidyverse (Hadley 2017), ggbiplot (Vu 2011), corrplot (Wei and Simko 2017), vegan (Oksanen et al. 2019).

Results

Dynamics of zones

Over the 2.5 year measurement period, and over all sites combined, there was a 47% decrease in the area occupied by *Cyperus*, a 43% increase in the area occupied by *Guilandina*, and a 49% increase in the area of bare soil zones (Fig. 3A). Considering the expansion of all ten halos, we estimated a reduction of more than 3,000 m^2 in the area occupied by *Cyperus* at our sites in 30 months. *Cyperus* zones contracted by roughly 100 m^2 per patch in each sampling period except for the very wet period of November 14-Jun 15, during which *Cyperus* zones decreased by roughly 60 m^2. Bare soil zones expanded by 30–50 m^2 per patch in the first two periods, were stable in the third period, which was exceptionally wet, and expanded by roughly 200 m^2 in the last period. In contrast to *Cyperus*, *Guilandina* zones increased by 160 m^2 per patch during the first three time periods, but retracted in the last period, totaling roughly 1200 m^2 in 30 months. Over all patches combined, the area occupied by *Guilandina* increased around 40 m^2 per month, bare soil expanded around 60 m^2 per month, and *Cyperus* retracted some 100 m^2 per month. Taking together, the field recordings show that *Guilandina* and bare soil zones rapidly eradicated *Cyperus* over time, and that these rates were affected by rainfall. The variation in the area occupied by bare soil zones is correlated positively with *Guilandina*, and the area occupied by *Cyperus* correlated negatively with the area occupied by *Guilandina* and bare soil (Fig. S4).

Removal experiment

Guilandina removal corresponded with a large initial decrease in adjacent bare soil and an even larger increase in area occupied by *Cyperus*, but over time the effect of the removal waned (Fig. 3B).

Six months after removal, across all sites, *Guilandina* cover showed a decrease, unsurprisingly, of 103 ± 27 m^2, bare soil decreased by 147 ± 23 m^2, and correspondingly *Cyperus* increased by 249 ± 33 m^2. Our field observation was that the *Cyperus* increase was due to recolonization of bare soil. Twelve months after aboveground *Guilandina* removal, however, *Guilandina* cover had increased back roughly to that before the removal and bare soil changed from an early decrease of 147 ± 23 m^2 to a decrease of 81 ± 51 m^2 (zones: $F = 29.93$, $P < 0.001$, zones*time after cut: $F = 6.24$, $P = 0.0054$, Table S1). Correspondingly, the gain of *Cyperus* after 12 months post-removal was only 92 ± 63 m^2. It is important to note that recolonization by *Guilandina* was due to the resprouting of underground parts and not by germination—since no seedlings were found in the expanding populations.

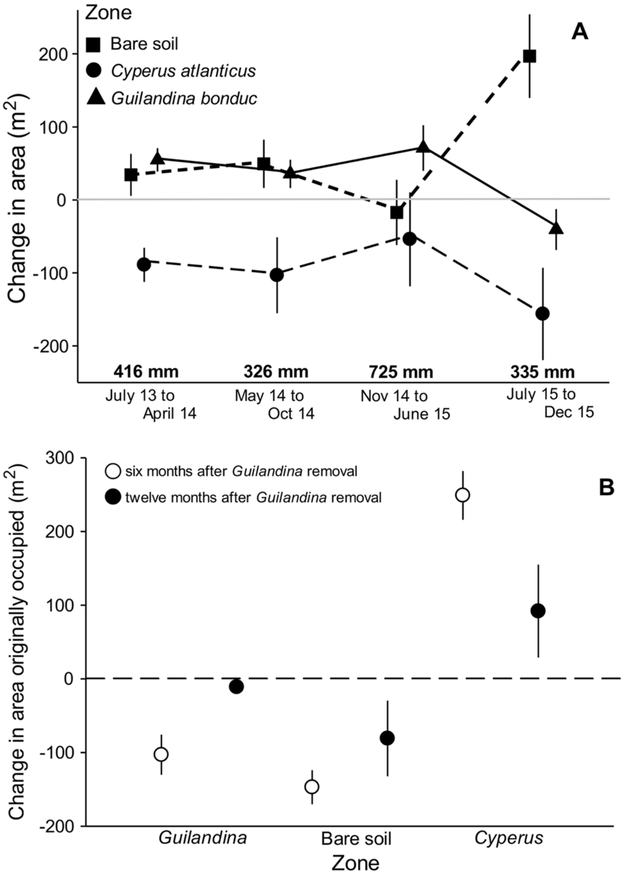


Fig. 3 **A** Changes in the areas occupied by *Guilandina bonduc, Cyperus atlanticus*, and bare soil over time on Trindade Island, Brazil. These represent the average of ten patches. Our first measurement was in July 2013, was relativized to zero for each zone. The second measurement was in April 2014, and the results represent the change from July 13 (first measure) to April 2014 (second measure), and so on. Error bars represent 1 SE. Average precipitation during the experimental period is also shown. **B**. Variation in the area (m^2) occupied by bare soil zone, by *Guilandina bonduc* zone and by *Cyperus atlanticus* zone six and 12 months after the removal of aerial part of *Guilandina* populations of six selected halos of three sites

Fine root abundance

Guilandina fine roots occurred in the soil of all zones but were much more abundant under *Guilandina* than in the bare soil or *Cyperus* zones, in which *Guilandina* root abundances were similar (Fig. 4, effect of species on roots, $F = 6{,}25$, $P < 0.001$, Table S2).

There were *Guilandina* fine roots beneath bare soil zones at all four sites, and under monodominant *Cyperus* zones at two sites (zones, $F = 18{,}32$, $P = 0.001$, plant species*zones, $F = 25.90$, $P = 0.001$, Table S2). In addition, during our field

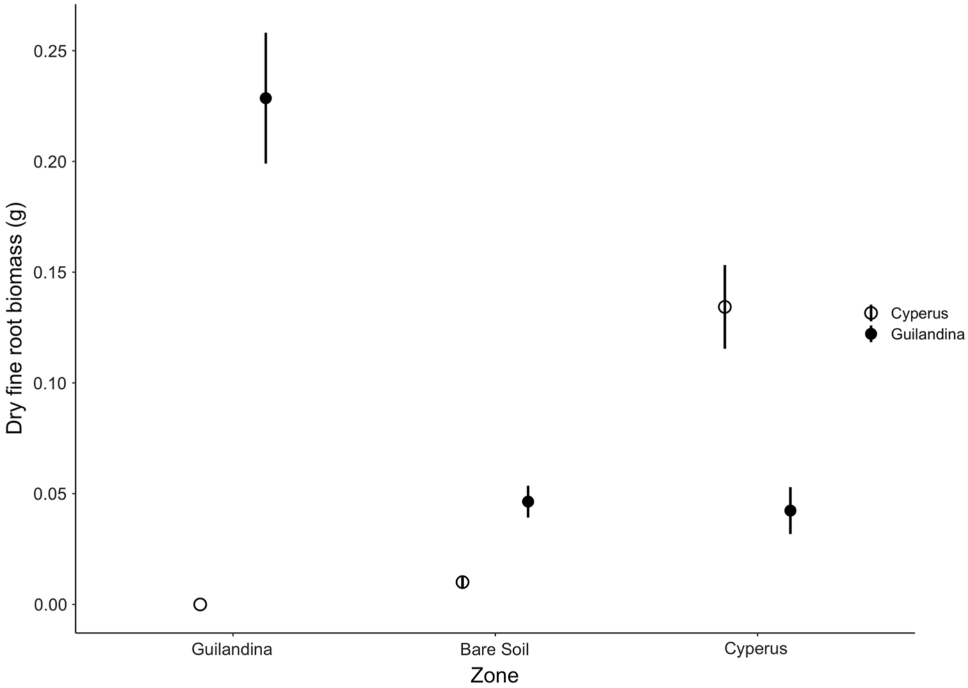


Fig. 4 Average of dry root biomass density (g / 3140cm^3 soil) of fine roots of *Guilandina bonduc* and *Cyperus atlanticus* quantified in soil samples collected under *Guilandina*, bare soil and *Cyperus* zones at 40 cm deep on the Trindade Island, Brazil

surveys we excavated dozens of large (~2–4 cm perimeter) lateral roots of *Guilandina* and these extended from at least 3 and up to14 meters from the edges of *Guilandina* zones through the bare soil zones and into living *Cyperus* zones (Fig S2). There were no fine *Cyperus* roots in *Guilandina* zones and roughly 15 times less *Cyperus* roots in bare soil zones than in *Cyperus* zones.

Allelopathy

Soil from under *Guilandina* increased shoot ($F = 24.072$, $P < 0.001$) and root biomass ($F = 13.569$, $P < 0.001$) of *Cyperus* seedlings by roughly 50% in comparison to soil from the bare soil zones and *Cyperus* zones (Fig. S5, Tables S3 and S4), indicating no allelopathic effects of *Guilandina*, but rather facilitative effects, in soils. Thus, soils removed from *Guilandina* patches showed no inhibition of *Cyperus*.

Soil nutrients

Chemical and physical analyses of the soils at the four sites showed that Site 1 contained higher amounts of organic matter, organic carbon, total nitrogen and iron, but lower amounts of magnesium in comparison with the other three sites (Table S5). The proportions of silt, clay and sand varied minimally among soil samples, and there were no differences among sites or zones (Table S5). Principal component analysis (PCA) revealed that soil nutrients and other edaphic characteristics as cation-exchange capacity (CEC) were very similar among the three zones (Fig. S6). The PCA plotted eight soil nutrients (total organic C, P, K, S, Ca, Mg, Al, N), soil pH, organic matter (OM) and CEC (Fig. S6). The first two axes explained 79.5% of variation. The PC1 was mostly associated with N and Mg, and PC2 was primarily associated with P, K and CEC. In sum, *Guilandina* did not relate with lower soil nutrient levels.

Soil water potential

Due to an atypically wet rainy season, the soils were exceptionally wet during our sampling periods. Regardless, soil water potentials were much lower in bare zones than in either the *Cyperus* or the *Guilandina* zones (zones, $F = 82.4616$, $P < 0.001$, Fig. 5). The lowest single soil water potential measurement was also in the bare soil zones, − 4.8 MPa. Over the course of our sampling period, soils in the *Cyperus* and *Guilandina* zones were significantly more likely to be water-saturated than soil in the bare soil zones (Fig. S7, Table 1A, B, Table S6). Moreover, soil water potentials at Sites 2, 3 and 4 were much lower than at site 1, where the species coexist (Fig. 6).

Leaf water potential

During the day, the mean leaf water potential of *Cyperus* leaves of plants growing with *Guilandina* was about 30% lower than that of *Cyperus* growing in pure stands ($F = 28.1331$, $P = 2.714\text{e-}07$, Fig. 7). At night, the mean water potential of *Cyperus* leaves of plants growing with *Guilandina* was more than 50% more negative than of

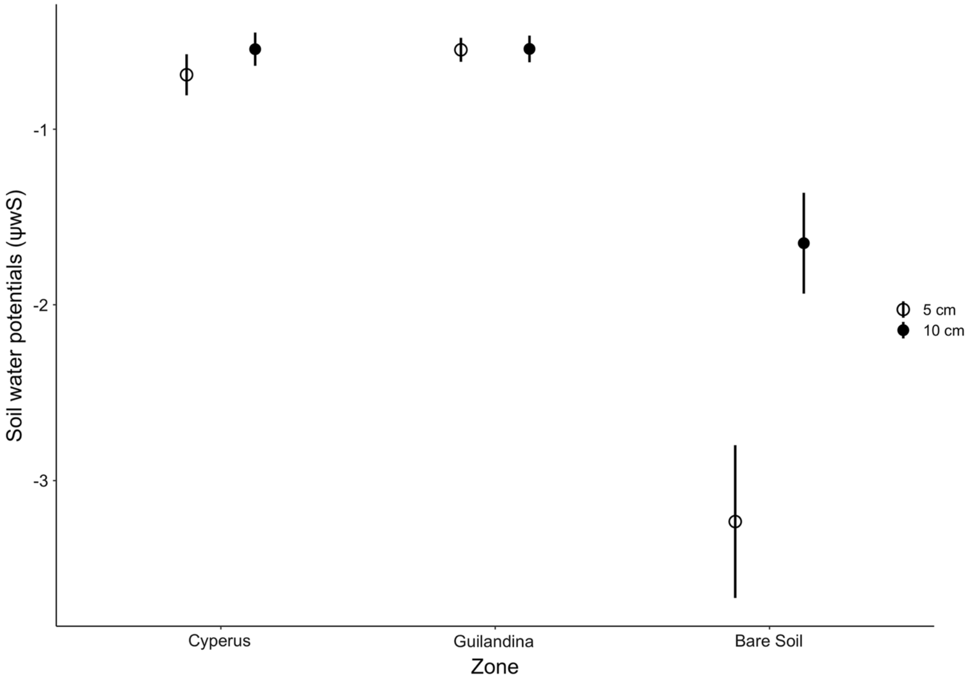


Fig. 5 Average soil water potential (ψwS, MPa) of soil samples collected at different soil depths (5 and 10 cm) on soils covered by monodominant stands of *Guilandina bonduc*, of *Cyperus atlanticus* and in bare soil zones. The values represent the mean across all four sites. Bars represent one standard error and significance was tested with analysis of variance for variables and interactions selected by the model at $p = 0.05$

Table 1 Type III Analysis of Variance comparing soil water potential of: **A** Under *Guilandina bonduc, Cyperus atlanticus* and bare soil zones, at 5 cm and 10 cm depth, model: log_wpsoil ~ depth + zone + depth * zone + (1|area/day/period); **B** At 5 cm and 10 cm depth at the four sites delimited for this study, model: log_wpsoil ~ depth + site + (1|zone/day/period); **C** Analysis of Variance comparing leaf water potential of *Cyperus* plants growing with *Guilandina* and growing in pure stands, at midday and midnight, model: log_wpleaf ~ zone*period + (1|area)

A	Sum Sq	Mean Sq	NumDF[1]	DenDF[2]	*F* value	*P*r(> F)
Depth	22.864	22.864	1	610.83	23.6060	1.504e-06 ***
Zone	159.741	79.871	2	625.53	82.4616	< 2.2e-16 ***
Deep*zone	12.283	6.142	2	611.12	6.3409	0.001881 **
B	Sum Sq	Mean Sq	NumDF[1]	DenDF[2]	*F* value	*P*r(> F)
Depth	26.37	26.370	1	620.53	21.742	3.822e-06 ***
Site	240.48	80.161	3	661.12	66.092	< 2.2e-16 ***
C	Sum Sq	Mean Sq	NumDF[1]	DenDF[2]	*F* value	*P*r(> F)
Zone	2.76451	2.76451	1	224	28.1331	2.714e-07 ***
Period	2.05549	2.05549	1	224	20.9178	7.934e-06 ***
Zone*period	0.29514	0.2951	1	224	3.0035	0.08446

[1]Degrees of freedom of the model, [2]degrees of freedom of the error

Cyperus growing in pure stands ($F = 20.9178$, $P < 0.001$, Table 1C). In this context, the presence of *Guilandina* was associated with substantially lower leaf water potentials of *Cyperus*.

Discussion

Considered together, our results indicate rapid competitive exclusion and displacement of the endemic *Cyperus atlanticus* by the pantropical *Guilandina bonduc* and suggests that competition for water might be a preeminent mechanism. First, over time *Guilandina* patches expanded simultaneously with bare soil zones that surround the patches, while *Cyperus* surrounding the halos contracted. These rapid changes in distributions corresponded with large roots of *Guilandina* extending into bare soil zones and under *Cyperus*, and the presence of *Guilandina* fine roots beneath bare soil zones and living *Cyperus* stands. In turn, soil water potentials were much lower in bare soils than in soils under *Guilandina* or *Cyperus*, and the water potentials of individual *Cyperus* plants were much lower

Fig. 6 Average soil water potential (ψwS, MPa) of soil samples collected at different soil depths (5 and 10 cm) at the four sites delimited for this study. The values represent the mean across the three zones (*Guilandina*, *Cyperus* and bare soil). Bars represent one standard error and significance was tested with analysis of variance for variables and interactions selected by the model at *p* = *0.05*

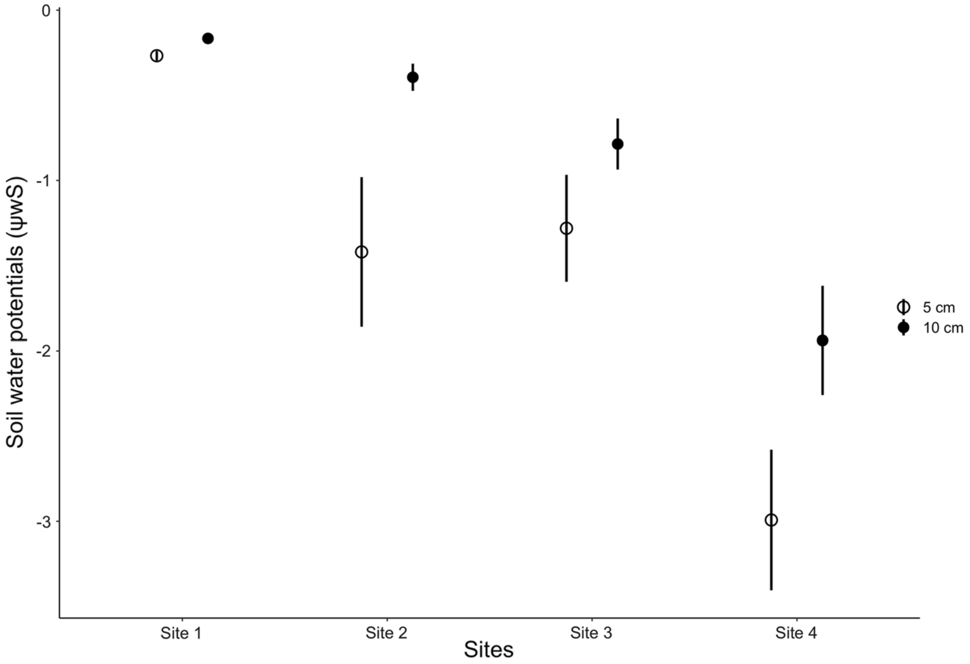
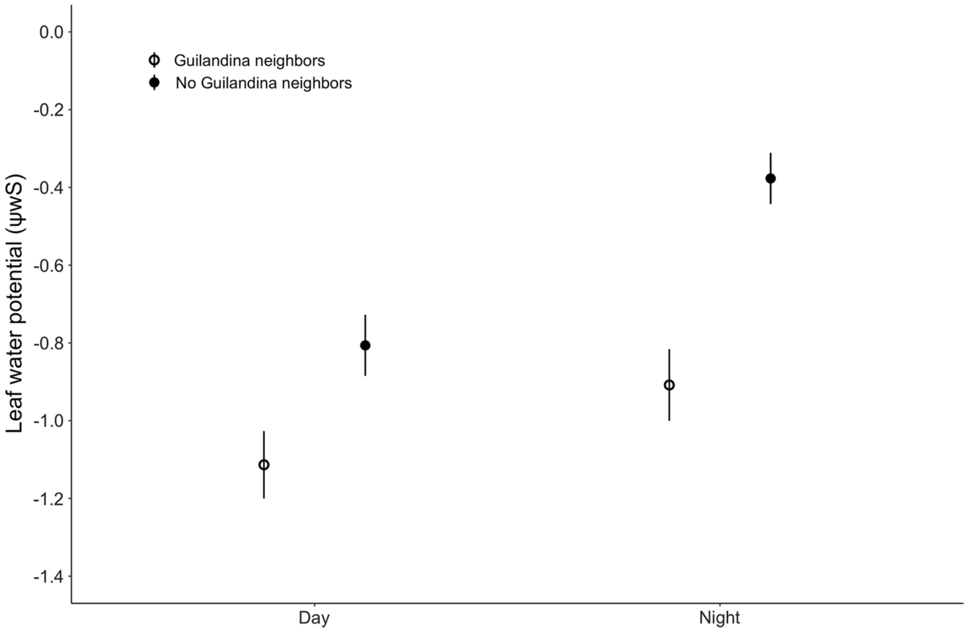


Fig. 7 Average leaf water potential (ψwS, MPa) at midday and midnight, of adult individuals of *Cyperus atlanticus* growing in mono-dominant stands or intermixed with individuals of *Guilandina bonduc*. The values represent the mean across all four sites. Bars represent standard error. Means with shared letters are not significantly different (ANOVA $P < 0.05$)



when co-occurring with *Guilandina* than when alone. Finally, when aboveground biomass of *Guilandina* was removed experimentally, bare soil zones contracted and were replaced to a large degree by *Cyperus*. As *Guilandina* grew back, the cover of both bare soils and *Cyperus* zones decreased. We propose a scenario in which *Guilandina* establishes, expands its roots systems beyond its canopies, these roots dry soils beneath *Cyperus* which kills it, and then *Guilandina* expands and repeats the process.

Our evidence for competition for water is somewhat unusual in a tropical environment, and perhaps more so when the lowest water potentials measured for *Cyperus* leaves in competition were roughly − 1.2 MPa, levels which would not create stress for most plant species. First, it is important to note that our measurement of leaf and soil water potential were taken during an exceptionally wet time, and it is likely that in drier periods *Guilandina* may have decreased *Cyperus* water potentials much more than we measured.

However, *Cyperus* species also appear to require unusually wet substrates and even small decreases in water potential might damage them. Most species in the genus are aquatic, and Rodiyati et al. (2005) found that *Cyperus brevifolius* and *Cyperus kyllingia* grew better in soils that were either maintained at 37% (field capacity) or 69% (flooded) water than soils at 14% water. Jones and Murthuri (1984) found diurnal patterns of *Cyperus papyrus* water potential reached a mid-day minimum of − 1.5 MPa. If *C. atlanticus* requires exceptionally wet conditions, such as other *Cyperus* species, the water potentials we recorded for *Cyperus* when growing with *Guilandina* could be inhibitory.

The strongest evidence for competition for water, in general, is the removal of competitors from around targets in the field, and then a response by the target that includes both improved water relations and metrics that relate to fitness (e.g., Ehleringer 1984; Callaway et al. 1996). We used removal experiments to show that *Guilandina* excluded *Cyperus*, but our evidence for exclusion via competition for water is based on correlations between the presence of roots, spatial variation in soil water potentials, and a correlation between reduced *Cyperus* water potential in the presence of *Guilandina*.

We have no evidence that *Guilandina* is an exotic invader on Trindade, but the effects of invasive species on native species and their water use may provide parallels. For example, invasion by *Acacia longifolia* into semi-arid Mediterranean dune pine forests increases whole-stand water use and decreases both the water use and photosynthetic rates of the native *Pinus pisaster* (Rascher et al. 2011). Caldeira et al. (2015) found that the invasive shrub, *Cistus ladanifer*, suppressed native oaks via competition for water. In South Africa, the water potentials of native *Acacia erioloba* trees increased substantially when invasive *Prosopis* tree species were removed (Schachtschneider and February 2013). And in an early review of mechanisms driving exotic invasions, Levine et al. (2003) found that the impacts of invaders often corresponded with differences in "transpiration rates, phenology, biomass of photosynthetic tissue or rooting depth" between invasives and natives. However, these water-based impacts have been measured in systems that are much more arid than ours.

Previous reports raised the possibility that the displacement of *Cyperus* by *Guilandina* could result from an allelopathic interaction (Carvalho-Silva et al. 2013). Indeed, the striking halos of bare soil around *Guilandina* shrubs and halos of dead and dying *Cyperus* are similar or even starker than patterns described for other species connected to allelopathy (Hierro and Callaway 2021). Much like in our case, *Polygonella myriophylla* is a shrubby perennial endemic to Florida with distinct bare zones surrounding aboveground patches (Weidenhamer and Romeo 1989). They conducted bioassays with soils collected from beneath *Polygonella*, bare zones, and surrounding vegetated areas and found that germination and seedling growth of grasses were suppressed in *Polygonella* and bare zone soil relative to soil from beneath other more distant species. In contrast with this study, our bioassays showed that soil from directly beneath the canopies of *Guilandina* had strongly positive effects on *Cyperus* biomass, relative to soil from the bare and *Cyperus* zones. However, this positive effect might not be related to soil nutrients since the soils from beneath the canopies of *Guilandina* and *Cyperus*, and from bare zones, showed similar nutrient contents and textures (see below).

Plants with nitrogen-fixing microbial mutualists commonly improve available soil nitrogen (Callaway 2007), and it might be that effects of soil directly beneath the canopies of the nitrogen-fixing *Guilandina* canopies, once removed from the complex effects of living roots, were unmasked in the controlled bioassays (see Callaway et al. 1991). Also, bulk effects of soil in bioassays might not reflect the effects of *Guilandina* roots on *Cyperus* roots in situ (see Schenk 2006). In other words, *Guilandina* roots might have had contact-based inhibitory effects on *Cyperus* that are not detectable in bulk soil (Mahall and Callaway 1991). As potentially allelopathic chemicals can rapidly attenuate in natural soil and in the time between soil collection and the bioassay (Inderjit et al. 2011), the allelopathic effects of *Guilandina* is still a possible mechanism. However, considering that both species coexist side by side at Site 1 with no noticeable effect on each other, this could hold only for Sites 2, 3 and 4. Overall, considering that the soil beneath *Guilandina* patches were *stimulatory* to *Cyperus*, potential allelopathic interaction behind the exclusion of *Cyperus* by *Guilandina* (Carvalho-Silva et al. 2013), was not supported by our studies.

Nutrient competition could also be a possible mechanism behind the exclusion of *Cyperus* by *Guilandina*. However, our soil analysis showed that, in general, the sites showed similar soil nutrient contents. The most striking differences were found in organic matter and carbon content, higher at the Site 1 in comparison to the other three sites. The analysis also revealed a very high CEC values for all sites, and a high saturation of the bases H^+ and Al^{+3} at the Site 1. At the Sites 2, 3 and 4, the samples revealed a soil less acidic and with a base saturation ranging from 78 to 92%, indicating a high availability of nutrients for plants. Overall, our analyses corroborate previous studies showing that soils occurring at both top hills and lower slopes of Trindade island are fertile (Clemente et al. 2009). Taking together, these results suggest that variations in soil characteristics as texture, nutrient content and pH would not be enough to explain the interaction between *Guilandina* and *Cyperus*, the rapid responses of *Cyperus* in the removal experiment, and the variation in their ranges associated to rainfall. These results indicate that the expansion/retraction dynamics of the halos at the lower slopes of the island might not be associated with soil nutrient variability and/or nutrient competition.

A puzzling pattern in our results is that the highest biomass of *Guilandina* roots occurred under *Guilandina*, where water potentials were relatively high. In contrast, water potentials were far lower in bare soil zones where *Guilandina* roots were 4–5 times less abundant than under *Guilandina*. If the spread of *Guilandina* roots into bare soil zones and *Cyperus* stands is important for extracting water from soils and ultimately eliminating *Cyperus*, then why were soils under *Guilandina* so wet? It is possible that the shrubby canopies of *Guilandina* shaded soils and decreased vapor pressure deficit (VPD) at the soil surface. Thus, the loss of vegetation cover exposed the bare soil to direct solar heating and excessive drying, but this would be inconsistent with competition for water being the cause of the exclusion of *Cyperus*. Soil water differences cannot be attributed to soil texture, as texture was very similar across zones in each site. It is also possible that hydraulic redistribution, which can occur in the wet tropics (Oliveira et al. 2005) and seasonal tropics (Scholz et al. 2002), moved water from deep soils to shallow subcanopy soils. However, why redistributed water would not flow through roots to soils with the lowest water potential, the bare zones, is not clear.

The climate of Trindade Island is tropical, is classified as wet, and without a true dry season, but there are several reasons why our results might not extend to typical wet tropical systems. First, precipitation can be much higher in other tropical regions and perhaps results such as ours could not be obtained in much wetter climates. Second, interactions in many, if not most, tropical communities involve far more species, and the very low diversity of our study system may have yielded results that are inherently different than those that would occur in more diverse assemblages. On the other hand, the simplicity of species-poor communities has allowed experimental investigation of competition for water in other biomes, thus simple communities may provide opportunities to understand interactions more clearly than in more complex communities (Fonteyn and Mahall 1978; Ehleringer 1984). Indeed, our studies might be extended to either tropical regions subjected to water seasonality, as savannas, or dry regions where water availability can limit plant growth.

The patterns of zones and soil water potentials we describe may provide the first empirical evidence, although incomplete, for the theoretically derived "root-augmentation feedback" mechanism for self-organized vegetation pattern formation, well represented in model studies (Meron 2012; Bennett et al. 2022). In this scenario, a plant extends roots beyond its canopy, extracts water from these distal areas, and forms relatively mesic subcanopy soils and relatively xeric soil surrounding the canopy. Over time, such feedbacks polarize these mesic and xeric microhabitats further, which can lead to strong spatial heterogeneity in vegetation patterning. Interestingly, model studies have focused on arid ecosystems, thus if *Guilandina* is driving root-augmentation feedback, it is doing so at much higher precipitation levels than models predict (see Gilad et al. 2007), suggesting that it might not only be applied to arid systems, but also to relatively wet systems with temporary dry periods or water shortage.

At one of our four sites, *Guilandina* and *Cyperus* appeared to coexist somewhat stably – Site 1, at a much higher elevation than the others. We do not have rainfall measurements at that elevation, but anecdotal evidence indicate that this site is far wetter than the other sites (Alves et al. 1998). Moreover, soil analysis showed that in Site 1 the amounts of total organic matter and carbon were much higher than at the other three sites. If competition for water is the main driver of the displacement of *Cyperus* by *Guilandina*, perhaps competitive exclusion occurs at the drier end of a gradient for these particular species, or at least for *Cyperus*, and the importance of competition wanes (not necessarily the intensity; see Brooker et al. 2005) in the wettest habitats on the island.

So, taking into consideration the potential variation in microclimate over much of the Trindade territory, we found competitive exclusion in the tropics, apparently via competition for water. While we demonstrated competitive exclusion experimentally, our evidence for competition for water is circumstantial—based on field recordings as soil water availability, dynamics of the zones and on a physiological trait (leaf water potential). With that caveat our results suggest that competition for water might be important in other relatively wet tropical communities, especially if the stronger competitor can drive soil water potential below that tolerated by neighbors. This has been shown in semi-arid systems (Callaway et al. 1996) and suggests important avenues of study in wetter systems, where intense competition is theoretically important (Dobzhansky 1950; MacArthur 1969; Bertness and Callaway 1994) and empirically demonstrated among dominant plant species (Uriarte et al. 2018; Yang et al. 2021; Weng et al. 2022). However, this empirical evidence is predominantly based on demographic correlations, thus future experimentation holds a great deal of promise.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00442-023-05352-7.

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Author contribution statement FB and AG planned and designed the research. AG, BR, GP conducted fieldwork and performed experiments. AG, EB, FB, RC analyzed and interpreted the data. RC wrote the manuscript with input from AG and FB.

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Data availability The data that support the findings of this study are available from the corresponding author upon request.

Code availability Not applicable.

Declarations

Conflicts of interest The authors declare that they have no conflict of interest.

Ethical approval Not applicable.

Consent to participate Not applicable.

Consent for publication Not applicable.

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