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Article

Invasiveness in *Schefflera* s.l.: do non-native species outperform phylogenetically related native species?

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Abstract: Can differences in biological attributes related to seed germination and seedling development between phylogenetically close native species and invasive non-native species help explain biological invasion potential in subtropical forests? Can the expression of these attributes vary according to different conditions of light when assessed experimentally? To answer these questions, we collected seeds of four phylogenetically close species, two of which are native (*Didymopanax angustissimus* Marchal and *Didymopanax* calvus (Cham.) Decne. & Planch.) and the other two are invasive non-native species (Heptapleurum *actinophyllum* (Endl.) Lowry & G.M. Plunkett, Heptapleurum arboricola Hayata) on coastal regions of southern Brazil. The seeds were set to germinate under different light conditions (100% and 50%) for a period of 180 days. We compared seed germination, seedling survival and growth between the native and invasive non-native species. H. *actinophyllum* showed higher proportions of germinated seeds, compared to the native D. calvus in T100. The native D. *angustissimus* showed higher Index of Velocity of Germination (IVG), compared to invasive non-native H. *arboricola* in the T50. The rate of survival of the invasive non-native species was higher at 50% of light. The higher germination proportion of the invasive non-native species help to explain their invasiveness regardless of light intensity. Our results suggest potential plasticity in *H. arboricola* for root/shoot biomass allocation under different light availability conditions. Both invasive non-native species are shade-tolerant, allowing them to germinate in the forest undergrowth. This trait may contribute to their establishment and invasion success in forests. Thus, both H. *actinophyllum* and H. *arboricola* should be considered a threat to closed canopy forests.
Keywords**:** G*rowth; invasive potential; invasive non-native plants; seed germination; shade tolerance; survival.*

Potencial de invasão de *Schefflera* s.l.: espécies exóticas superam nativas filogeneticamente relacionadas?

Resumo: As diferenças nos atributos biológicos relacionados à germinação de sementes e ao desenvolvimento de plântulas entre espécies nativas filogeneticamente próximas e espécies exóticas invasoras podem ajudar a explicar o potencial de invasão biológica em florestas subtropicais? A expressão desses atributos pode variar de acordo com as diferentes condições de luz quando avaliada experimentalmente? Para responder a essas perguntas, coletamos sementes de quatro espécies filogeneticamente próximas, duas das quais são nativas (*Didymopanax angustissimus* Marchal e *Didymopanax calvus* (Cham.) Decne. & Planch.) e duas espécies exóticas invasoras (*Heptapleurum actinophyllum* (Endl.) Lowry & G.M. Plunkett e *Heptapleurum arboricola* Hayata) em regiões costeiras do sul do Brasil. As sementes foram submetidas a diferentes condições de luz (100% e 50%) por um

período de 180 dias. Comparamos a germinação das sementes, a sobrevivência e o crescimento das mudas entre as espécies nativas e as exóticas invasoras. A proporção de sementes germinadas foi maior para a espécie exótica invasora *H. actinophyllum*, comparada a nativa *D. calvus*, em condições de 100% de luz. Ao contrário do que se esperava, a espécie nativa *D. angustissimus* apresentou maior velocidade de germinação, em relação às espécies exóticas invasoras em 50% de luz. Por outro lado, a taxa de sobrevivência das espécies exóticas invasoras foi maior em 50% de luz. A maior proporção de germinação das espécies exóticas invasoras ajuda a explicar seu potencial de invasão em relação à intensidade de luz. Nossos resultados sugerem potencial de plasticidade em *H. arboricola* para alocação de biomassa na raiz: parte aérea sob diferentes condições de luz. As duas espécies exóticas invasoras são tolerante à sombra. Esta característica pode contribuir para seu estabelecimento e sucesso de invasão em ecossistemas florestais. Assim, tanto *H actinophyllum* quanto *H. arboricola* podem ser consideradas uma ameaça a florestas densamente fechadas.

Palavras-chave: *Crescimento; germinação de sementes; plantas exóticas invasoras; potencial de invasão; sobrevivência; tolerância à sombra.*

Introduction

Invasion success by introduced plants has been explained by differences in ecological attributes of native and non-native species (Funk et al. 2008, Moodley et al. 2013, Leffler et al. 2014, Duffin et al. 2019). For example, seedlings of invasive species perform better in terms of germination, growth, and survival compared with co-occurring congener native species (Leicht-Young et al. 2007, Stricker and Stiling 2013). However, many comparisons do not take the phylogeny of compared species into account (Porté et al. 2011, Mathakutha et al. 2017, Yu and He 2021). Phylogenetically close species have similar biological attributes because they share a recent common ancestral (Antúnez et al. 2001, Van Kleunen et al. 2010). In a global meta-analysis, it has been shown that attributes such as fitness, height, growth rate and shoot allocation differed more between phylogenetically close invasive and non-invasive species compared with phylogenetically more distant species (Van Kleunen et al. 2010). Therefore, comparisons between the attributes of phylogenetically related species may offer a more robust basis for predicting invasiveness, based on the biological and ecological traits of an introduced species and its consequent invasion success (Van Kleunen et al. 2010, Stricker and Stiling 2013).

Invasion success may also be influenced by local environmental conditions such as water availability, nutrients in the soil, and light availability (Burns et al. 2006, Richards et al. 2006). Low light availability in forests may limit the survival of non-native species (Davis et al. 2000, Fridley et al. 2023). However, shade-tolerant non-native plants may invade forests, using different strategies to persist under different conditions of light (Martin et al. 2009, Rejmánek 2014, Berg et al. 2016, Medvecká et al. 2018). For example, shade-tolerant invasive non-native species may combine low survival with rapid growth under intermediate to high light conditions, and high survival with slow growth in conditions of lower incidence of light (Martin et al. 2010, Dechoum et al. 2015). On the other hand, shade-tolerant native species have attributes that minimize breathing and tissue renovation, preventing rapid growth and competitive dominance in conditions of higher incidence of light (Lusk and Jorgensen 2013, Sendall et al. 2016).

Although the number of experimental studies comparing co-occurring invasive non-native and native plants has increased in recent years, many of the comparisons do not consider the phylogeny of compared species (Porté et al. 2011, Mathakutha et al. 2017, Yu and He 2021). Important attributes shared by phylogenetically close species might be left aside in the determination of invasion success (Yu and He 2021). *Schefflera*, for a long time considered the largest genus of Araliaceae, has been segregated in five geographically coherent groups: Pacific, which includes the generic-type, Melanesian, Afro-Malagasy, Asian, and Neotropical clades (Plunkett et al. 2005). All species of the former Asian clade of *Schefflera* s.l. are now treated under *Heptapleurum* (Lowry and Plunkett 2020), while species of Neotropical *Schefflera* are currently arranged in five genera, of which *Didymopanax* accounts for most Brazilian species (Fiaschi et al. 2020). Despite *Heptapleurum* and *Didymopanax* are not sister-groups, they both belong to the Asian-Palmate clade of Araliaceae (Plunkett et al. 2019), which includes all species of the Asian and Neotropical clades of *Schefflera* s.l. Both groups include non-prickly woody plants with palmately-compound leaves and ligulate stipules, and their preferential habitats are tropical and subtropical forests from the sea level to more than 3,000 m a.s.l.

The general objective of our study was to verify how the biological attributes related to seed germination, seedling survival and growth differ between invasive non-native and native species of former *Schefflera sensu lato* (Araliaceae) on coastal regions of southern Brazil. These species currently belong to the genera *Heptapleurum* (non-native species) and *Didymopanax* (native species). The questions posed were: (1) Can differences in biological attributes related to seed germination and seedling development between phylogenetically close native and invasive non-native species help explain invasiveness in subtropical forests? (2) Can the expression of these attributes vary according to different conditions of light?

Materials and Methods

1. Study species and study area

The experiment was set up in the seedling nursery of Corrego Grande Park, in Florianopolis, Southern Brazil (27°35’53.35’’S; 48°30’39.88’’O). The local climate is Cfa type according to the Köppen-Geiger classification, humid mesothermal with a hot summer and no defined dry season. Four species of former *Schefflera* s.l. occurring in the study area were selected

for the study (Figure 1), two of which are non-native and invasive (*Heptapleurum actinophyllum* and *H. arboricola*), and two native species (*Didymopanax angustissimus* and *D. calvus*) (Figure 2).

Heptapleurum actinophyllum is a tree species native to the South of New Guinea and Northeast of Australia (Lowry and Plunkett 2020). It is considered invasive in Singapore, the United States, Puerto Rico, Cuba, Brazil, and Australia (CABI 2020, Instituto Hórus 2022). It can be found invading pastures, coastal dunes, degraded areas, and secondary forests (Gucker 2011, CABI 2020). *Heptapleurum arboricola* occurs naturally in humid forests or along rivers in China and Taiwan (Lowry and Plunkett, 2020, Instituto Hórus 2022). It is acknowledged as invasive in the United States, the Reunion Islands, Brazil, Chile, and on several Pacific islands (Instituto Hórus 2022). When outside its native range, it can grow in open areas as well as in forests (Atlas of Living Australia 2020, Instituto Hórus 2022). Both *Heptapleurum* species are frequently used as ornamental plants in tropical and subtropical regions (Chen et al. 2003, Lowry and Plunkett 2020). The seeds are bird-dispersed and germinate easily on several types of substrates, developing as epiphytes until the roots reach the ground (Marciniak et al. 2019).

Didymopanax angustissimus is endemic to Brazil and occurs throughout the Atlantic Forest domain. It grows in direct sunlight (heliophilous), is fast-growing, and a prolific seeder, forming dense seedling banks with high mortality rates (Armelin 2005). *Didymopanax calvus,* also endemic to Brazil, occurs in subtropical and tropical Atlantic forests in the south and southeast (Fiaschi and Plunkett 2018). Both native species have low germination rates, possibly due to physiological or tegumentary dormancy or to the percentage of seeds injured by insect larvae (Franco and Ferreira 2002, Ohashi and Leão 2005, Vilarinho et al. 2019). None of the native species are considered invasive anywhere in the world.

2. Seed collection and preparation

Seeds of the native species were obtained from trees located in protected areas, registered in the Floristic and Forest Survey conducted in the state of Santa Catarina (Vibrans et al. 2013) and available from the CRIA database - *SpeciesLink* (2018). The seeds of the invasive species were collected from plants in urban and peripheral areas. Two populations were selected for each species, and three to four mother

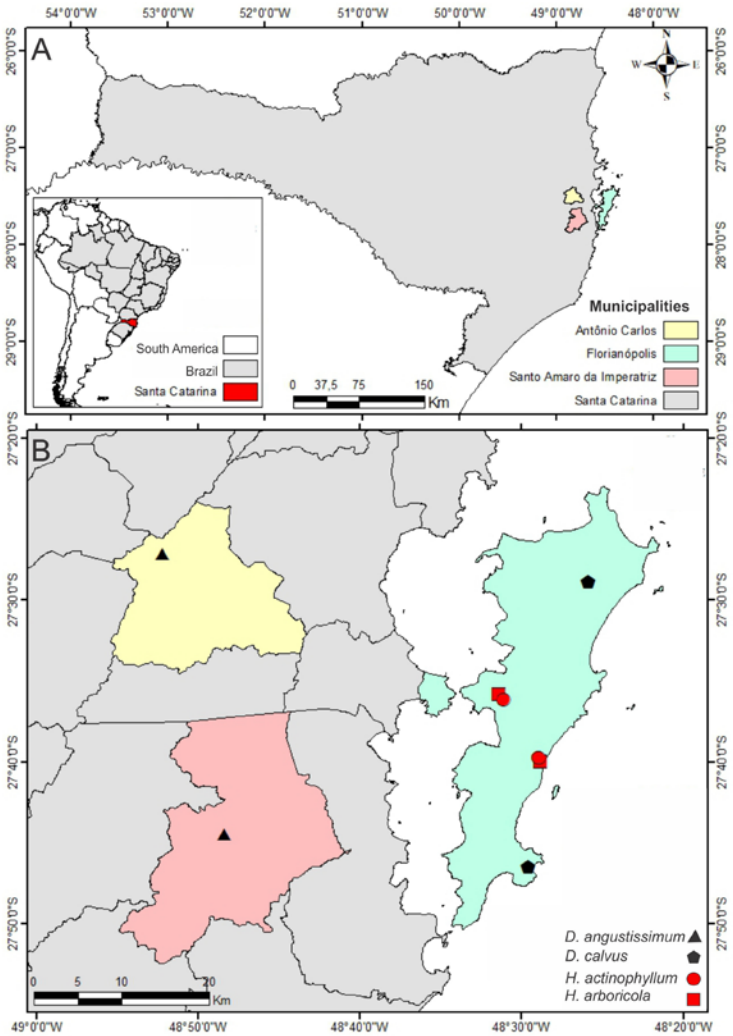

Figure 1. Location map of the former *Schefflera* s.l. species selected for the seed germination and seedling growth and survival experiments. A) Location of the state of Santa Catarina and the three municipalities in which the populations were sampled. B) Collection sites, different geographical shapes represent the different species, red shapes represent invasive non-native species, black shapes represent native species.

trees were selected for each population (Figure 1). A minimum number of three plants per population and six plants per species were selected. The selected plants were at least 10 meters apart in each population. The number of mother trees was low due to the difficulty in finding native individuals at the sites available for collection. Fruits were collected from the crown and from the ground. The seeds of the different plants and populations of the same species were mixed before being sowed. The seeds were processed for the pulp to be removed, disinfected with 70° alcohol, and dried at room temperature. Little developed seeds or seeds with granivory signs were discarded. In the case of native species, the rigid coat of the endocarp involving the seed was scarred in order to break the impermeable tegument (Carvalho 2008). The seeds of invasive non-native species were placed to germinate without prior treatment.

3. Experimental design

The seeds were sown in pots, with a volume of two liters (20cm height × 15 cm diameter), using a mixture of sand and fertilized soil (1:1). The pots were placed in the open, in natural conditions of temperature and rainfall, irrigated when the substrate dried, as needed. Two treatments were defined: 100% light intensity (T100) and 50% light intensity (T50). In T100, the seeds were exposed to solar radiation without protection; in T50, 50% shading was used to filter direct sunlight. One seed was sown per pot. A total of 160 seeds of *D. angustissimus* and *H. arboricola* were sown, with 80 seeds per treatment (T50 and T100). In the case of *H. actinophyllum*, 122 seeds were sown, 61 per treatment, and 200 seeds of *D. calvus*, with 100 seeds per treatment. Each pot was considered a replicate.

4. Data analysis

4.1. Germination

Seed germination was evaluated weekly for a period of 180 days. Hypocotyl height and diameter of the seedlings developed from the germinated seeds were measured every 30 days from the date of germination. The proportion of germinated seeds and index of velocity of germination (IVG) were calculated for each of the species in each of the treatments. The accumulated germination curve, which describes the time required for seeds in a given treatment to germinate over the course of the experiment (Aravind et al. 2019), was used to produce the germination curves. The index of velocity of germination (IVG) is the rate of germination in terms of the total number of seeds that germinate in a time interval (Aravind et al. 2019). We modelled the proportions of germinated seeds across species and treatments using a Generalized Linear Model (GLM) with a binomial distribution. In the model, the response variable was the number of successes (germinated seeds) and failures (non-germinated seeds) (Sühs et al., 2024). Similarly, the IVG was compared across species and treatments using a GLM with a Gamma distribution. For both comparisons, interactive models between species and treatment (species * treatment) were constructed, followed by contrast analyses. *p*-values for multiple comparisons were adjusted using the Holm-Bonferroni method (Holm 1979). Models were validated using graphic analysis of residuals.

4.2. Survival

Survival functions were estimated per species and per treatment using the Kaplan-Meyer method for censored data (Rich et al. 2010). As a result, new data were added to the curve as more seedlings died throughout the duration of the experiment (180 days). The comparison between species survival curves was made using a *Log-rank* test (Kaplan and Meier 1958). Seedling survival was evaluated for a period of 180 days after germination.

4.3. Growth

Relative growth rate based on plant height was calculated based on the seedling height values measured weekly for 180 days. After 180 days since germination each live seedling was removed from the plastic bag and the aerial part (shoot: hypocotyl, cotyledons, and leaves) was separated from the subterranean part (roots). The shoot and root were weighed separately for records of fresh mass. Leaves were detached and scanned for measurement using Image software (Rasband 1997) to generate leaf area data. Dry mass was obtained after the seedling parts were oven-dried at 60°C for 48 hours, then weighed. The root/shoot ratio was obtained from the dried material.

All analyses were conducted in R software (R Development Core Team 2014), using the "*survival*" and "*survminer*" packages (Therneau and Lumley 2013, Kassambara et al. 2017) for survival analysis, "*germinationmetrics*" (Aravind et al. 2019) to calculate index of velocity of germination, and "*emmeans*" and "*lmeans*" (Lenth and Lenth 2018) for pairwise comparisons.

Results

1. Germination

The total values of proportion of germinated seeds were higher for the invasive non-native species than for the native species. *Heptapleurum actinophyllum* germinated 37 of 122 (30%) seeds, while *H. arboricola* germinated 23 of 160 (15%). The native species *D. angustissimus* germinated 17 of 160 (10%) seeds, and *D. calvus*, 5 of 200 (2%) (Table 1). Multiple comparisons showed significant differences in the proportions of germinated seeds between the invasive non-native *H. actinophyllum* and the native *D. calvus* in T100, with the former displaying a higher proportion of germinated seeds (Table 1, Figure 3, Table 1 – Supplementary material).

2. Germination curve

Mean time for germination was shorter in treatment T50 for *H. arboricola* and *D. calvus* [24 (±5) and 27 (±0) days], while *H. actinophyllum* and *D. angustissimus* had higher mean values [65 (±37) and 77 (±19) days] (Figure 2). In treatment T100, *D. calvus* and *H. arboricola* had the lowest mean values for germination time [27 (±0) and 43(±39)], while *H. actinophyllum* and *D. angustissimus* had the highest mean values [45 (±17) and 169 (±56) days] (Supplementary material – Figure 1).

3. Index of velocity of germination (IVG)

Due to the low number of germinated seeds, *H. calvus* was excluded from the calculation of the mean and the comparison between the IVGs. The comparisons of means between species and treatments showed no differences for most species and treatments (Table 2). The results showed a difference between *D. angustissimus* and *H. arboricola* in the T50 treatment, where the former showed a higher average IVG (Table 2, Figure 4, Supplementary material – Table 2).

Table 1. Summary of germination metrics for four species under two light treatments (50% and 100% sunlight). The table displays the total number of seeds sown, the number of seeds that germinated, the average number of days to germinate with standard deviation (Days to germinate), the Index of Velocity of Germination (IVG – rate of germinated seeds per day) and lifetime (days) with standard deviation for each species and treatment. Check supplementary material (Tables 1 and 2) to verify specific contrasts made in the analyses.

Species	Treatment	Seeds sown	Germinated seeds	Days to germinate	IVG	Lifetime
D. angustissimus	T50	80	10	80 ± 26	0.02 ± 0.02	141 (±63.3)
	T100	80	7	147 ± 58	0.011 ± 0.003	137 (±41.9)
D. calvus	T50	100	3	28 ± NA	0.11 ± NA	150 (±51.9)
	T100	100	2	28 ± NA	0.071 ± NA	165 (±21.2)
H. actinophyllum	T50	61	23	79 ± 55	0.06 ± 0.04	165 (±32.4)
	T100	61	14	56 ± 21	0.082 ± 0.08	171 (±32)
H. arboricola	T50	80	13	29 ± 10	0.28 ± 0.31	120 (±60)
	T100	80	10	69 ± 54	0.083 ± 0.10	135 (±57)

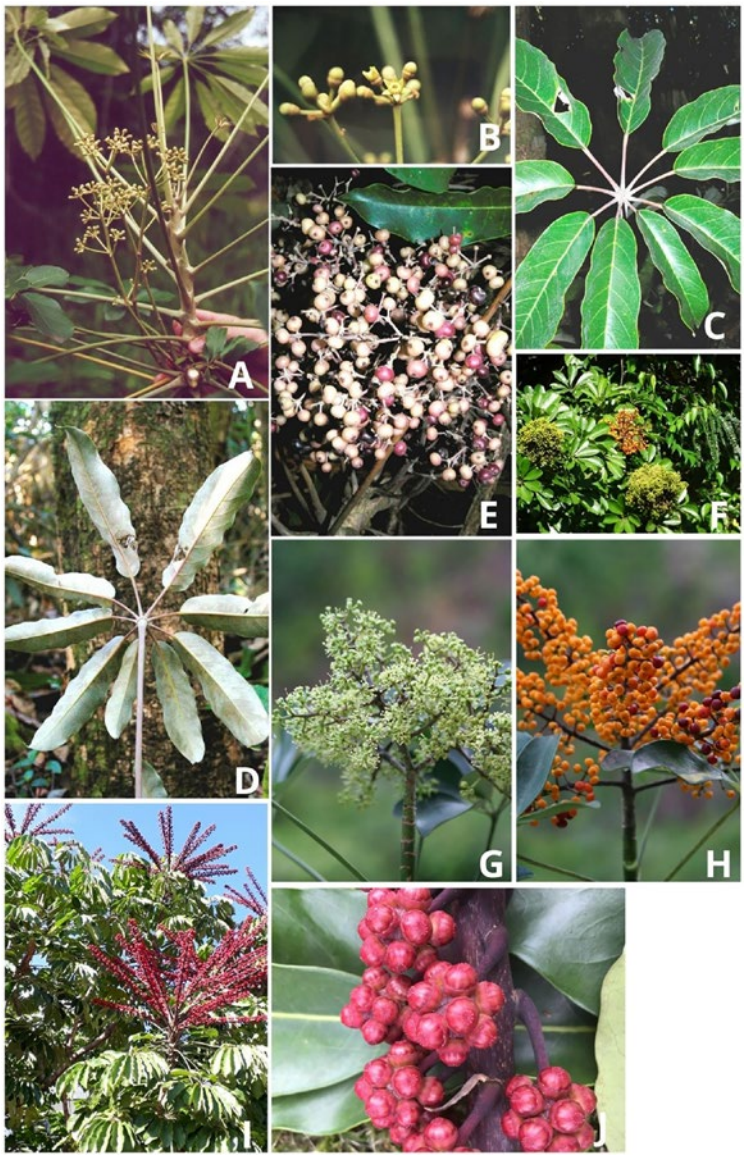

Figure 2. Species used to verify which biological attributes related to seed germination, survival and seedling growth differ between native and invasive non-native species of former *Schefflera* sensu lato (Araliaceae) in coastal regions of southern Brazil. **A**–**B**. *Didimopanax angustissimus*. **A**. Fertile branch. **B**. Inflorescence. **C**–**E**. *Didimopanax calvus*. **C**. Leaf, adaxial view. **D**. Leaf, abaxial view. **E**. Fruits. **F**–**H**. *Heptapleurum arboricola*. **F**. Habit. **G**. Inflorescence. **H**. Fruits. **I**–**J**. *Heptapleurum actinophyllum*. I. Inflorescence and leaves. **J**. Flower buds. Image credits to photographers Brisa Marciniak, Pedro Fiaschi and Sílvia Ziller.

Table 2. Mean germination velocity indices (IVG) of the native species *D. angustissimus* and the invasive non-native species *H. actinophyllum* and *H. arboricola* under two treatments: direct sunlight (T100) and 50% shade (T50). Different letters are not included in this table due to the specific contrasts made in the analyses. To verify the comparisons, check supplementary material - Table 2).

Species	Treatment	Mean	Std. Error	95% Confidence Interval	
				Lower Bound	Upper Bound
D. angustissimus	T50	40.3	13.53	12.19	68.48
	T100	87.3	35.86	12.69	161.86
H. actinophyllum	T50	16.2	5.02	5.71	26.59
	T100	12.2	5.02	1.77	22.64
H. arboricola	T50	3.6	2.09	-0.75	7.95
	T100	12.1	4.97	1.76	22.43

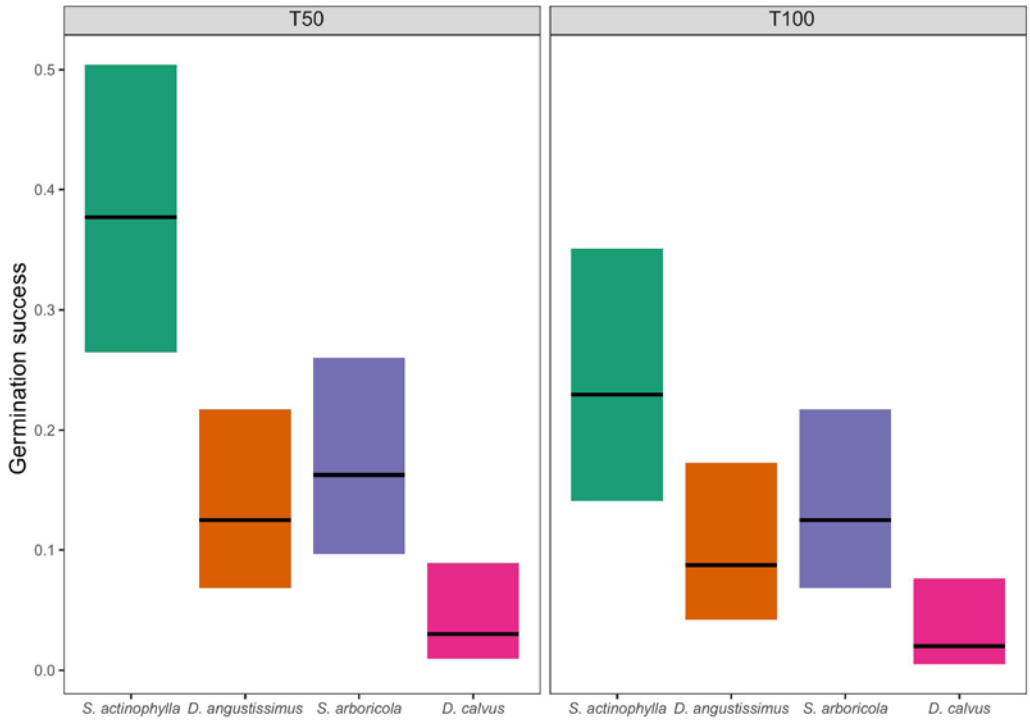

Figure 3. Model results for germination percentage. The Y-axix represents germination successes. The data was modeled using a binomial distribuition. The response variable is successes, with explanatory variables including the non-native invasive species *H. actinophyllum* an *H. arboricola*, as well as the native species *D. angustissimus* and *D. calvus*, across two treatments: direct sunlight (T100) and 50% protection from direct sunlight (T50).

4. Survival curve

Survival rates in terms of the proportion of seedlings that survived in treatment T50 (0.82 and 0.70, respectively) were higher for *H. actinophyllum* and *D. angustissimus*, and lower for *Didimopanax calvus* and *H. arboricola* (0.66 and 0.23, respectively). In treatment T100, *H. actinophyllum* had the highest survival rate (0.92), followed by *D. calvus* and *H. arboricola* with 0.50, and *D. angustissimus*, with the lowest rate (0.42). The curves obtained by the *Kaplan-Meier* estimator differed between the four species and between treatments ($X^2 = 19.5$, $df = 7$, *p-value* = 0.007; Figure 5).

The survival rate of *Heptapleurum actinophyllum* was the highest in both treatments at the end of the experiment; however, in treatment T50, it was lower than in treatment T100. On the other hand, the survival rate of *H. arboricola* was low in both treatments. The native species had better survival rates in T50 compared with treatment T100.

The survival rate of *Didimopanax angustissimus* was high during the first month of the experiment, but after 60 days it declined in both treatments. In the case of *D. calvus*, the survival rate declined after 90 days in treatment T50, and after 150 days in treatment T100. The survival rate of *Heptapleurum actinophyllum* was higher during the initial two months in treatment T100 and during the first three months in T50. The survival rate of *Heptapleurum arboricola* declined in the first month in both treatments, and continued to fall until the 150th day of the experiment.

The mean lifetime was longer in the T100 treatment for most species (*D. calvus*, *H. actinophyllum*, *H. arboricola*) (Table 1). Only the native *H. angustissimus* had a longer lifetime in T50 treatment (Table 1).

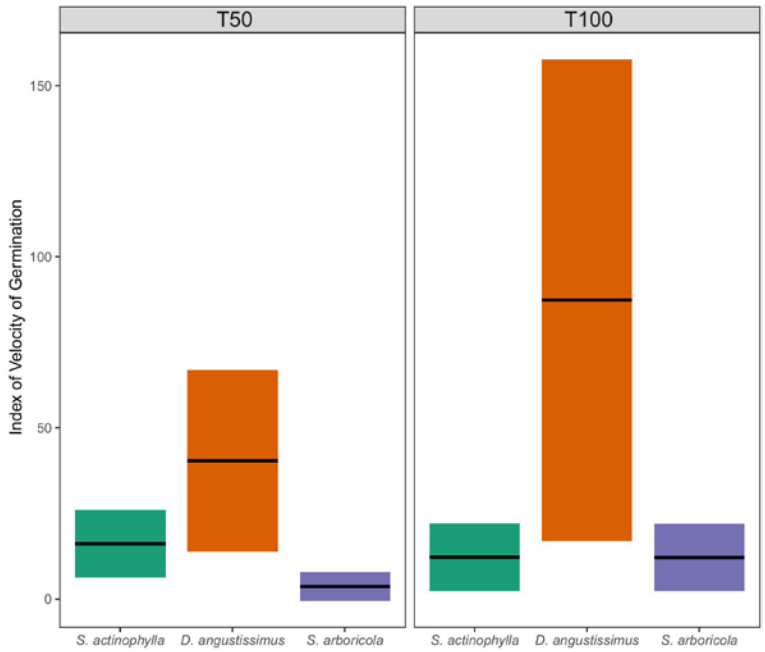

Figure 4. Model results for the Index of Velocity of Germination (IVG). The Y-axis represents IVG, which is the rate of germinated seeds per day. The data were modeled using a Gamma distribution with an inverse link function. The response variable is IVG, with explanatory variables including the non-native invasive species *H. actinophillum* and *H. arboricola* as well as the native species *D. angustissimus*, across two treatments: direct sunlight (T100) and 50% protection from direct sunlight (T50).

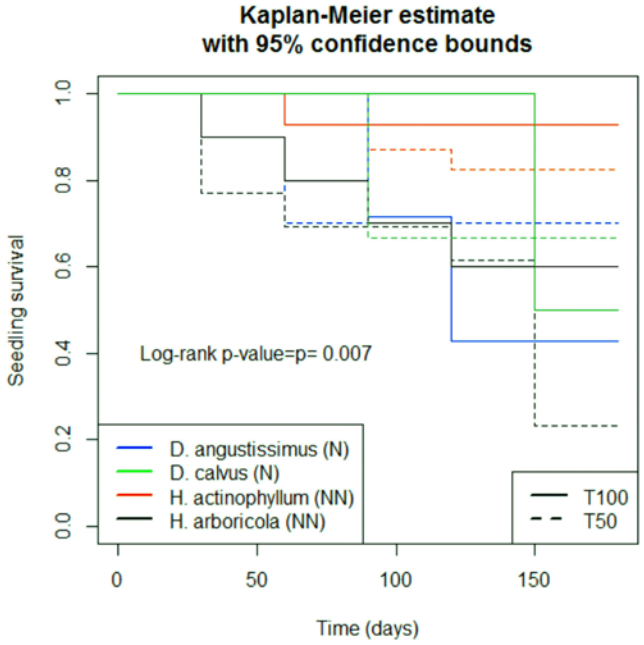

Figure 5. Survival curves of seedlings of the native species *D. angustissimus* and *D. calvus* and of the invasive non-native species *H. actinophyllum* and *H. arboricola* in two treatments: direct sunlight (T100) and 50% protection from direct sunlight (T50). NN: non-native, N: native.

4.1. Growth

Given the low number of germinated seeds of the native species (*D. angustissimum*: 14; *D. calvus*: 5), it was not feasible to compare the results on growth parameters. The results are available in the supplementary material – Table 5. The root/shoot ratio was higher for *Heptapleurum arboricola* than for *H. actinophyllum* (estimate = −0.18, SE = 0.09, *t* value = −1.97, $p = 0.055$). On the other hand, the leaf area means (estimate = −30.85, SE = 18.05, *t* value = −1.70, $p = 0.095$), total dry mass (estimate = −0.28, SE = 0.19, *t* value = −1.49, $p = 0.144$), and relative growth rate based on height (estimate = −0.0008, SE = 0.005, *t* value = 1.40, $p = 0.168$) did not differ between species. No difference was found in the means between treatments T100 and T50 per species (Supplementary material – Table 5).

Discussion

We observed differences in germination and survival parameters between native and invasive non-native species of former *Schefflera* s.l. The germination proportion was higher for the invasive non-native species *H. actinophyllum* compared to the native *D. calvus* under full sunlight. In the comparison between treatments for each species, *H. actinophyllum* exhibited a higher germination proportion under 50% light compared to full sunlight. The native *D. angustissimus* showed a higher germination velocity (mean IVG) than the invasive *H. arboricola* under 50% light. Non-native species generally had higher survival rates under 50% light, with *H. actinophyllum* showing the highest survival in both light conditions.

The germination velocity of the native *D. angustissimus* was higher than that of *H. arboricola* under 50% sunlight. This result contrasts with most comparative studies between invasive non-native and native species (e.g., Dickson et al. 2012, Wainwright et al. 2012, Kardol et al. 2013, Wainwright and Cleland 2013, Gioria and Pysek 2017). Rapid germination has often been considered a key characteristic that facilitates invasion by non-native species (Gioria and Pysek 2017,

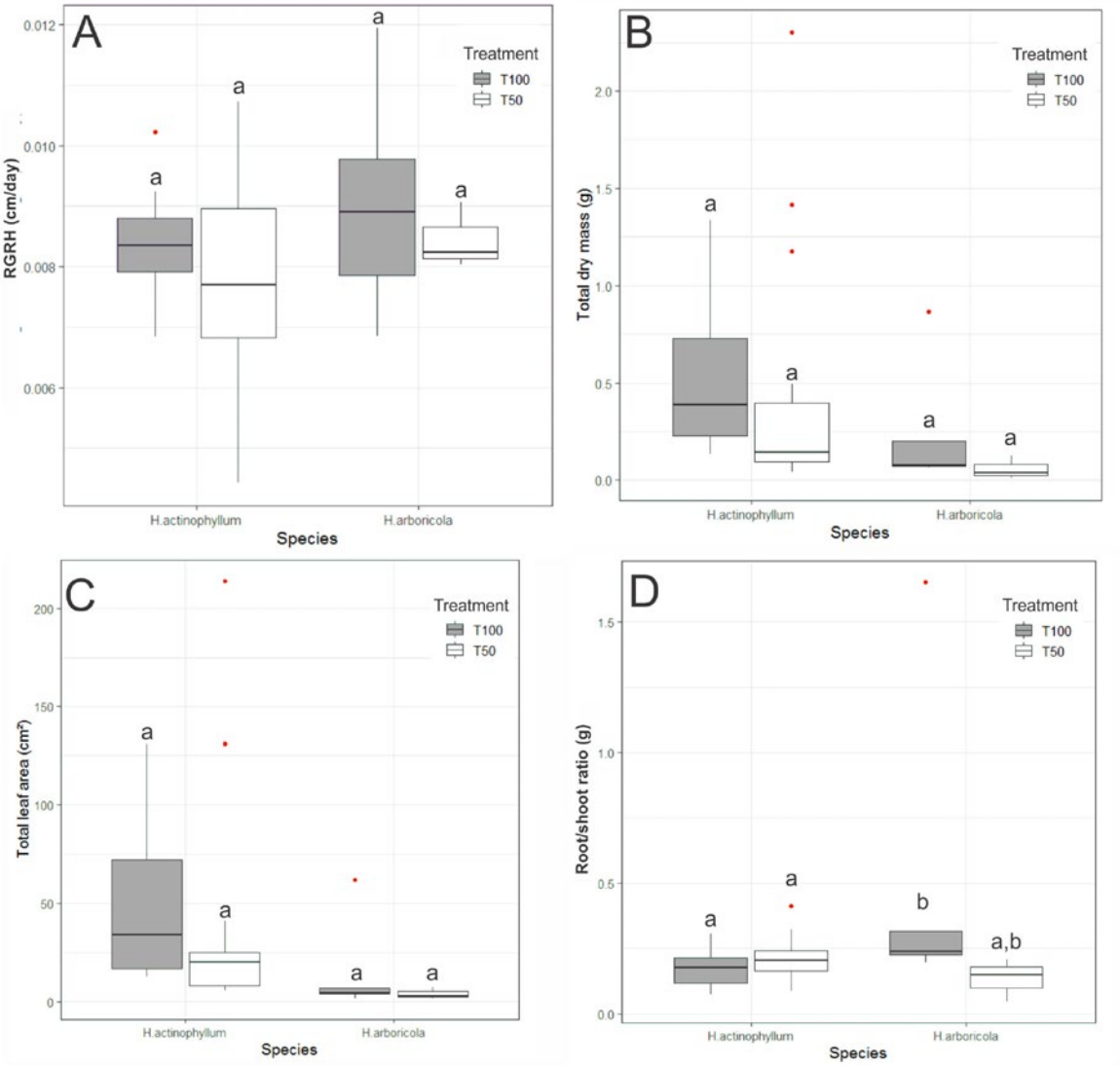

Figure 6. A) RGRH – Relative growth rate based on height; B) Total dry mass; C) Total leaf area; D) Root/shoot ratio. The central line in the box indicates the median, the higher and lower lines, the quartiles 25 and 75%, vertical lines on top and at the bottom of each boxplot represent maximum and minimum values in the database. *Outliers* were verified using the *"Dharma*" package in R software; only the red dot in graph D represents an outlier for *H. arboricola*; the other dots are data away from the mean, but not considered outliers by the *"Dharma"* package. There is no significant difference between groups that share the same letter.

Gioria et al. 2018). However, slower germination may be equally important as a strategy to avoid competition, promoting successful establishment (Gioria et al. 2018), as long as predation is low. Early germination can also present risks, as environmental conditions that trigger germination may not indicate the onset of suitable conditions for growth and development (Wainwright et al. 2012). For example, in regions with seasonal rainfall, seedlings may face water deficits or high temperatures after brief rainfall events that initially promote seed germination (Wainwright et al. 2012, Willis et al. 2014).

The germination proportion of the invasive non-native species *H. actinophyllum* was higher than that of the native *D. calvus* under full sunlight. Even though the seeds of the native species were scarified and seeds damaged by granivory were discarded, only 5% of the *D. calvus* seeds germinated. The low germination rate was a limiting factor encountered when working with these species. The low viability we proposed was based on previous studies that used native species of the same genus, such as Armelim (2005) for *D. angustissimus* (15% predictability). Additionally, this result supports findings from other studies that observed low germination rates for *D. angustissimus* (*e.g.* Armelin 2005, Anastácio 2010, Vilarinho et al. 2019), suggesting the possibility of physiological dormancy (Ohashi and Leão 2005). There were differences in germination proportion of *H. actinophyllum* between treatments, with higher rates observed under 50% light. This suggests greater shade tolerance, enabling the species to invade the forest undergrowth. Consequently, invasion by this species may pose a threat to tropical and subtropical forests with closed or seasonally closed canopies (Olson 2001). Established populations of *H. actinophyllum* in Brazil include degraded areas, undisturbed subtropical humid forest and coastal scrub (*restinga*) remnants (Instituto Hórus 2024). Additionally, both species of

Heptapleurum can grow as epiphytes, meaning their seeds can germinate and grow on tree trunks, rocks, or even on built structures, such as roofs and walls (Instituto Hórus 2024). This ability to grow on different types of substrates further contribute to the threat these species can pose to diverse environments.

The invasive non-native species *H. arboricola* and *H. actinophyllum* are widely cultivated in Brazil for ornamental purposes (Lorenzi et al. 2003). Cultivated species undergo selective breeding and often differ from wild species in ornamental traits and ecological attributes (Chrobock et al. 2011). Human-mediated selection for certain characteristics may thus contribute to observed differences between invasive non-native and native species, such enhanced germination potential (Chrobock et al. 2011). Studies comparing individuals from cultivated and wild populations of the same species have shown that seeds from cultivated plants germinate more quickly and in greater proportions than those from wild plants (Wilson and Mecca 2003, Chrobock et al. 2011). Therefore, targeted selection for traits like rapid and complete germination in cultivated plants may increase their potential to become invasive (Chrobock et al. 2011).

The root/shoot ratio results suggest that *H. arboricola* exhibits higher plasticity in response to varying light conditions, allocating more biomass to roots under higher light exposure and favoring shoot growth when light is limited. Such shifts in biomass allocation likely play a crucial role in seedling survival within shaded forest understories. Generally, adjustments in biomass allocation are characteristic of woody invasive species adapting to low-light environments within forests (Leicht-Young et al. 2007, Granata et al. 2020). Low light availability is a limiting factor for plant growth in forest ecosystems (Chazdon et al. 1996, Pattinson et al. 1998). Thus, the ability to develop mechanisms for efficient light capture is a significant determinant of the competitive ability of plants that can thrive in low-light conditions (Chazdon et al. 1996, Pattinson et al. 1998). Phenotypic plasticity enables plants to occupy a wide range of ecological niches, aiding the success of biological invasions, particularly during the establishment phase (Matesanz et al. 2010, Godoy et al. 2011). Our study highlights the potential of the non-native species examined, particularly *H. arboricola*, to invade forest borders, clearings, or the forest interior under closed canopies.

Conclusion

Differences in germination and survival were observed between invasive non-native and native species in the former *Schefflera* s.l.. The higher germination proportion of the invasive non-native species *H. actinophyllum*, compared to the native species, contributes to its initial establishment. The greater germination proportion under T50 for *H. actinophyllum* may indicate that the species is shade-tolerant. Our results suggest potential plasticity in *H. arboricola* for root/shoot biomass allocation under different light availability conditions. Both invasive non-native species are shade-tolerant, allowing them to germinate in the forest undergrowth. This trait may contribute to their establishment and invasion success in forests. Thus, both *H. actinophyllum* and *H. arboricola* should be considered a threat to closed canopy forests.

Supplementary Material

The following online material is available for this article:

Table S1 – Results of the comparison by pairs of germination proportions between treatments, per species.

Table S2 – Results of the comparison by pairs between indices of germination velocity (IVG) between treatments, per species.

Table S3 – Mean total life time (days) and standard deviation per species and per treatment; and percentage of seedlings that survived until the end of the experiment (180 days).

Table S4 – Comparisons between growth parameters means conducted by pairs between species by contrast.

Table S5 – Means and total standard deviation per species, and means and standard deviation per treatment and per species.

Figure S1 – Cumulative germination curves of the invasive non-native species seeds *H. actinophyllum* and *H. arboricola* and the native species *D. angustissimus* and D. calvus in two treatments: direct sunlight (T100) and 50% protection from direct sunlight (T50).

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Author Contributions

Amanda Angélica Carmes: delineated the study; located the species populations and collected seeds for the experiment; cared for the seedlings; performed the statistical analyses; wrote the text; contributed to revisions and discussions in the manuscript; gave final approval for publication.

Rafael Barbizan Sühs: performed the statistical analyses; wrote the text; contributed to revisions and discussions in the manuscript; gave final approval for publication.

Pedro Fiaschi: delineated the study; located the species populations and collected seeds for the experiment; wrote the text; contributed to revisions and discussions in the manuscript; gave final approval for publication.

Michele S. Dechoum: delineated the study; located the species populations and collected seeds for the experiment; wrote the text; contributed to revisions and discussions in the manuscript; gave final approval for publication.

Conflicts of Interest

The authors declare that they have no conflict of interest related to the publication of this manuscript.

Data Availability

Suporting data are available at <https://doi.org/10.48331/scielodata.AS5JTZ>.

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