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ORIGINAL PAPER

The danger of non-native gardens: risk of invasion by *Schefflera arboricola* associated with seed dispersal by birds

Brisa Marciniak · **Michele de Sá Dechoum** · **Tânia Tarabini Castellani**

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Abstract The success of invasion by non-native species can be influenced by positive interactions established in the area of introduction. For instance, seed dispersal by birds can increase seed rain, seed germination, and, as a consequence, the probability of establishment of new invasion *foci*. *Schefflera arboricola,* an ornamental shrub with fruits largely consumed by birds, is invasive in several countries. To our knowledge, this is the first research project on mechanisms that might explain the success of *S. arboricola* in areas where it is invasive. The main aim of this study was to assess the invasiveness of *S. arboricola* associated with seed dispersal by birds. Fruit availability and frugivory interactions with local birds were registered and the germination percentage of seeds not consumed by birds was compared to the germination of seeds collected from bird feces. Our results show that frugivory and seed dispersal by native birds increase the establishment of *S. arboricola.* In addition, intrinsic species traits such as extended flowering and fruiting, high percentage of seed germination, early germination due to frugivory, and ability to establish in different microhabitats facilitate invasion by *S. arboricola*. Given the intensive horticultural use of *S. arboricola* and seed dispersal interactions with generalist birds, there is an imminent risk of invasion in forest remnants close to wherever *S. arboricola* is cultivated. We recommend that adult plants of *S. arboricola* are eliminated from gardens and semi-natural areas close to protected areas as a prevention measure to avoid invasions and impacts on natural habitats.

Keywords Biological interaction · Frugivory · Invasive non-native plant · Management · Protected area · Seed dispersal · Seed germination

Introduction

The rate of species introduction is increasing worldwide (Seebens et al. 2017), which facilitates the establishment of ecological interactions between introduced and indigenous species (Richardson et al. 2000; Aslan et al. 2015). Such interactions may be positive for introduced species in the sense of helping them overcome biotic and abiotic barriers inherent to biological invasions (Traveset and Richardson 2011; Richardson and Pyšek 2012). Animal-dispersed

B. Marciniak (✉) · M. de Sá Dechoum · T. T. Castellani
Programa de pós-graduação em Ecologia, Universidade Federal de Santa Catarina, Campus Universitário s/n – Córrego Grande, Florianópolis, SC 88040-900, Brazil
e-mail: brisamarciniak@gmail.com

M. de Sá Dechoum · T. T. Castellani
Departamento de Ecologia e Zoologia, Universidade Federal de Santa Catarina, Campus Universitário, s/n, Córrego Grande, Florianópolis, SC 88040-900, Brazil

invasive non-native plants seem to have an advantage in the process of biological invasion compared to invasive plants with other dispersal syndromes (Buckley et al. 2006; Muñoz and Ackerman 2013; Traveset and Richardson 2014). Integration of non-native plants in invaded communities is facilitated because dispersal networks tend to be generalist (Morales et al. 2009). Besides, some traits of introduced plants attractive to resident frugivores also facilitate the establishment of new interactions. These traits include fleshy fruit, attractive fruiting displays (e.g. abundant fruit crop and attractive colors), energetically rich fruit and fruit production at different times than indigenous species (Richardson et al. 2000; Gosper et al. 2005; Kueffer et al. 2009).

When non-native species are attractive to frugivores, animals tend to reduce consumption of indigenous fruit, and foraging spots in the landscape are altered (Kueffer et al. 2009; Mokotjomela et al. 2013). In this sense, invasive non-native plants that produce fleshy fruits can interfere in interactions between indigenous plants and frugivores (Heleno et al. 2013), changing the structure of seed dispersal networks in biotic communities (Aizen et al. 2008) and the structure of interactions developed along the evolutionary scale (Traveset and Richardson 2006, 2014). Reduced consumption of indigenous fruit may lead to lower success rates in seed dispersal and recruitment of indigenous plants (Traveset et al. 2012) with consequential changes in species composition of the plant community and the associated indigenous fauna (Traveset and Richardson 2006, 2014).

Generalist birds are among the main dispersal agents of invasive non-native plants (Gosper et al. 2005; Richardson and Rejmánek 2011; Traveset and Richardson 2014). Different attributes of birds can affect the establishment of introduced species. The efficiency of propagule dispersal depends on the treatment seeds receive between entrance through the beak and passage through the gastrointestinal tract (scarification process), as well as on the habitat where seeds are defecated (Schupp et al. 2010; Jordaan et al. 2011). Seed dispersers usually affect plant germinability (Traveset 1998). Pulp removal performed by seed dispersers (Robertson et al. 2006) can anticipate seed germination and increase the percentage of germination of fleshy-fruited invasive alien plants (Jordaan et al. 2011; Amodeo et al. 2017). If a bird travels over long distances and/or passage through the gastrointestinal tract takes long, it is more likely that seeds are defecated farther away from the source, favoring the establishment of new invasion *foci* (Trakhtenbrot et al. 2005). Besides, passage through the gastrointestinal tract may increase germination percentage and favor species establishment by breaking seed dormancy (see Panetta and Mckee 1997; Amodeo et al. 2017; Dlamini et al. 2018; Vélez et al. 2018).

Intra-populational traits in non-native plants may be related to attraction for disperser birds and consequently influence removal rates and seed transport in the landscape (Foster 1990; Saracco et al. 2005; Blendinger et al. 2008). For example, individual fruit abundance was a relevant predictor of bird visitation rates to *Schefflera morototoni* fruits in Costa Rica (Saracco et al. 2005) and of bird dispersal of *Sapium sebiferum* seeds in the USA (Renne et al. 2000). Crop size and plant height were important predictors of fruit removal success and removal efficiency by birds in fruits of *Casearia corymbosa* in Mexico (Ortiz-Pulido et al. 2007). Interindividual variations in plant height, fruit size and sucrose content in *Henriettea succosa* were important predictors in the structure a plant-frugivore network in Brazil (Crestani et al. 2019). In addition, considering the perspective of prevention in biological invasions, individual variations may be useful to set control priorities for introduced species at the population level (Buckley et al. 2006). For example, systematic control can be applied with priority to individuals that potentially compete more strongly with indigenous species for seed dispersal agents (Farwig and Berens 2012).

Horticulture and ornamental use are the main pathways of introduction of invasive non-native plants (Hulme et al. 2008; Van Kleunen et al. 2018; Guo et al. 2019). The use of invasive species in gardens and public and private green areas increases the availability of propagule sources in the landscape, facilitating seed spread to the vicinity by frugivore birds that visit the plants (e.g. Silva et al. 2013). Spread may as well affect nearby protected areas (Foxcroft et al. 2011). Several frugivore bird species use forest habitats as well as open areas (e.g. with isolated trees and shrubs in grassland matrices, gardens and low vegetation) and deposit seeds as they move around (Pizo 2004, 2012). Therefore, the more sources of propagules in the landscape and the higher the consumption by birds, the higher the transportation of propagules and the likelihood of establishing new invasion *foci* (Moody and Mack 1988; Gosper et al. 2005; Amodeo and Zalba 2013). The landscape surrounding protected areas, often altered by different human uses, may be a source of propagules of invasive species (Dechoum et al. 2015a). Other landscape features such as streams and roads can also facilitate dispersal (Foxcroft et al. 2011).

Schefflera arboricola (Hayata) Merr (Araliaceae) is widely used across the globe as an ornamental plant (Chen et al. 2002). Dwarf schefflera, as it is popularly known, is indigenous to low altitude subtropical forests in Taiwan and China (Ohashi 1993; Wu et al. 2007a), where it grows along stream banks and is sometimes an epiphyte (Wu et al. 2007b). It is considered invasive in the United States (in Hawaii and Florida), the Fiji Islands, Singapore and Brazil (Santa Catarina 2012; Ziller and Dechoum 2013; Brazil National Invasive Alien Species Database 2018). Fruits are rich in lipids and known to be consumed by birds, which potentially spread the seeds to other areas (Starr et al. 2006; Lorenzi and Souza 2008; Romahn 2009; Silva 2015).

Despite common use of the species in many countries, ecological studies on the invasion ecology of *S. arboricola* do not exist or have not been found. This is therefore, to our knowledge, the first ecological study on invasion by *S. arboricola* including ecological aspects of interactions between the species and the receiving environment. The main goal of our study was to assess the invasive potential of *S. arboricola* in an area of Atlantic Forest based on aspects related to seed dispersal by birds. The following hypotheses were tested: (a) high individual fruit production by *S. arboricola* positively influences frugivory by birds and; (b) germination of *S. arboricola* seeds is increased by frugivory. The specific objectives were to: (a) assess the reproductive phenology and resource offer by *S. arboricola*; (b) describe frugivore interactions between *S. arboricola* and local birds; (c) assess individual attributes of *S. arboricola* associated with frugivory by birds; and (d) assess *S. arboricola* seed germination percentage with and without effects of frugivory. We expect this study to advance the knowledge on dispersal of fleshy-fruited invasive species, providing clear directions for the implementation of management strategies for these species.

Materials and methods

Study system

Schefflera arboricola is a semi-woody shrub that can grow up to 5 m in height (Ohashi 1993). The fruits are ovoid, approximately 5 mm long and 4 mm wide. The color varies from orange to purple. Fruits are grouped in infructescences growing on fruit stems located at the apex of reproductive branches (Lorenzi and Souza 2008; Romahn 2009). Fruits are consumed by birds (Starr et al. 2006), and seeds have been found in bird feces (Toledo 2018) and in seed rain (Begnini 2011). The seeds are orthodox and able to germinate on trees, rocks, or soil; seedlings can grow on the same substrates (Becwar et al. 1983; Foxcroft et al. 2008). Dwarf schefflera grows in full sunlight, half-shade or full shade (Gilman 1999).

Sampling was conducted in Atlantic Forest remnants adjacent to the gardens of the Plaza Caldas da Imperatriz Hotel (27°43′56.8″S, 48°48′36.5″W), located in the municipality of Santo Amaro da Imperatriz, state of Santa Catarina, Brazil (Fig. 1), between 188 and 244 meters of altitude. The hotel property is situated on the northern limit of the Serra do Tabuleiro State Park (STSP), a protected area that covers almost 85,000 hectares (FATMA 2009). The study site is located in the Serra do Mar Coastal Forests ecoregion, in the Tropical and Subtropical Moist Broadleaf Forests biome (Olson et al. 2001), part of the Atlantic Forest hotspot (Myers et al. 2000). The climate in the region is humid mesothermal (Cfa) according to the Koeppen classification (Cfa), characterized by the absence of a dry season and hot summers (Peel et al. 2007). The mean monthly temperature varies between 15 and 25 °C. Annual rainfall is 1600 mm, with highest rainfall in January and April (CIRAM/EPAGRI 1990–2000).

Schefflera arboricola plants present in the green areas of the Plaza Caldas da Imperatriz Hotel grow on different substrates, from tree crowns and rocks along the river to buildings and structures (personal observation). They are able to grow at different heights from the ground and under different light conditions, from full sunlight in gardens to shaded areas inside forest remnants. The *S. arboricola* plant closest to the STSP is approximately 400 meters away from the border.

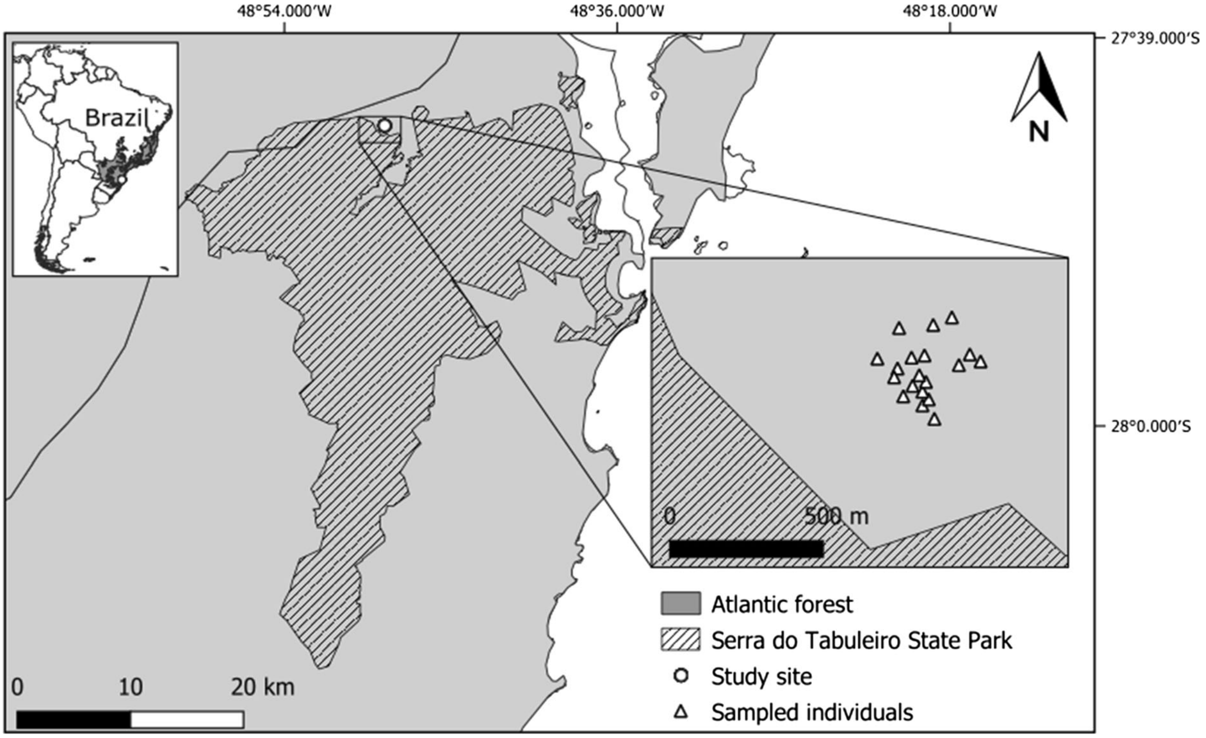

Fig. 1 Location of the study site (white circles) in southern Brazil, in the Atlantic Forest hotspot, and STSP (Serra do Tabuleiro State Park) (diagonal stripes). The detail shows the location of *Schefflera arboricola* plants studied (white triangles) and northern limit of the STSP

Data collection

A total of 19 adult *S. arboricola* plants were selected and georeferenced. A distance of 30 meters was established as minimum distance between plants. Each plant was visually analyzed to define the substrate (rock, tree or soil). The following measurements were taken for each individual plant: height (IH), corresponding to the maximum height of the aerial part of the plant in relation to the substrate; total height (TH), consisting of IH plus the height of the substrate in relation to the ground; and two measures of crown diameter (CD), equivalent to the width of the crown projection on the ground. Height (IH and TH) was measured by visual estimation, while crown diameter (CD) was measured using a 50 m measuring tape. Elliptical crown area (EA) was calculated based on the ellipsis of the crown area using the formula $\pi \times$ radius 1 $\times$ radius 2.

Reproductive phenology and resource offer

The phenological assessment of *S. arboricola* was carried out fortnightly between August, 2017, and August, 2018. The presence or absence of flowering or fruiting phenophases was observed each time on all branches of all the 19 plants selected. Flowering was marked by the occurrence of flowers in anthesis, and buds were generally found along with fully open flowers. Fruiting was observed on reproductive branches with immature fruit (green color) and/or mature (orange to purple). Whenever two phenophases were observed on the same branch, we considered the most frequent one.

The intensity of phenophases was assessed by adapting Fournier's intensity index (1974), which compares the number of branches with a certain phenophase to the total number of branches per plant. On each assessment day the plants were classified in five phenophase intensity classes: level 0 (absence of phenophases), level 1 (phenophase present on 1–25%

of branches), level 2 (phenophase present on 26–50% of branches), level 3 (phenophase present on 51–75% of branches) and level 4 (phenophase present on 76–100% of branches). The Fournier percent index of intensity (PII) was estimated fortnightly by the sum of individual values of intensity classes of all plants in each phenophase (Σ_{Idata}) divided by the maximum possible value (total number of plants multiplied by 4) according to the formula: PII = $(\Sigma_{\mathrm{Idata}}/4\ \mathrm{N}) \times 100$ (Fournier 1974; Galetti et al. 2003).

Circular histograms were developed with data from the periodic flowering and fruiting assessments in which 360° represent 365 days in the year and 22 days of phenological intensity assessments were converted and rescaled to circular data between 0° and 360°. The mean angle (*a*) (mean date), the respective circular standard deviation (CSD), the peak of the phenophase (modal angle) and the length of the mean vector (*r*) were calculated for each phenophase. The length of the mean vector (*r*) represents the concentration of data around the mean date, varying from zero (uniformly distributed throughout the year) to one (concentrated around the mean angle) (Morellato et al. 2010). A Rayleigh *Z* test of parametric uniformity was applied to determine the significance of the mean angle; if significant, some seasonality occurred and the intensity of the phenophase was concentrated around the mean angle (Morellato et al. 2010). These data were analyzed using the Circular package (Agostinelli and Lund 2017) in R environment, version 3.4.4 (R Core Team 2018).

An estimate of the quantity of fruits and seeds produced by *S. arboricola* plants was calculated based on nine fruiting branches collected from four adult plants in the population not used for frugivory observations. The branches were wrapped in fine cloth bags while the fruits were still immature, then the fruits were collected once matured. The total numbers of stems, infructescences and fruits were quantified. Thirty mature fruits were collected at random from each fruiting stem and the total number of seeds per fruit was counted. Total mean fruit production was estimated by calculating (mean number of fruiting branches/plant) × (mean number of stems/branch) × (mean number of infructescences/stem) × (mean number of fruits/infructescence). The result of this calculation was then multiplied by the mean number of seeds per fruit, resulting in the estimation of the total mean seed production per plant (Silva 2015). Dry weight, width, length and thickness of 30 seeds of *S. arboricola* from the fruit collection of the Ecology of Biological Invasions, Management and Conservation Lab at the Federal University of Santa Catarina, registered under the code ME100, were measured for the analysis of seed size. These seeds were collected in the exact same area of the current study by Begnini (2011) in a previous study.

Frugivory interactions with birds

Focal observations of plant crowns were made fortnightly for periods of 20 min (Jordano and Schupp 2000) with the aim of describing frugivory interactions of *S. arboricola* with local birds. The number of plants observed in each focal observation was different because only individuals with mature fruits were observed. The total number of plants observed per day varied between three and thirteen plants. These observations were made in the morning (between 6 and 11am), when birds were more active (Pizo and Galetti 2010). The order of observation on *S. arboricola* plants was altered on each visit so that each plant was observed at different times. The following parameters were considered: the species of visiting birds, the number of birds and the number of fruit intake by individual bird, as well as foraging behavior (Galetti et al. 2003). When a group was observed feeding, only the amount of fruits consumed by one bird was counted and the presence of other birds was registered. The bird species were visually identified in the field and verified according to the list published by the Brazilian Ornithological Records Committee (2014). Each bird species observed was classified in terms of feeding habits, body size and use of habitat, based on bibliographic references (Sick 1997; Begnini 2011; Sigrist 2014).

Linear Mixed Effects Models (LMM) using the nlme package in R environment, version 3.4.4 (R Core Team 2018), were built in order to verify whether a larger availability of *S. arboricola* fruits positively influences frugivory by birds (Pinheiro et al. 2018). The number of visits and the number of fruits consumed by birds during each visit were used as response variables. The explanatory variables used as fixed effects were: number of branches with fruits (BF) (counted in each visit), measurements of IH, TH and EA of each plant (measured in the beginning of study), and the interaction of all variables. We used the number of branches with fruits that we counted instead of the estimated number of fruits in the crown as response variable because we consider that data counted are more robust than data estimated. As a consequence, the number of fruiting branches was used as proxy of crop size. Time (individual sampling days) was considered a random effect and incorporated in the model as a co-variable due to temporal autocorrelation (repeated measurements). Explanatory variables were selected by excluding correlated variables and through automated model selection using the packages corrplot (Wei and Simko 2017) and MuMIn (Barton 2018), respectively, in R environment version 3.4.4 (R Core Team 2018). Models were selected by means of the Akaike information criterion (AIC). The most parsimonious model was the one with the lowest AIC value.

Seed germination

A germination test was performed using seeds consumed and not consumed by birds in order to evaluate whether frugivory benefited germination. The non-consumed seeds used in this experiment were collected directly from the crowns of *S. arboricola* plants. Seeds that had passed through the gastrointestinal tract of birds were collected from square seed traps measuring 0.54 × 0.54 m supported by four aluminum poles installed at 0.50 m from the ground. Eight traps were placed under the influence of the crown of 15 *S. arboricola* plants, totaling 120 seed traps in the study site. Four traps were set directly under the crown, and the other four at a distance of two meters beyond the limit of the crown projection of each plant. Seed traps were checked fortnightly for a year in order to collect bird feces with *S. arboricola* seeds. To isolate the effect of fruit ingestion (scarification process) the seeds in both conditions—passed through the gastrointestinal tract (condition with frugivory) and seeds reserved for control (condition without frugivory)—were washed with running water over a sieve and left to dry at air temperature.

A total of 436 seeds in conditions with and without frugivory were placed on vermiculite substrate in plastic trays measuring 28 × 33 × 6 cm. Each seed of the first treatment was paired with a seed of the second, totaling 218 seeds in each treatment. Each tray was split in half with a divider, and the same quantity of paired seeds were placed in each half on dates that varied with collection in the field. The pairs of seeds (subjected to frugivory and not subjected) were planted at the same time and received the same watering regime. Trays were checked every 2 days for 60 days and the number of germinated seeds was registered. Germination was characterized by protrusion of the radicle. All seeds used in this experiment were visually evaluated to make sure they were not damaged. The experiment was carried out in the greenhouse managed by the Center for Biological Sciences (CCB) of the Federal University of Santa Catarina (UFSC), in Florianopolis (SC, Brazil).

Germination data were analyzed using Generalized Linear Mixed-Effects Models (GLMM) with the package lme4 (Bates et al. 2015) in R environment, version 3.4.4 (R Core Team 2018). The response variables in each model were: germination velocity (number of days it took the seeds to germinate) using the Poisson distribution, and the proportion of seeds germinated in each treatment, which used a binomial distribution. Treatment type (with or without frugivory) was considered as fixed effect while pairs were considered as random effect in each model.

Results

Among the 19 adult *S. arboricola* plants observed in this study, nine used rocks as substrate (n = 9) and eight used trees (n = 8). Only two plants were rooted directly in the soil (n = 2). The mean CD of the19 plants observed was 7.28 m (SD = ± 2.28) and the mean crown area (ellipsis) was 40.25 m^2 (± 26.16). Mean IH, which corresponded to the height of the aerial part of the plants in relation to the substrate of fixation, was 6.23 m (± 2.11); mean TH, which considered the height of the substrate in relation to the ground, was 8.29 m (± 3.77).

Reproductive phenology and resource offer

Flowering and fruiting phenophases occurred during the whole year of observation of *S. arboricola* plants, but the highest intensity was seasonal. Seasonality can be verified both by visual analysis of the circular histograms of intensity (Fig. 2) and by intermediate *r* values and significant values in Rayleigh tests ($p < 0.001$). Three of the 19 plants did not undergo reproductive phenophases in the observation period.

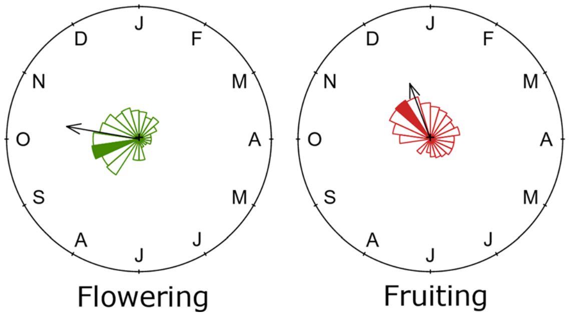

Fig. 2 Circular histogram of Fournier percent index of intensity for each *Schefflera arboricola* reproductive phenophase between August, 2017, and August, 2018 in green areas of the Plaza Caldas da Imperatriz Hotel, municipality of Santo Amaro da Imperatriz, Santa Catarina State, Brazil. Green bars represent flowering and red bars represent fruiting as well as the respective intensities on the dates of each fortnightly observation. The filled bars represent the peaks of each phenofase (date of highest intensity). The arrow points to the mean angle (*a*). Arrow length represents the value of *r*, which varies between 0 and 1, and shows the concentration of the phenophase around the mean angle (degree of seasonality)

Flowering was not observed only in one visit (May, 2018), occurring in the visits between August, 2017, and August, 2018 (Fig. 2). The flowering peak occurred at angle 252.49°, equivalent to the date of September 13, 2017, when the population reached maximum flowering intensity. The mean angle (*a*) for flowering was 279.92° (03 October, 2017), which corresponds to the date around which flowering was more concentrated. The length of the mean vector ($r = 0.55$) revealed that the concentration of intensity around the mean (*a*) was intermediate, therefore neither totally concentrated nor uniform throughout the year; but there was a moment in the year when the data were more grouped (*a*), showing a slight seasonal pattern between the end of winter and spring (Fig. 2, Rayleigh test: $p < 0.001$).

Fruiting did not occur in the population between August and September, 2017, but was observed in all other visits between October, 2017, and August, 2018.The peak of fruiting intensity occurred at 315.58°, equivalent to 16 November, 2017—the date when maximum fruiting intensity was observed. The mean angle (*a*) for fruiting was 339.64°, corresponding to 03 December, 2017, date around which fruit production was concentrated. The results for fruiting intensity and flowering intensity were similar. The length of the mean vector ($r = 0.44$) revealed that the concentration of intensity around the mean angle (*a*) was intermediate, tending to be distributed throughout the year; but there was a moment in the year when data were more grouped (*a*), showing a slight seasonal pattern in spring (Fig. 2, Rayleigh test: $p < 0.001$).

Each fruit contained 5.86 (SD = ± 0.19) seeds on average whereas each reproductive branch bore 456.11 (± 222.06) fruits. As a consequence, each branch had a mean of 2672.8 seeds. The means of seed measurements were 0.23 (± 0.01) cm in width, 0.36 (± 0.01) cm in length, 0.07 (± 0.02) cm in thickness, and 0.0034 g in dry mass. Maximum fruit production observed at the fruiting peak was 196 branches with fruits in a single individual. Conversely, individuals with the lowest fruit production had between one and six reproductive branches during the period of low fruiting. On average, *S. arboricola* plants sampled offered between 456.11 and 89,397.56 fruits during one reproductive season in the study area.

Frugivory interactions with birds

After 39 h of focal observations of *S. arboricola* crowns bearing fruit, 84 visits of birds feeding on fruit were registered. In 60 of these visits, we registered intake of 281 fruits by 14 bird species (Table 1). Thraupidae was the most representative bird family, with six species and 60.7% of visits (n = 51 visits), followed by Turdidae, with four species and 15.5% of visits (n = 13).

Among the species interacting with *S. arboricola*, Golden-chevroned Tanager (*Tangara ornata*) and Sayaca Tanager (*Tangara sayaca*) accounted for 48% of all interactions (n = 39). These species also consumed a larger number of fruits (197 fruits, 70.1% of total consumption). Sayaca Tanager (*T. sayaca*) stood out for accumulating 48% (n = 135) of total fruit consumption (n = 281), while Pale-breasted Thrush (*Turdus leucomelas*) consumed the largest quantity of fruits per visit (n = 10).

An evaluation of feeding habits showed that, among the 14 bird species observed, most were frugivores (eight species), followed by omnivores (five species) and insectivores (one species). As for habitat use, none of the bird species were exclusive to any of the habitats considered in this study: forests, forest borders, secondary forests (initial/intermediate stages) and gardens. All bird species observed were of small size, with total body length between 12 and 25 cm.

Table 1 Birds that interacted with *Schefflera arboricola* at the Plaza Caldas da Imperatriz Hotel, municipality of Santo Amaro da Imperatriz, Santa Catarina State, Brazil

Family	Species	Common name	S	F	H	NV	NC	I %
Fringillidae	*Euphonia violacea* (Linnaeus, 1758)	Violaceous Euphonia	12	FR	1,2,3	6	10	1,66
Thraupidae	*Tachyphonus coronatus* (Vieillot, 1822)	Ruby-crowned Tanager	18	FR	1,2,3	3	0	0
	Tangara cyanocephala (Statius Muller, 1776)	Red-necked Tanager	13,5	FR	1,2	5	7	1,4
	Tangara cyanoptera (Vieillot, 1817)	Azure-shouldered Tanager	18	FR	1,2,3	2	1	0,5
	Tangara ornata (Sparrman, 1789)	Golden-chevroned Tanager	18	FR	1,2	15	62	4,13
	Tangara palmarum (Wied, 1823)	Palm Tanager	18	FR	2,3	2	4	2
	Tangara sayaca (Linnaeus, 1766)	Sayaca Tanager	17	FR	1,2,3	24	135	5,62
Turdidae	*Turdus amaurochalinus* Cabanis, 1850	Creamy-bellied Thrush	22	ON	2,3	9	34	3,77
	Turdus flavipes Vieillot, 1818	Yellow-legged Thrush	20	ON	1,2,3	1	2	2
	Turdus leucomelas Vieillot, 1818	Pale-breasted Thrush	22	ON	2,3	1	10	10
	Turdus rufiventris Vieillot, 1818	Rufous-bellied Thrush	25	ON	2,3	2	0	0
Tyrannidae	*Elaenia* sp.	Elaenia	15	FR	1,2	11	11	1
	Pitangus sulphuratus (Linnaeus, 1766)	Great Kiskadee	22	ON	2,3	1	1	1
	Camptostoma obsoletum (Temminck, 1824)	Southern Beardless Tyrannulet	9	IN	2,3	2	4	2
					Total	84	281	

Habitat (H): 1- forests, 2 - forest edges, initial/intermediate successional stages, 3 - anthropic environments (gardens, parks and cities). Feeding behaviour (F): *FR* frugivores, *ON* omnivores; *IN* insectivores. *S* Body size (cm). *NV* number of visits. *NC* total number of fruits consumed by the species. *I %* percentage of fruit intake per visit. Nomenclature of species registered according to the list by the Brazilian Committee of Ornithological Records (2014). Classification of dietary habits, body size and habitats according to Sick (1997), Sigrist (2014) and Begnini (2011)

The best model explaining the number of visits by birds included resource offer (individual number of branches with fruit) and total height (Table 2). Resource offer was the variable that best explained the number of visits by birds in the reproductive period of *S. arboricola* ($t = 3.411$, $p < 0.001$). The model that best explained the number of fruits consumed by birds included interactions between resource offer (individual number of branches with fruits), total height and crown area. Resource offer and total height were the variables that best explained the the number of fruits consumed, being marginally significant ($t = -1.955$, $p = 0.05$) (Table 2).

Seed germination

In the germination test, 67.2% (n = 293) of the total number of seeds germinated (n = 436; 218 seeds per treatment). Of 218 seeds sowed in each treatment, 57.7% (n = 126) of the seeds germinated in the treatment with frugivory and 76.6% (n = 167) germinated in the treatment without frugivory. In the paired analysis between treatments, seeds that did not go through the gastrointestinal tract of birds germinated in larger numbers ($z = 5.25$, $p < 0.001$) (Fig. 3a), but seeds that passed through the gastrointestinal tract of birds germinated faster (17.19 days ± 0.32) than

Table 2 Results of the LMM on the number of bird visits to *Schefflera arboricola* plants and number of *Schefflera arboricola* fruits consumed by birds at the Plaza Caldas da Imperatriz Hotel, municipality of Santo Amaro da Imperatriz, Santa Catarina State, Brazil

Variables	t-value	*p* value
Number of visits		
BF	3.411	0.0009
TH	1.569	0.1426
Number of fruits consumed		
BF	− 1.828	0.07
TH	1.099	0.2974
EA	1.046	0.3201
BF * TH	1.955	0.0529
BF * EA	1.778	0.0779
TH * EA	− 1.075	0.3076
BF * TH * EA	− 1.767	0.0798

Number of branches with fruits (BF), total height in relation to substrate (TH) and elliptical crown area (EA)

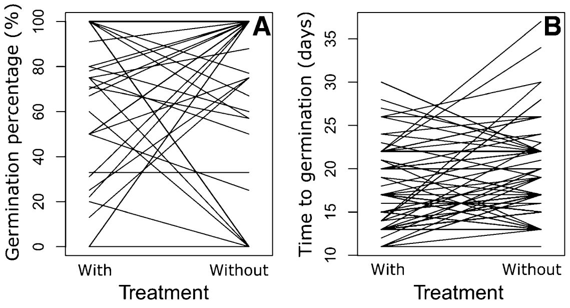

Fig. 3 Paired *S. arboricola* tests of germination percentage (**a**) and time to germination in days (**b**) with seeds that passed through the gastrointestinal tract of birds (Treatment "with" frugivory) and seeds that were not consumed by birds (Treatment "without" frugivory)

those which did not (18.81 days ± 0.33) (Fig. 3b). This trend was corroborated in the paired test between treatments, which proved that seeds that passed through the gastrointestinal tract of birds protruded the radicle in less time (z = 106.36; $p < 0.001$).

Discussion

Our first hypothesis considered that *S. arboricola* plants with a higher offer of fruits would positively influence frugivory by birds. This hypothesis was corroborated by the fact that the increase in resource offer represented by the number of branches with fruits in *S. arboricola* plants best explained the number of visits by birds. The second hypothesis, on the other hand, was partially corroborated, as *S. arboricola* was only partially benefited by frugivory, considering that fruit intake by birds increased germination velocity, which may in turn favor plant establishment. On the other hand, some seeds that passed through the gastrointestinal tract of birds may have been damaged, resulting in a lower percentage of germination compared with seeds that were not ingested. Even so, regardless of the gastrointestinal tract, the total germination percentage of *S. arboricola* was high.

Some traits that confirm the invasive potential of *S. arboricola* have been confirmed as a result of this study: plasticity, given the ability to establish on several types of substrate and along the vertical stratification of forests; high seed germination percentage; early germination; seed dispersal by birds; and flowering and fruiting extended throughout the year. The phenology and fruit production by *S. arboricola* observed in this study may facilitate the establishment of frugivory interactions with local birds. According to Westcott and Fletcher (2011), non-native species that bear fruit for long periods or at times when resources are scarce, offer abundant food resources and attractive fruiting displays are more used by birds. The results of a phenological study carried out in the same forest type of the present study observed low food production by indigenous species in the period between July and September (Mantovani et al. 2003). Our observations show that the extended phenology of *S. arboricola* covers this period of scarcity, which tends to favor the establishment of interactions with birds.

Jordaan et al. (2011) conducted a study on frugivory of invasive non-native species and found that pulp removal resulted in significantly higher germination rates and earlier germination. Our results may be partially related to pulp removal performed both manually and by birds in the germination tests (Jordaan et al. 2011). The significant differences found in the treatments show that while passage through the gastrointestinal tract of birds accelerates germination of *S arboricola* seeds, some seeds lose viability. Scarification may have different results for invasive non-native plants, for example, the scarification process enhances germination success of *Prunus mahaleb* (Amodeo et al. 2017). The variation in germination response can be explained by the different influence on pulp removal and scarification that each seed dispersal syndrome generates (Amodeo et al. 2017). In our study the feces founded may originate from a variety of frugivores that feed on *S. arboricola* fruits. Seed retention time in the digestive tract varies according to each seed disperser (Traveset 1998), which affects germination and helps explain the variation observed in seed germination. Even if germination percentage of *S. arboricola* seeds is reduced when passing through the gastrointestinal tract of birds, 57.7% of the seeds germinated earlier when compared to seeds not subjected to frugivory. When plants germinate faster, they may benefit from early access to environmental resources (e.g. space) and reduced competition in the initial phase of establishment, which contribute to increased invasive potential (Gioria et al. 2018). Early germination and high germination rates contribute to the high invasive potential of *S. arboricola*, possibly confering competitive advantage for the species in the process of establishment.

Frugivory interactions were mostly explained by resource offer, and partially by plant height in relation to the ground. Several studies have found that fruit crop positively influences frugivory events (Navarro et al. 2018) and the number of fruits removed (Ortiz-Pulido et al. 2007; Pizo and Almeida-Neto 2009). This is related to better foraging opportunities for frugivorous birds through the provision of a larger amount of food (Saracco et al. 2004). Conversely, different results have been found for the relationship between plant height and fruit removal. Whereas plant height was positively associated with fruit removal efficiency by birds for *Casearia corymbosa* in its native range in Tropical dry forest fragments in Mexico (Ortiz-Pulido et al. 2007), it was not an important predictor for bird frugivory events for *Cecropia pachystachya* in its native range in Atlantic forest remnants (Navarro et al. 2018). Plant height is related to different forest strata (canopy, midstory, understory), and can be related to different frugivores that are able to feed on different vertical strata (Schleuning et al. 2011). In our study, the fixation of *S. arboricola* on varied vertical strata created opportunities for interaction with bird species that use different strata of the forest as habitat. Our results reveal that both forest stratification and resource offer of *S. arboricola* plants influence the choice of birds regarding which plants to visit.

As for the number of fruits consumed, total plant height (TH) was marginally significant, which probably means that non-tested traits were also relevant to determine this interaction. For example, consumption may be influenced by the existence of other food sources in the surroundings (Carlo 2005), as noted by Saracco et al. (2005) on fruit intake of *Schefflera morototoni*. This specificity of the environment can lead to spatial autocorrelation based on the similarity between spatially close individuals and consequently, similar responses of the response variables (Legendre 1993). In addition, individuals sampled at the edges of gardens can be more apt to receive frugivore visits than individuals inside the forest (Menke et al. 2012). Or still, the existence of competitive interactions between bird species may have influenced visit—agonistic interactions were observed between *T. sayaca* and *T. ornata* at a time of low resource offer (only one reproductive branch), but no such behavior was observed when resource offer was high (personal observation).

Fruits in the genus *Schefflera* attract generalist frugivores (Snow 1981). All bird species observed feeding on *S. arboricola* fruits are potential seed dispersers of the invasive species, especially Sayaca Tanager (*Tangara sayaca*), the species of more intense interaction with *S. arboricola* fruits, highest number of visits and of fruit intake, and Pale-breasted Thrush (*Turdus leucomelas*), which consumed the highest percentage of fruits per visit (Table 1). Thraupidae and Turdidae were the bird families with more species visiting fruits of *S. arboricola*, the majority of which in the family Thraupidae (61.7%). These same families often appear among those which interact more intensely with plants in frugivory and seed dispersal studies in the Atlantic Forest, and are therefore considered good seed dispersers of ornithocoric species (Pizo 2004; Guix 2007; Alves 2008; Athiê and Dias 2012; Ikuta and Martins 2013). Birds in the family Thraupidae predominantly use visual orientation for feeding (Sick 1997), preferring fruits of red to purple colors (Wheelwright and Janson 1985). Besides, they are considered generalist frugivores, feeding on a large variety of fruit, according to availability, and usually feeding on small fruit with small seeds (Sick 1997). This corroborates the results obtained in this study, as *S. arboricola* produces small reddish-purple fruit with small seeds (< 15 mm width, see Gosper and Vivian-Smith 2010).

Intake of *S. arboricola* fruits by *T. sayaca* and *T. leucomelas* was also observed by Toledo (2018), who found *S. arboricola* seeds in the feces of these species. This shows that these birds function as *S. arboricola* seed dispersers (Toledo 2018). As for the efficiency of dispersal, quantitative traits such as high visitation rate and fruit removal, as well as qualitative traits, such as handling and seed digestion, were observed for *T. sayaca*. Despite being a chewing bird, the behavior of chewing on fruit is not always observed, as birds were sometimes seen swallowing whole fruits. This behavior was also noted in a study by Casetta et al. (2002), who considered the species an efficient seed disperser. *Tangara sayaca* has also been shown to be an important seed disperser of other non-native species, such as guava (*Psidium guajava*) (Silva et al. 2013) and cherry tree (*Muntingia calabura*) (Figueiredo et al. 2008). These factors imply that this species is potentially the most effective disperser of *S. arboricola* seeds. The introduction or use of *S. arboricola* in the native range of *T. sayaca*, therefore, increases the potential of biological invasion by this non-native plant.

An assessment of the habitats where *S. arboricola* seeds were dropped by birds showed that the species established on various types of substrate and that the movement of birds in the landscape facilitates the spread of seeds between habitats where germination may be favored. Most birds observed feeding on *S. arboricola* fruits occupy different habitats (Table 1). *Tangara sayaca* and *T. leucomelas* are especially recognized for using the most varied habitat types, including small forest fragments, hedges, isolated trees and pastures (e.g. Pizo 2004). These species are considered important for moving seeds around (Pizo 2012). Birds of the genus *Tangara* are also capable of flying long gap distances, crossing fragments up to 425 meters away (personal communication). The probability of a *S. arboricola* seed to be dropped on a favorable substrate and subsequently establish a nascent invasion *focus* is therefore increased.

Conclusions

Identifying the factors that contribute to the spread of invasive species is a relevant step towards improving the management of biological invasions (Caplat et al. 2012). Our study showed that the reproductive biology of *S. arboricola* and mutualistic interactions with indigenous birds which act as seed dispersers can largely explain invasive ability and offer valuable information for management. Control actions focused on reducing the amount of fruit available are necessary to reduce the number of seeds spread by birds (Amodeo and Zalba 2015). Considering the individual variations in *S. arboricola* assessed in this study, we recommend the control of reproductive adults with more intense fruit production as a priority (e.g. reproductive branches). These measures can help reduce the arrival of propagules in non-invaded areas (Dechoum et al. 2015b). Preventing invasion by *S. arboricola* in protected areas requires the control of plants established inside these areas as well as in the surroundings (buffer zones) (Foxcroft et al. 2011). Early detection and rapid response plans for the eradication of new invasion *foci* are essential to prevent reinvasion after initial management (Amodeo and Zalba 2015). Considerable efforts must be invested to increase public awareness on the impacts of invasive non-native species used in gardens, especially of people in the surroundings of protected areas (Foxcroft et al. 2008). Local communities should be involved in the planning and implementation of management strategies (Potgieter et al. 2019).

On a regional scale, management actions should be implemented to prevent the use and spread of *S. arboricola*. To prohibit sales and planting of the species would be the first step as a precautionary measure. We recommend promoting the replacement of *S. arboricola* by indigenous plants with similar functional traits (Funk et al. 2008) that also provide food to resident frugivores in order to reduce the risk of invasion by *S. arboricola* in protected areas. Some examples of native plants that could be regionally used to replace *S. arboricola* are: *Eugenia uniflora* (Myrtaceae), *Schinus terebinthifolius* (Anacardiaceae), *Allophylus edulis* (Sapindaceae) and native species of the genus *Schefflera* (e.g. *S. morototoni* and *S. calva*) (Araliaceae). This paper provides information for decision-making on biological invasions by *S. arboricola* as well as useful recommendations for other invasive plants that produce fleshy fruits and invade subtropical forests. Furthermore, it stresses the relevance of considering ecological aspects in studies on biological invasions, such as interactions between non-native species and resident species in the receiving environment, as these may be useful for the development of prevention, eradication or control plans in protected areas.

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