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Understanding willow invasion in subtropical highlands

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Abstract Willows invade many riparian environments around the world. Understanding the environmental factors that affect the establishment of non-native invasive plants, as well as characterizing population structure and stages of invasion, are crucial steps to define priority areas for monitoring and management. In this study, we characterized the population structure of the hybrid invasive tree *Salix*×*rubens*, determined the stage of the invasion process, and identified relevant factors for the establishment of regenerating plants in a subtropical riparian system in southern Brazil. We assessed population structure by measuring stem perimeter and height of plants sampled along river banks and riverbeds along several rivers, and measured environmental variables that may explain abundance patterns of regenerants. We showed that the majority of regenerants developed in riverbeds. The species seems to be transitioning between the establishment and dispersal phases of the invasion process. The abundance of regenerants was affected mainly by the abundance of nearby *S.*×*rubens* adults. Abundance of regenerants was negatively influenced by canopy openness, an unexpected result since *S.*×*rubens* is considered light-demanding. Our study provides insights for management strategies of *S.*×*rubens*, which must focus on searching sites along rivers where adult trees are present.

Resumen Los sauces invaden numerosos ambientes riparios alrededor del mundo. Comprender los factores ambientales que afectan el establecimiento de plantas exóticas invasoras, así como caracterizar la estructura poblacional y las etapas del proceso de invasión, son pasos cruciales para definir áreas prioritarias para su monitoreo y manejo. En este estudio caracterizamos la estructura poblacional del árbol híbrido invasor *Salix*×*rubens*, determinamos la etapa del proceso de invasión e identificamos factores relevantes para el establecimiento de renovales en un sistema ripario subtropical en el sur de Brasil. Evaluamos la estructura poblacional midiendo el perímetro del tallo y la altura de los individuos localizados en las riberas y cauces de varios ríos, y medimos las variables ambientales que pueden explicar los patrones de abundancia en la regeneración. Demostramos que la mayoría de los renovales estaban en los cauces de ríos. La especie estudiada parece encontrarse en la transición entre las

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fases de establecimiento y dispersión en el proceso de invasión. La abundancia de los renovales fue afectada principalmente por la abundancia de los adultos cercanos de *S.*×*rubens*. La abundancia de los renovales fue afectada negativamente por la abertura del dosel, un resultado inesperado debido a que *S.*×*rubens* es luz-dependiente. Nuestro estudio aporta perspectivas para estrategias de manejo de *S.*×*rubens*, las cuales deben centrarse en la búsqueda de sitios cercanos a ríos donde árboles adultos de *S.*×*rubens* están presentes.

Keywords Establishment · Invasion process · Population structure · Regeneration

Palabrasclaves Establecimiento · Estructura poblacional · Proceso de invasión · Regeneración

Introduction

Understanding which traits contribute to certain plants being more invasive than others (i.e., invasiveness) is a relevant goal in the study of biological invasions. However, invasion potential is not equal among all populations of invasive plants and depends on the site of introduction (Rejmánek et al. 2013), among other factors. After introduction, a species must overcome at least two barriers to become invasive (Blackburn et al. 2011; Richardson et al. 2000). The first is the survival and reproduction barrier, overcome when a species establishes a population—this phase of the invasion process is named establishment; subsequently, the dispersal barrier is overcome when the species establishes new populations away from the introduction site—this is the dispersal or dissemination phase of the invasion process. In addition, the definition of adequate management interventions will vary according to the stages of the invasion process. In most of the cases, eradication is feasible only when the invader has not passed the dispersal phase; after that, long-term control programs must be implemented to reduce abundance and/or contain the invader distribution, potentially reducing negative environmental impacts. Thus, to understand which biotic and abiotic factors limit or promote the establishment and dispersal of new plants and populations is critical for determining whether and where a plant species may become invasive (McAlpine and Jesson 2008), as well as for providing better guidance for management strategies.

Riparian environments are highly susceptible to biological invasions since they serve as ecological corridors for many species and act as vectors for propagules that are deposited along the banks of watercourses (Renöfält et al. 2005; Richardson et al. 2007). These environments cover the zone from the watercourse margin to the extent where community structure is affected by flooding (Naiman and Décamps 1997). Riparian environments provide several ecosystem services, such as food provision, regulation of water temperature, erosion control, sediment filtering, and nutrient control (Hood and Naiman 2000). Biological invasions in riparian environments can lead to direct physical, hydrological and biological impacts (Tickner et al. 2001; Richardson et al. 2007; Gallardo et al. 2016), affecting the human economy and human wellbeing (Speziale et al. 2012). For instance, invasive willows (*Salix* spp.) can increase the sediment load, reduce water flow capacity, alter flooding regimes and shading conditions, decrease litter decomposition and displace native species (Cremer 2003; Greenwood et al. 2004; Holland-Clift and Davies 2007; Budde et al. 2011). Thus, the effective management of biological invasions in riparian environments is crucial for conserving their ecological integrity and sustainable ecosystem functions.

In southern Brazil, species in the genus *Salix* have been cultivated for wicker production particularly in riparian ecosystems at high altitudes (Sühs et al. 2020a). *Salix*×*rubens* is most commonly cultivated in the region. It is recognized as invasive in riparian areas in the state of Colorado, USA (Shafroth et al. 1994), in the Argentine Patagonia (Budde et al. 2011; Thomas et al. 2015), in Australia (Greenwood et al. 2004), and in southern Brazil (Sühs et al. 2020a). Vegetative propagation through water-dispersed branches is a fundamental pathway for dispersal (Thomas et al. 2012). Additionally, sediment and hydrological characteristics can also affect the establishment and distribution of pioneer plants in riparian areas, including *Salix* species (Francis et al. 2006; Osterkamp and Hupp 2010; Mosner et al. 2011). Young plants of invasive *Salix* are commonly found in higher densities near river channels in areas more susceptible to flood and drought regimes (Francis et al. 2006; Gehrig 2010; Mosner et al. 2011). The presence of adults, high incidence of light, and low

competition for space (Newsholme 1992; Sher et al. 2002; Moggridge and Gurnell 2009) are other factors positively correlated with the establishment and growth of *Salix* plants. Since dispersal mainly occurs via rivers, obstacles and low-flow pockets may play an important role in retaining propagules and facilitating establishment.

Understanding the environmental factors that affect the establishment of non-native invasive plants, as well as characterizing population structure and stages of the invasion process, are crucial steps to define priority areas for monitoring and management. Additionally, these steps may also provide guidance for the implementation of protocols for commercial cultivation, helping to prevent the dispersal of invasive species through river corridors. In this context, our objectives were to characterize the population structure of the hybrid invasive tree *Salix*×*rubens*, determine the stage of the invasion process, and identify relevant factors for the establishment of regenerating plants in a subtropical riparian system in southern Brazil. Considering that the species primarily disperses through water, we expected the abundance of regenerants to be higher in shallow, slow current waters, on sites with high canopy openness and presence of adults. Moreover, we expected sites with flatter terrain and low cover of herbaceous vegetation and litter to also favor the abundance of regenerants.

Materials and methods

Study system

Our study was carried out in the São Joaquim National Park (SJNP—latitude: 28.19° S, longitude: 49.53° W), a protected area in southern Brazil. The climate in this area is humid mesothermal without a defined dry season and cool summers (Cfb type, Köppen-Geiger climate classification—Kottek et al. 2006). The landscape is shaped by mosaics of Araucaria forests and high altitude grasslands (Sühs et al. 2020b). Several water sources are present in the region, forming contributors of important rivers such as the Pelotas River and the Canoas River, the main tributaries of the Uruguay River.

The genus *Salix* has a cosmopolitan distribution, except for the absence of native species in Australasia (Gehrig 2010). *Salix humboldtiana* Willd. is the only species in the genus native in southern Brazil (Marquete et al. 2015). The species mainly cultivated in the region is *Salix*×*rubens* (Schrank), a hybrid of *Salix alba* and *Salix fragilis*, introduced in southern Brazil in the 1930s (Wagner et al. 2009). In Australia, this species is listed as a "Weed of National Significance" for being invasive in riparian environments (Adair et al. 2006). *Salix* species are dioecious shrubs or trees that produce lightweight seeds dispersed by water or wind (Moggridge and Gurnell 2009). However, vegetative reproduction is reported as the main dispersal and establishment means for *S.*×*rubens* (Shafroth et al. 1994; Cremer 2003; Budde et al. 2011; Thomas et al. 2012). Branches of *S. fragilis* hybrids can easily break off and flow downstream during flood events and windstorms; as a consequence, reproduction via vegetative propagation has been commonly registered (Beismann et al. 2000; Cremer 2003). These vegetative regenerants generally have higher survival rates and tolerate a wider range of environmental conditions when compared to seedlings developed from sexual reproduction (Moggridge and Gurnell 2009; Asaeda et al. 2011), accelerating biological invasion processes (Budde et al. 2011). Also, it is unlikely that the regenerants are suckers since most willows do not sprout shoots from roots (Cremer 2003). The likely source of the willow presence within SJNP appears to be associated with abandoned small-scale cultivation areas near former residential houses.

Data collection

Thirteen transects of 200 m each were established in parallel to river watercourses in the São Joaquim National Park (SJNP). Before establishing the transects, we conducted an active search to find adult plants in sites adjacent to watercourses. We placed the center of each transect at the location of the tallest *S.*×*rubens* adult or on a cluster with the highest number of adults. Each transect covered 100 m upstream and 100 m downstream from the center, and was four meters wide in only one side of the river bank. Since plants of *S.*×*rubens* can grow in the water, we looked for these invasive plants in the riverbed up to a maximum distance of five meters, depending on the river width. Watercourses width ranged from 1.15 m to 16.5 m. Transects were at least 250 m distant from each other (Supplementary files—Fig. 1).

We conducted an active search for these invasive plants along the transect, including the riverbed. We only recorded plants rooted at the time of sampling, measuring stem perimeter at ground level (PGL) and height of each sampled plant. Additionally, we recorded the position of sampled plants in relation to the stream (in the riverbed or on the river bank). The data were collected in April, 2021.

The characterization of environmental variables was performed in every 50 m section along the transect, only in the river bank. The abundance of *S.*×*rubens* adults and juveniles in each 50 m section was recorded. The environmental variables evaluated, related to the river were: current velocity, width, and depth. For ground cover, the proportions of rock, litter, herbaceous vegetation, and the percentage of bare soil were estimated in a 1 m^2 quadrat. Slope was calculated at the center of each quadrat. Canopy openness refers to the percentage of light that passes through the canopy to the ground, and was measured from photographs directed at the forest canopy and taken at 15 cm above the ground at the center of each quadrat. Photographs were converted to black and white, the number of white pixels in each photograph was computed and the sum considered as canopy opening. A summary table with the computed statistics for explanatory and response variables can be found in the supplementary material (supplementary files, Table 1).

Data analysis

We used stem perimeter at ground level (PGL) and height to describe the population structure of *Salix*×*rubens* and classify the sampled plants as regenerants or adults. Based on field observations, we defined regenerants as plants with PGL less than or equal to 10 cm. To assess the effect of environmental factors on the establishment of regenerants, we built generalized linear mixed-effects models (GLMM) using regenerant abundance as the response variable and the transect as a random effect variable. Since the sampled area of the riverbed varied between transects due to the variable width of rivers, we incorporated the sampled area as an offset term in the models (in logarithm form, to match the distribution of the chosen family). We used the negative binomial distribution family as it fitted the data better. The variance inflation factor (VIF) was used to remove collinear variables, whenever VIF > 3 (Zuur et al. 2009). With this procedure, the variables proportion of ground cover by herbaceous vegetation and river width were removed due to high collinearity. The variable percentage of bare soil was not included in the models due to a high incidence of zero values. The models were built considering the following fixed-effect variables: river depth, river current velocity, proportion of ground cover by litter and rocks, slope, canopy openness, and abundance of *Salix*×*rubens* adults. Since a high density of *S.*×*rubens* adults can negatively affect regenerants (due to a reduction on light availability and/or resource competition), we included the quadratic term of the adult abundance in the models. Additionally, we built one model with an interaction term between abundance of adults and canopy openness to access whether adult abundance could interfere with light availability.

Fixed-effect variables were classified into four groups (following (Ceolin and Giehl 2017): river-related variables (river depth and current velocity), ground cover and topography variables (proportion of litter, rocks, and slope), canopy-related variables (canopy openness), and dispersal-related variables (abundance of adults and its quadratic term). We built seventeen models, including one model with all four groups of variables, alternative models with a single group of variables, models with the joint action of two and three groups, one model with the interaction of adults and canopy openness, and a null model (intercept-only). Model selection was based on the Akaike Information Criterion corrected for small samples (AICc), and validation was performed through residue validation (Zuur et al. 2009). The performance of the selected model was evaluated using marginal pseudo-R^2 (log-normal approximation), which refers to the variance explained by fixed-effect variables. All analyses were conducted using the R software (R Core Team 2020), with the glmmTMB package (Magnusson et al. 2020) for GLMM models, MuMIn (Barton 2009) for accessing model performance, DHARMa (Hartig 2016) for model validation, and visreg (Breheny and Burchett 2017) to visualize the effects of the model selected.

Results

Population structure of *Salix*×*rubens*

A total of 203 plants of *S.*×*rubens* were sampled. The stem perimeter of the majority varied between 0 and 30 cm (Fig. 1A), and height between 0 and 100 cm (Fig. 1B). Lower perimeter and height classes generated the highest density values (Fig. 1 A and B). Regenerants (PGL less than or equal to 10 cm) accounted for 104 plants (51%), none of which exceeded two meters in height (Fig. 2). Regenerants were mainly present in the riverbed (63%), whereas adults were mainly on the river bank (87%) (Fig. 2).

Factors influencing the establishment of *Salix*×*rubens* regenerants

Among all 17 models built to assess the influence of environmental factors on regenerant establishment (Table 1), the most parsimonious model (with the lowest AICc value) contained the variables adult abundance (Estimate = 0.773, Std error = 0.29,

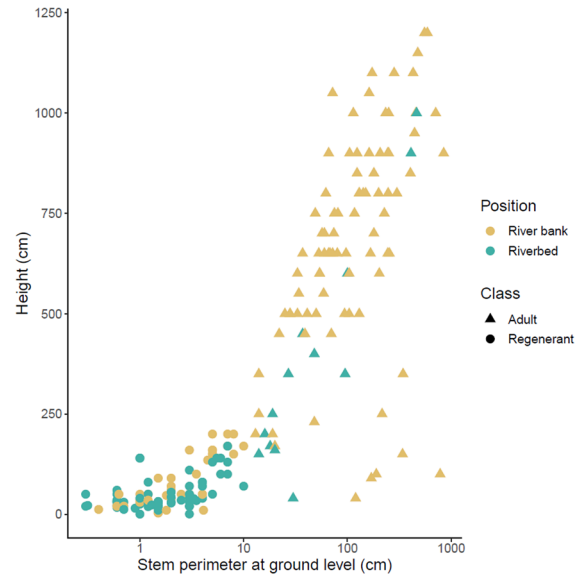

Fig. 2 Relationship between stem perimeter and height of *Salix*×*rubens* sampled in riparian environments in subtropical highlands, Brazil. Stem perimeters are expressed in log(x + 1) for better visualization. Triangles represent adult trees and circles represent regenerants of *Salix* x *rubens*. The location of each plant was classified as riverbed (blue) or river bank (light brown)

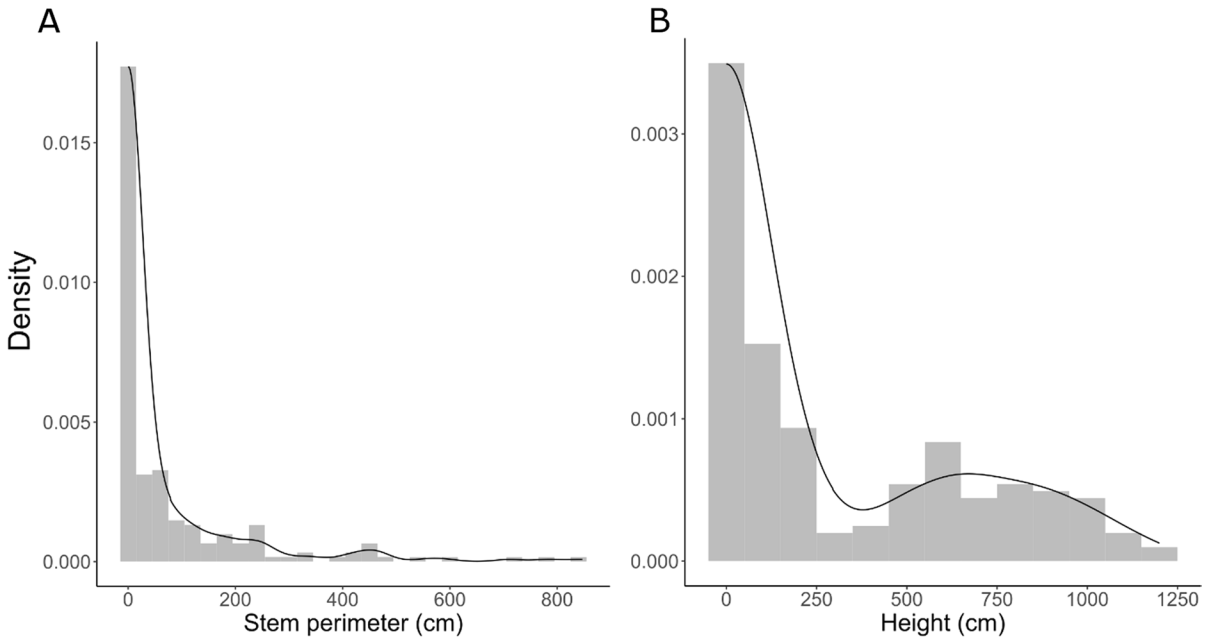

Fig. 1 Population structure represented by density plots of perimeter **A** and height **B** classes of *Salix*×*rubens* plants sampled in riparian environments in subtropical highlands, Brazil

Table 1 List of the 17 models built to understand the abundance of *Salix*×*rubens* regenerants sampled in riparian environments in subtropical highlands, Brazil

M	slp	cnp	dpt	rck	ltr	vlc	adt	adt^2	adt:cnp	df	logLik	AICc	delta	wgt
m.11	−	+	−	−	−	−	+	+	−	6	−58.73	131.94	0.00	0.60
m.8	−	−	−	−	−	−	+	+	−	5	−61.47	134.66	2.72	0.15
m.17	−	−	−	−	−	−	−	−	−	3	−64.72	136.09	4.15	0.08
m.3	−	+	−	−	−	−	−	−	−	4	−64.10	137.30	5.36	0.04
m.13	−	+	+	−	−	+	+	+	−	8	−58.42	137.35	5.41	0.04
m.9	−	−	+	−	−	+	+	+	−	7	−60.02	137.43	5.49	0.04
m.2	−	−	+	−	−	+	−	−	−	5	−63.26	138.24	6.30	0.03
m.6	−	+	+	−	−	+	−	−	−	6	−62.77	140.00	8.07	0.01
m.12	+	+	−	+	+	−	+	+	−	9	−58.69	141.18	9.24	0.01
m.10	+	−	−	+	+	−	+	+	−	8	−61.07	142.64	10.71	0.00
m.4	+	−	−	+	+	−	−	−	−	6	−64.24	142.94	11.00	0.00
m.5	+	+	−	+	+	−	−	−	−	7	−63.32	144.04	12.10	0.00
m.14	+	−	+	+	+	+	+	+	−	10	−59.13	145.59	13.65	0.00
m.7	+	−	+	+	+	+	−	−	−	8	−62.70	145.90	13.96	0.00
m.15	+	+	+	+	+	+	+	+	−	11	−58.35	147.80	15.86	0.00
m.1	+	+	+	+	+	+	−	−	−	9	−62.25	148.32	16.38	0.00
m.16	+	+	+	+	+	+	+	−	+	11	−61.09	153.29	21.35	0.00

M = model list, slp = terrain slope, cnp = canopy openness, dpt = river depth, rck = ground cover by rocks, ltr = ground cover by litter, vlc = river current velocity, adt = abundance of *S.*×*rubens* adults, adt:cnp = interaction of *S.*×*rubens* adults with canopy openness, df = degrees of freedom, logLik = log Likelihood, delta = delta AICc and wgt = AICc weights. "+" stands for the presence of the variable in the model and "−" stands for the absence of the variable in the model

$p < 0.01$), adult abundance in its quadratic form (Estimate = − 0.060, Std error = 0.03, $p < 0.05$) and canopy openness (Estimate = − 0.058, Std error = 0.03, $p < 0.05$). Residuals were considered appropriate, with no deviations regarding normality, heteroscedasticity, or dispersion. Fixed-effect variables accounted for 63% of the differences in regenerant abundance (lognormal approximation of marginal pseudo-$R^2 = 0.63$). Regenerant abundance showed a negative quadratic relationship with adult abundance, with the highest abundance of regenerants observed whenever five to eight adult plants were present (Fig. 3A). Canopy openness was negatively associated with regenerant abundance, with higher abundance of regenerants occurring when canopy openness was below 30%, i.e., in denser canopies (Fig. 3B).

Discussion

The abundance of *S.*×*rubens* regenerants was affected mainly by the abundance of nearby adult plants, with a peak of regenerant abundance observed near the presence of approximately six adults. Regenerant abundance was negatively influenced by canopy openness, an unexpected result based on the current knowledge that *S.*×*rubens* is a pioneer species, thus more frequently establishing in areas with high incidence of light. Since the interaction between abundance of adult plants and canopy openness did not explain the abundance of *S.*×*rubens* regenerants, it is possible that a higher density of *S.*×*rubens* adults affects regenerants through other mechanisms, such as competitive exclusion or niche preemption. The majority of regenerants occurred in the riverbeds of sampled rivers, which is probably related by the dispersal mechanism (vegetative propagation by water-dispersed branches). The invasive species is likely in the transition between establishment and dispersal in the invasion process, considering that there was not a widespread distribution of established populations in the study area. The analysis of population structure and the relationship between regenerant abundance and environmental factors provide insights for *S.*×*rubens* management strategies in the region.

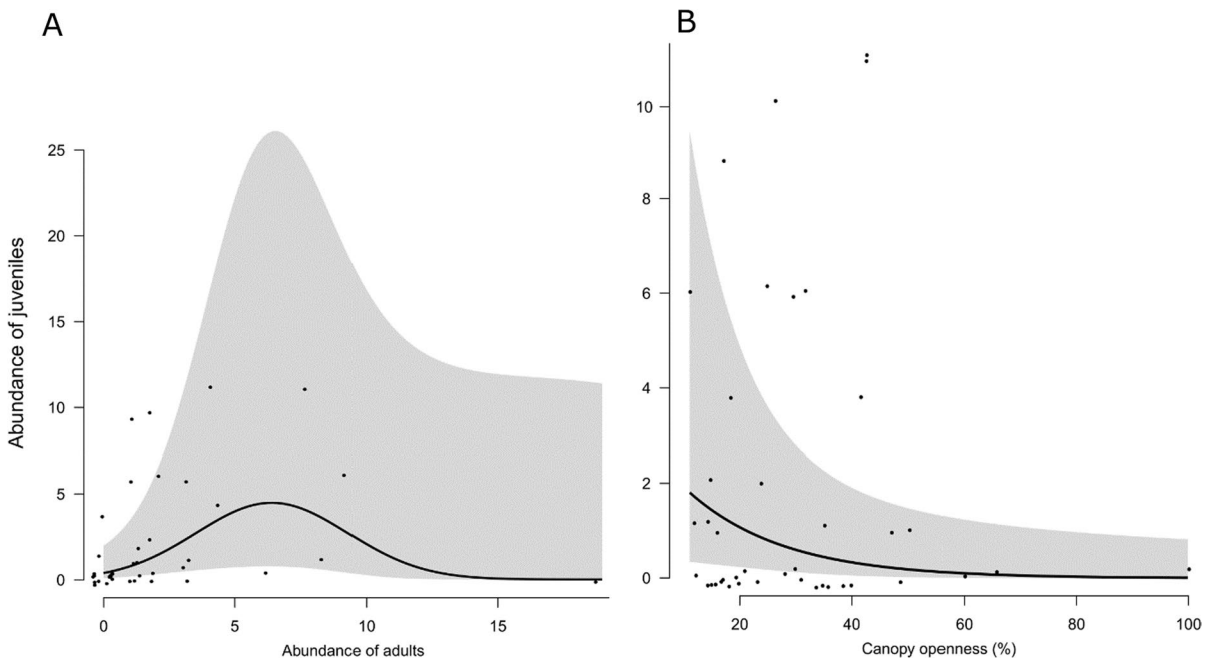

Fig. 3 GLMM effects of variables that influence the abundance of *Salix*×*rubens* regenerants sampled in riparian environments in subtropical highlands, Brazil. A = quadratic relationship of the number of adults affecting regenerants and B = negative relationship of canopy openness and regenerants. Shaded areas indicate confidence intervals. Black dots represent the sampled data points

The observed pattern suggests that the abundance of *S.*×*rubens* regenerants is facilitated by the presence of adults, but tends to decrease at higher densities of adult plants. The presence of adults may not only provide new propagules but also contribute to the incorporation of organic matter into the sediment (Holland-Clift and Davies 2007; Gehrig 2010). Additionally, adults offer protection against fluvial disturbance that might eliminate regenerants (Moggridge and Gurnell 2009). On the other hand, high densities of adults can inhibit the establishment of regenerants by hindering the access of younger plant root systems to the water table, especially at greater distances from the riverbed, thereby restricting them mostly to river margins (Mosner et al. 2011). Thus, the presence of adults in more distant areas from the river indicates that the species is able to grow beyond the preferred habitat. However, the concentration of regenerants in the riverbed or river bank may be related to the need for water, characteristic of many *Salix* species, especially because lower parts of floodplains often retain high moisture in the soil (Francis et al. 2006).

The pattern observed is similar to what was found for the native species *Salix martiana* in the Central Amazon floodplain, where smaller plants and higher densities were observed in areas more susceptible to river flood and recession regimes (Oliveira and Piedade 2002). Similarly, juveniles of the invaders *Salix babylonica*, *S. fragilis*, *Salix*×*crysocoma*, and *S.*×*rubens* established within one to two meters from the river bank, not farther away than five meters from adult plants in southern Australia (Gehrig 2010). The proximity to adults favors vegetative reproduction as vegetative propagule dispersal occurs through water with greater interference from obstacles, allowing for quicker establishment compared with seeds of the Salicaceae family, which disperse over greater distances due to their light weight (Shafroth et al. 1994). The high abundance of regenerants in the riverbed and river banks observed in our study indicates a pattern of distribution through vegetative reproduction. Moreover, we have not so far observed the occurrence of invasive *Salix* plants with seeds in the region of the study.

We showed that higher regenerant abundance was related to closed canopies, a result that contrasts with the expected low shade tolerance of Salicaceae species (Karrenberg et al. 2002). Trees of the Salicaceae family are more commonly pioneers in riparian areas of temperate regions (Hupp and Osterkamp 1996; Gurnell 1997), with establishment favored in habitats of exposed soils and high incidence of light. Closed canopies are characterized by the presence of trees, which can lead to reduced water velocity and sediment transport (Liotta 2001; Riis 2008; Thomas and Leyer 2014), thereby favoring the establishment of regenerants. Although we did not characterize the herbaceous vegetation, we observed that environments with higher canopy openness tended to be dominated by grasses, which may hinder the establishment of trees due to competition.

It has been shown that populations of *Salix*×*rubens* are densely distributed along rivers and floodplains in the region of the study, many of which are distant from the original plantations (Sühs et al. 2020a). Given the historical use and trade of willow in the region, we expected a similar distribution pattern within the boundaries of the protected area in the study. However, despite conducting an extensive survey, we found fewer regenerants than expected, with some sites lacking regenerants altogether, although there were a few areas with dense clusters and isolated adult plants. As the invasive *Salix*×*rubens* tends to form monospecific clusters (Sühs et al. 2020a), this pattern suggests the existence of environmental, historical, and/or temporal differences related to the invasion process between the protected area and the surroundings. Studies in invaded areas outside the protected area could provide insights into these differences and help develop guidelines for commercial cultivation to prevent spread through rivers, such as prohibiting plantations along watercourses and removing *S.*×*rubens* trees in areas from where it can easily spread (Sühs et al. 2020a). Considering the current early stage of *S.*×*rubens* invasion, urgent management actions must be implemented aiming at eradicating the species in the protected area. The scenario developed in Australia in which *S.*×*rubens* altered the composition and reduced the abundance of terrestrial arthropods (Greenwood et al. 2004), and impacted bird assemblages (Holland-Clift et al. 2011), must be avoided. In the same context, the subaquatic roots of *Salix* can modify rivers by forming a dense cover that alters river banks and creates islands (Read and Barmuta 1999; Cremer 2003; Moggridge and Gurnell 2009), leading to changes in river flow (Richardson et al. 2007). Such condition was observed in one of the sampled rivers in the study region. Therefore, we emphasize the importance of an eradication project for *S.*×*rubens* in the protected area.

Limitations and perspectives

Although a high abundance of *S.*×*rubens* regenerants can be explained by the presence of adults and canopy openness, future research should be directed to understand the effects of willow plantations on biological invasions. For instance, explore whether factors like the size and proximity of willow plantations have a substantial influence on willow invasion. Investigating the relationships between the size of plantations and the extent of invasion, as well as the distance between plantations and invaded areas, could shed light on the mechanisms driving willow invasion in riparian ecosystems as well as guide strategies to mitigate and prevent further invasions. Additionally, assessments on the efficiency of different management actions, as well as restoration techniques to mitigate the negative effects of *S.*×*rubens* invasions, are necessary. Although river-related variables did not have a significant effect on regenerants in our study, we still recommend future studies to collect such information, given its importance in other systems (e.g.: floods: Thomas et al. 2015). We emphasize that management actions must be performed following current legislation and expert advice (e.g.: Holland-Clift and Davies 2007). Additionally, the development of specific legislation to regulate the species usage near watercourses (Sühs et al. 2020a) is crucial to prevent future invasions.

Conclusions

Our study showed that there is a higher abundance of *Salix* × *rubens* regenerants and an intermediate number of adults (between five to eight adults) on sites with low light availability (*i.e.,* closed canopies) in invaded riparian forests. We also showed that characteristics related to the river (water current and depth), ground cover (litter and forbs cover), and terrain

(slope) play a small role in regenerant abundance. This result indicates that management actions must focus on searching sites near rivers where adult plants tend to be present.

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Author contributions L.O. Becker, R.B. Sühs and M.S. Dechoum designed the study and analyzed the data. L.O. Becker collected the data and wrote the first draft of the manuscript. All authors contributed during the writing and revision processes of this manuscript.

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Data availability The datasets generated during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

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