Research Article

Riparian degradation, stream position in watershed, and proximity to towns facilitate invasion by *Hedychium coronarium*

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Abstract

Hedychium coronarium is an invasive plant widespread in the Brazilian Atlantic forest, especially in riparian areas. However, its distribution along streams is not continuous and the factors that are related to its local occurrence are unknown. We investigated which natural and anthropogenic drivers, particularly concerning dispersal and disturbance, facilitate establishment of *H. coronarium*. We sampled 148 randomly chosen riparian sites (each containing two plots) in a subtropical basin in southern Brazil and recorded presence/absence of the plant and some environmental variables *in situ*; other variables were extracted via GIS software. We performed a GLMM with presence/absence as the response variable, sampling site as a random factor and five predictors: intensity of ecosystem degradation, dominant type of terrestrial vegetation, river substrate size class, Strahler stream order and downstream distance to the nearest urban centre. Our results point out that invader presence is favoured by local human disturbance (high riparian degradation and presence of non-native forest), and possibly dispersal, as there is a higher *H. coronarium* presence probability in proximity to urban centres. Furthermore, a higher presence probability in downstream sections (higher Strahler order) might be explained by hydrologic dispersal of rhizome fragments. Our study illustrates that in the case of riparian invasions it is important to consider terrestrial and aquatic drivers, both natural and anthropogenic.

Key words: non-native species, introduced species, spatial patterns, plants, riverine corridors, GLMM

Introduction

Riparian forests are the interface between land and water, and they are among the most biologically diverse ecosystems on the planet (Tockner and Stanford 2002). This high species richness is due to the environmental heterogeneity of riverine areas (Naiman et al. 2005; Wintle and Kirkpatrick 2007), visible in longitudinal and lateral gradients of geomorphic features, in seasonal/yearly changes in water and nutrients flows and in patterns of natural disturbances (Naiman et al. 2005). Flood pulses, particularly when of short duration but high intensity, are one of the major drivers that create

a spatio-temporally heterogeneous environment with multiple habitats (Ward et al. 1999; Tockner et al. 2010).

Riverine vegetation performs many important functions, such as stabilization of stream channel (Barling and Moore 1994), provision of critical habitat and movement corridors for wildlife (Sparks 1995; Naiman and Décamps 1997), and water purification and provisioning (Peterjohn and Correll 1984); therefore, these areas are highly attractive for human exploitation (Tockner et al. 2010). Worldwide, riparian forests are often subject to anthropogenic alteration (Connolly and Pearson 2005); the main threats for these ecosystems are land conversion, pollution and species introductions (Lord and Clay 2006; Wahyuni 2016). Several studies have shown that anthropogenic alteration of landscapes is associated with the introduction of exotic plant species that can become invaders of moderately degraded riparian ecosystems (Planty-Tabacchi et al. 1996; Hierro et al. 2006); forest clearing and subsequent abandonment, for example, leads to open environments that are highly prone to invasion (Haider et al. 2016). In many parts of the world, riparian forests are being eliminated to make space for economic activities or residential properties; this causes the extension of the road network into more pristine areas, which—in turn—can favour the spread of invasive plant species by providing sources of propagules and transport mechanisms via vehicle and foot traffic, which is favoured by proximity to urban areas (Watterson and Jones 2006).

Once non-native species have been introduced in a riparian forest, the same factors that promote high species richness can favour spread of exotics throughout the watershed (Naiman and Décamps 1997; Hood and Naiman 2000; Catford et al. 2012). The process of fluvial erosion, for example, is associated to high-intensity floods and can cause the uproot of vegetation and subsequent creation of patches open to colonization (Goodson et al. 2001; Steiger et al. 2005). Propagules of non-native invaders can also travel long distances thanks to hydrological dispersal, thus propagating invasion in new reaches of the river (Watterson and Jones 2006; Nilsson et al. 2010; Catford and Jansson 2014).

One of the most common invasive plants in Brazilian riparian areas is *Hedychium coronarium* (Koenig, 1783) (Zenni and Ziller 2011). Currently, the Global Biodiversity Information Facility (GBIF) contains 1119 occurrence records of *H. coronarium* in 45 countries all over the world ("Human observation" only – GBIF.org 2020), and in many of them it is considered a highly invasive weed (Lim 2014). In spite of this, the natural history and ecology of *H. coronarium* are still quite understudied in comparison to other species of the same genus such as *Hedychium gardnerianum* (Sheppard ex Ker Gawl., 1824), recognized as one of the 100 worst invaders of the world. *H. coronarium* is detrimental for local riparian plants, as it forms dense stands that overcome native species (Kissmann 2000) and inhibits the growth of seedlings (Costa et al. 2019). Control and restoration

techniques for *H. coronarium* have only recently been examined (Machado et al. 2020).

In this study we investigated factors associated with the occurrence of *H. coronarium* in the riparian forests of the Maquiné river basin, Rio Grande do Sul, southern Brazil. In this region, *H. coronarium* is considered an invasive species (Rolim et al. 2015) and in our study area, this plant has been present for more than 100 years as the oldest museum record in the region is from 1934 (PACA-AGP 1351, Herbário Anchieta, Unisinos, Brazil), but it has been previously recorded in eastern Brazil in the 19th century (Petersen 1890). Studies have demonstrated that the longer an invasive plant resides in a given region the more likely it is to spread into different habitats, therefore strengthening its invasive potential (Pyšek et al. 2015; Feng et al. 2016). In the study region, *H. coronarium* has an uneven distribution in riparian forests, ranging from high-density patches to areas where it is virtually absent. Therefore, the main objective of this study was to examine factors influencing its distribution including dispersal and disturbance drivers, both anthropic and natural.

In this context, the Maquiné watershed is an interesting study system as in the beginning of the 20th century its subtropical forest was largely converted to agricultural lands, some of which were subsequently abandoned (Becker et al. 2005; Pasquetti et al. 2009); currently, most of the human impact on the landscape consists of land clearing for small agricultural business or residential properties. A rural road network in proximity of the streams and the presence of two small urban centres can facilitate dispersal of non-native species (Watterson and Jones 2006; McLean et al. 2017); in addition, the streams of the Maquiné basin are often subject to natural disturbance in the form of high-energy flash floods that modify stream banks and create new openings for plants to establish (Becker et al. 2005).

With this knowledge in mind, we expect anthropogenic disturbance to promote *H. coronarium* presence in Maquiné riparian forests; we also hypothesize that areas with more intense fluvial geomorphic processes have a higher incidence of *H. coronarium*. In addition to disturbance, we believe that hydrologic and terrestrial dispersal of vegetative propagules can also favour the presence of *H. coronarium* in riparian areas.

Materials and methods

Study area

We recorded the occurrence of *H. coronarium* in riparian areas along six streams in the Maquiné river basin, in southern Brazil (Figure 1). The climate in the region is humid subtropical with high annual rainfall (1400–1800 mm/y) and no marked dry season (Hasenack and Ferraro 1989). At the beginning of the 20th century, the area witnessed a massive conversion of the subtropical humid forest to agricultural lands, but in the last 50 years
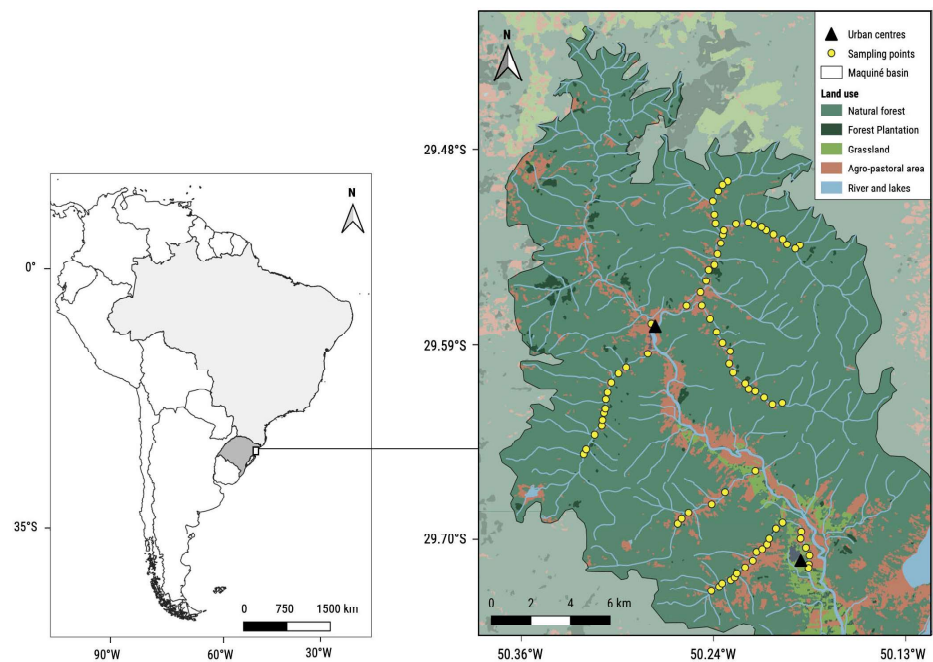
Figure 1. A) Geographic location of the study area (white rectangle) in the state of Rio Grande do Sul (dark grey), Brazil (light grey). B) Sampling sites in the Maquiné river watershed and their associated land use.

there has been a decrease of the land exploitation and a regeneration of native vegetation (Becker et al. 2005; Pasquetti et al. 2009).

The streams of the Maquiné watershed are characterized by harsh hydrological and geomorphic fluvial processes that can constrain the establishment and persistence of plants in the riparian areas (Bendix and Hupp 2000). Such streams have marked longitudinal profiles, flowing from elevations of approximately 800 meters above sea level (m.a.s.l.) to 50 m.a.s.l. in only 5–10 km of length. Channel width of the studied streams varied between 5 and 22 m (mean 10.8 m). High rainfall events are common throughout the year (but mainly in spring and summer) and, because of the pronounced elevation profile of the Maquiné basin, result in high-energy flows and flash floods, which physically affect stream habitats (further detail on stream physical characteristics can be found in Camana et al. 2016). Pictures of the stream bank can be seen in Supplementary material Figure S1.

Land use in riparian areas is heterogeneous, consisting predominantly of native vegetation interspersed by small scale agriculture, small farms and exotic tree stands (*Pinus* sp., *Eucalyptus* sp.) (Pasquetti et al. 2009).

Study species

Hedychium coronarium is a rhizomatous plant of the Zingiberaceae family native to the Himalayan region. Its reproduction is both sexual—with the production of white zygomorphic flowers—and asexual – via rhizomatic propagation (De Souza and Correia 2007). *Hedychium coronarium* has recognized commercial value in different fields: essential oils from its rhizome have several clinical properties (Joy et al. 2007), while its flowers
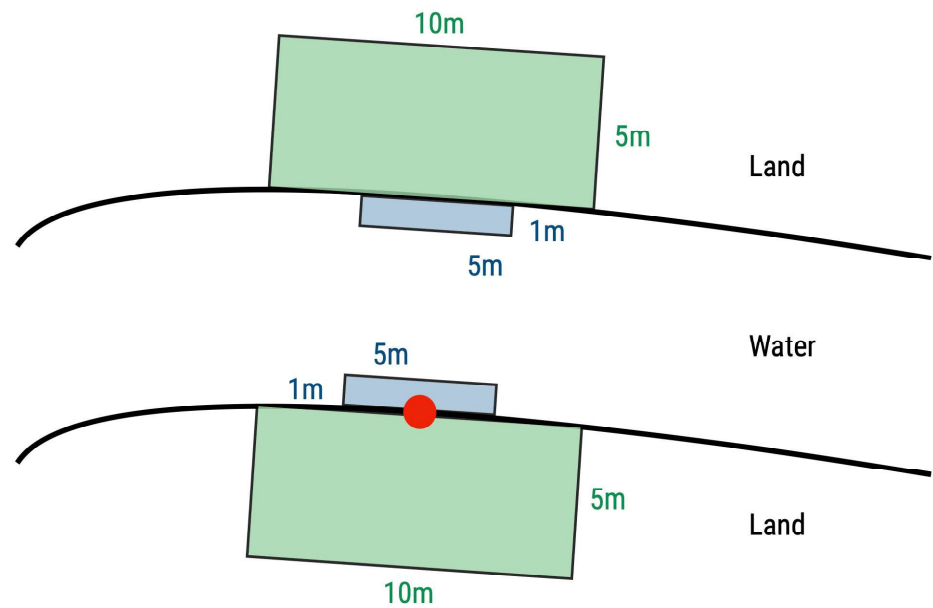
Figure 2. Sampling scheme for each site. Two terrestrial 10 × 5 m plots (green rectangles) are set up, one centred on the GPS coordinate (red dot) and the other one in parallel position on the opposite bank. On the water side, each plot is next to an aquatic 5 × 1 m plot for substrate size assessment. All plots have their longer side adjacent to the bank.

can be used for ornamental purposes or to produce perfume (Verma and Bansal 2010). It can tolerate a wide range of environmental conditions and it can exhibit different invasion strategies according to soil moisture, plant community composition, and intensity of competition (Chiba de Castro et al. 2016). Ramet growth dynamics can be highly seasonal in regions of seasonally dry climate (Chiba De Castro et al. 2020).

Field data collection

We sampled riparian areas of six tributaries of the Maquiné river (Água Parada, Encantado, Forqueta, Garapiá, Ouro, and Pinheiro), which are similar in width and longitudinal profile. We used tools in ArcGIS 10.5.1 (ESRI 2011) to generate 148 random sampling sites coordinates along the stream network (Figure 1), with a minimum spacing of 100m between sites and covering a wide distance gradient (0.05–17.1 km) to downstream urban centres (Barra do Ouro or Maquiné, Figure 1).

Each sampling site consisted of two paired plots, one on each stream bank (left and right); in total, we sampled 148 sites and therefore 296 paired plots. Each plot consisted of two parts: the first was a 10 × 5 m rectangle on land, with the longest side adjacent to the watercourse and the second was smaller parcel (5 × 1 m), adjacent to the bank but in the water (Figure 2); the random site coordinate was the midpoint of both parcels longer side. In each terrestrial plot, we recorded the presence or absence of *H. coronarium*. We chose not to make abundance estimates because local riparian forest patches can present several vertical layers and can be very dense, so that rapid assessment of abundance would be prone to observer

Table 1. Set of collected variables. For each variable, we present the name, the way it was measured or quantified, the source (either field or GIS measurement, see Methods for detailed information), and how it was assumed to affect invasion.

Variable	Measurement	Method	Driver	How it affects the invasion process
Presence of fluvial geological processes	Categorical: erosion, deposition or transition	Visually assessed in the field	Dispersal	Depositional channel sites have a higher chance for vegetative propagules to arrive and persist
Strahler stream order	Integer numbers (one to four)	GIS analysis	Dispersal	If *H. coronarium* occurs in lower-order streams, these may act as propagule sources for higher-order (passive downstream transport of rhizome fragments by streamflow)
Downstream distance to the nearest urban centre	Distance along river course (km) from site to an urban area	GIS analysis	Dispersal	Occurrence is expected to increase with proximity to urban centres, due to human-mediated dispersal
Dominant size class of river substrate	Seven size classes: < 0.2 cm; 0.2–1.6 cm; 1.6–6.4 cm; 6.4–25cm; 25–50 cm; 50–100 cm; > 100 cm	Visually assessed in the field	Fluvial disturbance	Physical disturbance of stream banks by repeated removal and deposition of larger stream rocks (especially larger ones) can disturb (kill or remove) other plant species and favour the arrival, establishment or re-sprout of *H. coronarium*.
Stream reach slope	Angular degrees (°)	GIS analysis	Fluvial disturbance	Similarly to stream substrate size, stream slope is a proxy for fluvial disturbance. Steeper channel slopes imply harsher flow (especially during high flow events)
Density of buildings	% of buildings cover in a 100 m radius buffer around each site	GIS analysis	Local anthropic disturbance	Human disturbance can facilitate invasive plant establishment
Intensity of ecosystem degradation	0 (absent) to 3 (high)	Visually assessed in the field according to Karr (1999)	Local anthropic disturbance	Human disturbance can facilitate invasive plant establishment. High-integrity sites should not have traces of human presence such as trash, water pipes, fire remains or man-made structures
Intensity of agricultural activity	0 (absent) to 3 (high)	Visually assessed in the field according to Karr (1999)	Local anthropic disturbance	Agricultural management can disturb native communities and physical habitat, favouring invasive plant establishment. High-integrity sites should have no agricultural use
Canopy cover	0% to 100%	Visually assessed in the field	Local anthropic disturbance	Human disturbance can facilitate invasive plant establishment. High-integrity sites should have almost 100% canopy cover
Perturbation of understory vegetation	0 (absent) to 3 (high)	Visually assessed in the field	Local anthropic disturbance	Human disturbance can facilitate invasive plant establishment. High-integrity sites should have an undisturbed understory
Intensity of livestock disturbance	0 (absent) to 3 (high)	Visually assessed in the field according to Karr (1999)	Local anthropic disturbance	Livestock can remove competitor species and affect the physical environment, thus facilitating *H. coronarium* establishment. High-integrity sites should have little to no sign of livestock presence
Dominant type of terrestrial vegetation	Arboreal native; arboreal non-native; shrub; herbaceous; bare soil	Visually assessed in the field	Local anthropic disturbance	Human disturbance can facilitate invasive plant establishment and previous habitat alteration by non-native species can facilitate the arrival of other invasives. High-integrity sites should have the forest as dominant vegetation type

error. On the other hand, more accurate—but time consuming—methods to assess ground cover by *H. coronarium* would imply in a much smaller total sample size for this study.

For each plot we recorded several predictor variables, both in the field and through GIS analysis; Table 1 illustrates how each of these variables fit into our hypothesis and how we believe it would influence *H. coronarium* presence. In each plot we reported canopy cover (visually assessed by the same person and intended as percentage of the canopy layer above the parcel occupied by vegetation), type of dominant terrestrial vegetation (arboreal
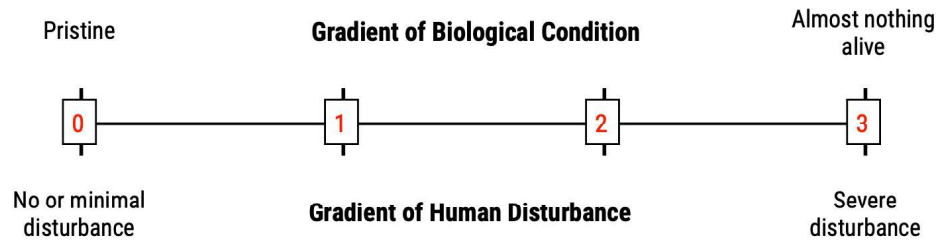
Figure 3. Scheme representing how ecosystem integrity is defined both by a biological and an anthropogenic gradient. Numbers in red indicate the levels we implemented to describe perturbation of understory vegetation, intensity of ecosystem degradation, livestock disturbance, and agricultural activity. Adapted from Karr (1999).

native, arboreal non-native, shrub, herbaceous, bare soil), perturbation of understory vegetation, and intensity of livestock disturbance, agricultural activity, and ecosystem degradation (alteration of the natural state by human activity); the latter four variables were assessed on a scale of zero (pristine) to three (very degraded) implementing the ecosystem integrity scheme described in Karr (1999) (Figure 3), which takes into account both gradient of biological condition and gradient of human disturbance. In each aquatic plot we assessed the presence of fluvial geological processes (erosion/deposition/transition) and dominant river substrate size class (< 0.2 cm; 0.2–1.6 cm; 1.6–6.4 cm; 6.4–25 cm; 25–50 cm; 50–100 cm; > 100 cm); both variables were visually assessed.

GIS analysis

We used ArcGIS (ESRI 2011) to extract values for Strahler stream order (positive whole number used in hydrology to indicate level of branching in a river system, with higher numbers corresponding to the outermost tributaries – Strahler 1957), stream segment slope (degrees), downstream distance to the nearest urban centre (km). Strahler order determination along the stream network was based on a modelled stream network (SEMA 2018, 1:25.000 scale), using the Rivex tool (Hornby 2017). Distance to nearest downstream urban centre was measured along the stream network instead of the road network because road maps were not available for the whole study area; this procedure is plausible since human occupation and roads in the Maquiné river basin are parallel and close to the main streams due to topological constraints. We used the Network Analyst extension in ArcGIS to calculate the distance to nearest urban centres. The density of buildings in a 100 m radius buffer (% building cover) around each site was assessed by visual analysis of high-resolution GoogleEarth images (Google Earth Pro 2019). In QGIS (QGIS Development Team 2019), we overlaid a grid of 10 × 10 m cells on the area occupied by the 100 m-radius buffer and counted the number of cells where buildings were present. Stream slope was calculated from a digital elevation model (DEM) generated in ArcGIS, based on terrain contour data at a 1:50.000 scale (Hasenack and Weber 2010).

Data analysis

We performed all statistical analyses in the R statistical environment (Version 3.6.3 – R Core Team 2019). We tested 15 different Generalized Linear Mixed Models (GLMM) (McCulloch and Searle 2000) and a null model (Table S1), formulated according to factors identified in other studies that focused on the characterization of riparian invasions; we then selected the definitive model via comparison of models' AIC (Akaike 1998). All continuous variables were scaled, and we checked a priori for collinearity between variables using Kendall rank correlation test. We selected a model with five fixed predictors: intensity of ecosystem degradation, dominant type of terrestrial vegetation, river substrate size class, Strahler stream order and downstream distance to the nearest urban centre. For river substrate size, the final value in each plot was the average value of the class it belonged to. Since presence/absence of *H. coronarium* is a binary response variable, all GLMMs had a binomial distribution and link function logit, using the package "lme4" (Version 1.1 – Bates et al. 2015); the GPS coordinate of each plot was included as a random independent variable with two levels (one per bank) to avoid spatial correlation between plots. Maximum Likelihood was estimated using the Laplace approximation (Liu 1993) and the significance of fixed effects was checked with a Wald χ^2 test (Kenward and Roger 1997). Collinearity between variables was once again tested assessing the VIF of the model with the "car" package (Version 3.0 – Fox and Weisberg 2019) using a threshold of 3, as recommended by Hair et al. (2019). Since the estimated coefficients of the model are in terms of log(odds) of *H. coronarium* presence, for an easier comprehension we visualized the results using the "effects" package (Version 4.1 – Fox and Weisberg 2019), which converts log(odds) to probability.

Model validation was carried out using the "DHARMa" package (Version 0.2.4 – Hartig 2019), which creates readily interpretable residuals graphs for GLMMs by transforming the residuals to a standardized scale (0–1) via a simulation-based approach similar to parametric bootstrapping. To support the visual model validation, we tested simulated residuals for normality with a one-sample Kolmogorov-Smirnov test (Kolmogorov 1956) in the "DHARMa" package and we tested overdispersion using the package "blmeco" (Version 1.3 – Korner-Nievergelt et al. 2015), using 1.4 as threshold as suggested by Korner-Nievergelt et al. (2015). Conditional and marginal errors of the final model were assessed with the package "performance" (Version 0.5.0 – Lüdecke et al. 2020). To assess how the model will generalize to an independent data set, we implemented a method that relies on the ROC (Receiver Operating Characteristic) curve (Pearce and Ferrier 2000), which is formed by plotting the probability of predicting a real positive against the probability of predicting a false positive; the area under the curve (AUC) is an evaluation of the model performance: the closer the

Table 2. Output of the final model, including estimate and standard error of each fixed predictor. For the predictor dominant type of terrestrial vegetation, the level "Arboreal native" is used as reference and therefore not shown.

| Variable	Estimate (log-odds)	Standard error
(Intercept)	1.5032	0.4591
Strahler stream order	1.6207	0.4412
Dominant size of river substrate	0.3467	0.2636
Dominant type of terrestrial vegetation (Arboreal non-native)	2.3211	0.8271
Dominant type of terrestrial vegetation (Shrub)	1.0289	1.0443
Dominant type of terrestrial vegetation (Herbaceous)	−1.2509	0.7310
Dominant type of terrestrial vegetation (Bare soil)	−1.9830	0.9969
Intensity of ecosystem degradation	0.9113	0.3065
Downstream distance to nearest urban centre	−1.3546	0.4181

value is to 1, the more valid is the model. Using the package "cvAUC" (Version 1.1.0 – LeDell et al. 2014), we calculated a cross-validated AUC estimate and confidence interval.

Results

Hedychium coronarium was found in 205 out of 296 randomly chosen sites (69.3%), indicating a frequent occurrence along the sampled streams. The model coefficients are shown in Table 2. The residuals met the assumptions of normality (one-sample Kolmogorov-Smirnov test, D = 0.05, p-value = 0.44) and there was no overdispersion (dispersion = 0.78). The conditional R^2 of the model was 0.761 and the marginal was 0.391. There was no collinearity among variables. The variance of the random effect was 5.087 with a standard deviation of 2.255. The cross-validated AUC had a value of 0.983 (lower CI = 0.972, higher CI = 0.994), signifying that the model has a good predictive ability even on unseen data. The Wald χ^2 test indicated that Strahler stream order, type of dominant terrestrial vegetation, downstream distance to nearest urban centre and intensity of ecosystem degradation were the most significant predictors.

We found a strong and clear positive correlation (estimate = 0.9113, s.e. = 0.3065) between intensity of riparian degradation and *H. coronarium* presence (Figure 4A), with high levels of disturbance associated to a presence probability close to 1.

The dominant type of terrestrial vegetation also proved important in explaining the presence/absence of *H. coronarium*. The category with the largest positive effect on presence probability is arboreal non-native vegetation (estimate = 2.3111, s.e. = 0.8271), followed by arboreal native vegetation (estimate = 2.3111, s.e. = 0.8271) and shrubs (estimate = 1.0289, s.e. = 1.443) which overlap and present a moderate uncertainty (Figure 4B). The categories with the most negative effect on the presence of *H. coronarium* were herbaceous vegetation (estimate = −1.2509, s.e. = 0.7310) and bare soil (estimate = −1.9830, s.e. = 0.9969), both of which possess a large uncertainty value (Figure 4B).
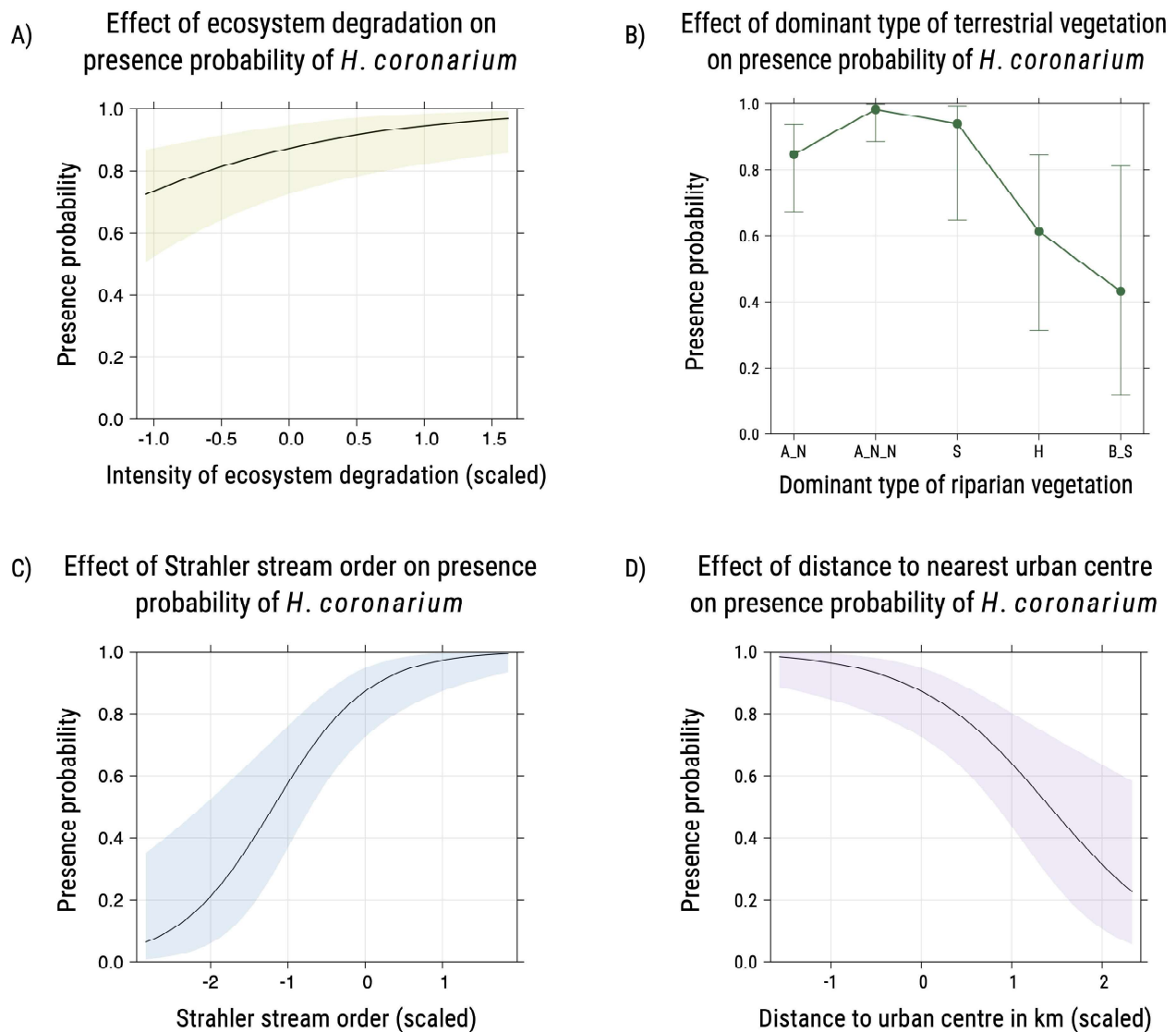
Figure 4. Visualization of the model results. Effect of A) intensity of ecosystem degradation, B) dominant type of riparian vegetation, C) Strahler stream order and D) downstream distance to nearest urban centre on the probability presence of Hedychium coronarium. Shaded areas represent 95% confidence interval. In B): A_N = Arboreal Native; A_N_N = Arboreal Non-Native; S = Shrub; H = Herbaceous; B_S= Bare Soil.

We found a positive correlation (estimate = 1.6207, s.e. = 0.4412) between Strahler stream order and presence of *H. coronarium* (Figure 4C), with riparian sites of high-order rivers (downstream position in the watershed and larger size) being more likely to host the plant; this correlation is more certain for high values of Strahler stream order than for low values.

According to our results, downstream distance to the nearest urban center has a negative correlation (estimate = −1.3546, s.e. = 0.4181) with presence of *H. coronarium* (Figure 4D); the greater the distance from the urban area, the less likely it is for the species to occurr.

The χ^2 test highlighted that dominant size of river substrate is not a very significant predictor. It seems that larger substrate size are associated with a higher chance of finding *H. coronarium*; however, there is a very high uncertainty and the output of the model showed a log(odds) coefficient (0.3467) just slightly larger than its standard error (0.2636) (Table 1).

Discussion

Our results suggest that occurrence of *H. coronarium* in riparian areas is influenced by local anthropogenic drivers (ecosystem degradation and—consequently—dominant type of terrestrial vegetation), but also by dispersal drivers, both natural (water flow and position in the stream network, given by Strahler order) and human-mediated (distance to nearest urban centre).

When determining priority areas for invasive species management, it is important to consider anthropogenic presence and land-use change. An *in situ* measure of ecosystem degradation provides a good indication of areas at risk of non-native establishment or that are already invaded. Human alteration of landscapes negatively impacts those native species that are poorly adapted to more frequent or new forms of disturbance (Shea et al. 2004) and creates "novel niches" that can be occupied by alien species more tolerant of such conditions (Moles et al. 2008). In our case, most of the severely degraded areas were near of openings that connected the road to the stream; such corridors can serve several purposes, such as accessing an elevated bridge or reaching an agricultural area, often consisting of a non-native trees plantation. The vegetation in these areas is often patchy and somewhat unhealthy, due to the frequent passage of people, which increases the possibility of introduction and establishment of alien plants (Niggemann et al. 2009; Park et al. 2019), such as *H. coronarium*.

The existance of forest plantations—expecially of *Pinus* sp. and *Eucalyptus* sp. (dark green in Figure 1B)—and the necessity of their owners to access them often could explain the strong association between arboreal non-native vegetation and presence of *H. coronarium*. Alien trees, expecially when in a plantation configuration, deeply modify ecosystem processes and characteristics (De Stefano et al. 2020; Franzese et al. 2020) and therefore create an inbalance that can favour the entrance of alien species and hinder the native ones (Padmanaba and Corlett 2014). Introduced pine trees (*Pinus* sp.), for example, are known to make soil pH more acid (Amiotti et al. 2000), which might be unfavourable for local plant species but does not constitute an obstacle for *H. coronarium* (Gilman 2014). Riparian trees seem to be beneficial for *H. coronarium* as they provide partial shadow, which is ideal for the optimal growth of this species (CABI 2019). Furthermore, Santos et al. (2005) noticed a strong influence of partial shade on *H. coronarium* sexual reproduction: individuals that were exposed to full sunlight or high levels of shadow (60–95%) did not produce viable seeds; therefore, a riparian habitat with intermediate canopy cover (provided by trees or shrubs) can favor both growth and reproduction of this species. Regarding herbaceous vergetation, our results differ from the ones of Haider et al. (2016), who found that the species was strongly associated with herbaceous patches.

This discrepancy might be ascribed to the different landscape evolution of the two study areas: while the one from Haider et al. (2016) was mostly converted to grassland in the 1950s, ours had only recent and small (much less < 1 ha) herbaceous patches along stream margins, often as gardens inside residential properties; perhaps *H. coronarium* was not present in our herbaceous plots because of frequent maintenance of the area by residents.

When studying distribution of riparian plants, it is important to consider that watercourses can act as vehicles for hydrologic dispersal of both sexual and asexual propagules (Nilsson et al. 2010; Sarneel 2013). Vegetative propagules can usually float better than seeds (Sytsma and Pennington 2015) and can therefore travel large distances and reach downstream sections of the hydrological network (Riis and Sand-Jensen 2006; Thomas et al. 2006). A similar mechanism would explain why the presence probability of *H. coronarium* is greater in downstream (higher Strahler order) streams of the Maquiné basin, and it would suggest a "small-to-large reach" dispersal pattern. Even though we did not assess dispersal *per se*, this finding provides support for our hypothesis concerning importance of natural dispersal of propagules for *H. coronarium* establishment. Once vegetative propagules of *H. coronarium* reach a new area of the riverbank, the rhizome high sprouting capacity and fast growth (Kissmann and Groth 1999) can favour its establishment; furthermore, Oliveira Costa et al. (2019) have shown that rhizomes of *H. coronarium* negatively affect seedlings of a native riparian pioneer tree, which could explain how they are able to colonize also less disturbed areas.

Finally, we also found support for our anthropogenic dispersal hypothesis, which postulated that *H. coronarium* would be more dominant in areas closer to urban centres. Maquiné and Barra do Ouro are small towns immersed in a rural landscape and they are the most densely populated area of the basin; here, frequent usage of *H. coronarium* as a garden plant could be another reason that favours its establishment in natural habitats: ornamental species are in fact amongst the most often naturalized non-native species (Mack and Lonsdale 2001; Lambdon et al. 2008). In addition, fast growth and asexual reproduction are characteristic that allow garden species to easily escape into natural and semi-natural habitats (Marco et al. 2010). Furthermore, in small towns residential gardens are often closer to the edge of the inhabited area, which would ease even further the introduction of non-native plants (McLean et al. 2017). Besides garden escape, vehicle traffic is another known driver of species dispersal from urban to natural areas (Von Der Lippe and Kowarik 2008). Both Maquiné and Barra do Ouro are an obligated transit point to reach the most upstream areas of the region and are therefore crossed by a large amount of vehicles traveling across the watershed, potentially mediating propagule dispersal.

Conclusion

Determining drivers of non-native species distributions is one of the many steps necessary to deal with the threat posed by biological invasions. In our study case, riparian degradation, proximity to anthropic areas, vegetation structure and position in watershed proved important to facilitate establishment of *H. coronarium*. Going back to our original question as to why *H. coronarium* has an uneven distribution in the watershed riparian forests, our results point out that these drivers are heterogeneously distributed in the landscape, explaining at least in part why *H. coronariu*m has not occupied riparian areas in spite of its long lasting presence in the region. Riparian degradation, for example, is more common near small farms and residential properties or near points that allow stream crossing by people and domestic animals. The higher presence probability associated with downstream sections of the river can indicate a unidirectional transport of propagules, which also can create an imbalance in the frequency of occurrence of this plant. Finally, human transit along the watershed roads—which seems favour propagule dispersal—is also not uniform as some areas are rarely accessed while others are visited more frequently, increasing propagule pressure.

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Supplementary material

The following supplementary material is available for this article:

Figure S1. Photographs of the streambank configuration and vegetation in the Maquiné watershed. Photo by the authors.

Table S1. List of GLMM models that were evaluated.

This material is available as part of online article from:

http://www.reabic.net/aquaticinvasions/2021/Supplements/AI_2021_Bellini_Becker_SupplementaryMaterial.pdf