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Natural and anthropogenic factors facilitate invasion of riparian corridors by *Hedychium coronarium*

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Resumo

Os ecossistemas subtropicais são caracterizados pela falta de informação sobre muitas espécies introduzidas. O *Hedychium coronarium* é uma planta invasora amplamente difundida na Mata Atlântica brasileira, principalmente em corredores ribeirinhos. Nosso objetivo é investigar se fatores naturais e antropogênicos facilitam o estabelecimento de *H. coronarium*. Com base na amostragem aleatória de 296 parcelas ao longo de riachos de uma bacia subtropical, registramos a presença / ausência da planta e variáveis ambientais locais; outras foram extraídas usando software de SIG. Realizamos um GLMM com presença / ausência como variável resposta, riacho de amostragem como fator aleatório e sete preditores: a) proximidade à área urbana, b) degradação da área local e c) abundância de silvicultura não-nativa, todos os quais tiveram efeito positivo sobre a probabilidade de presença de *H. coronarium*; d) tipo de vegetação local, segundo a qual a presença de árvores favorece o invasor; e) tamanho do substrato do riacho e f) ordem do riacho de Strahler, ambos com relação positiva com a probabilidade de ocorrência da planta; g) inclinação do rio, que teve um pequeno efeito negativo. Nossos resultados apontam para a influência da presença humana local na ocorrência de *H. coronarium*, possivelmente devido à remoção da competição, facilitação por outras plantas exóticas e fornecimento de propágulos; o último também é possível através da hidrocória, como mostrado pela maior probabilidade de ocorrência em rios de ordem superior. A ação perturbadora de um grande substrato durante as enchentes também pode criar oportunidades de estabelecimento para o *H. coronarium*. Se as avaliações em escala fina não forem possíveis, o manejo deve se concentrar nas áreas mais próximas dos centros urbanos, já que elas estão mais expostas a distúrbios humanos.

Palavras-chave: Especie não-nativa, Mata Atlântica, Bacia subtropical, GLMM

Abstract

Subtropical ecosystems are characterized by a lack of information on many introduced species. Hedychium coronarium is an invasive plant widespread in the Atlantic Forest biome of Brazil, especially in riparian corridors. We aim at investigating whether natural and anthropogenic factors facilitate the establishment of H. coronarium. Based on a random sampling of 296 plots along streams of a subtropical basin, we recorded the presence/absence of the plant and local environmental variables; others were extracted using GIS software. We performed a GLMM with presence/absence as response variable, sampling stream as a random factor and seven predictors: a) proximity to urban area, b) local area's degradation, and c) abundance of exotic silviculture, all of which had a positive effect on the presence probability of H. coronarium; d) type of surrounding vegetation, according to which the presence of trees favors the invader; e) size of stream's substrate and f) Strahler's stream order, both of which had a positive relationship with the plant's presence probability; g) stream's inclination, which had a small negative effect. Our results point out to the influence of local human presence for the occurrence of H. coronarium, possibly due to competition removal, facilitation by other exotic plants and propagule supply; the latter is also possible through hydrochory, as shown by the greater presence probability in higher-order rivers. Disruptive action from a large substrate during floods can also create establishment opportunities for H. coronarium. If fine-scale assessments are not possible, management should focus on areas closer to urban centers, as they are more exposed to human disturbance.

Keywords: Non-native species, Atlantic Forest, Subtropical basin, GLMM

Summary

General introduction

Many animal and plant species have been transported far from their original range and introduced in a new one thanks to human action, either consciously or not (McNeely 2001). In invasion ecology there is a lot of confusion regarding the terminology; here, we refer to the one defined by Richardson *et al.* (2000) in their schematization of the invasion process (Fig. 1 of General Introduction -G.I.).

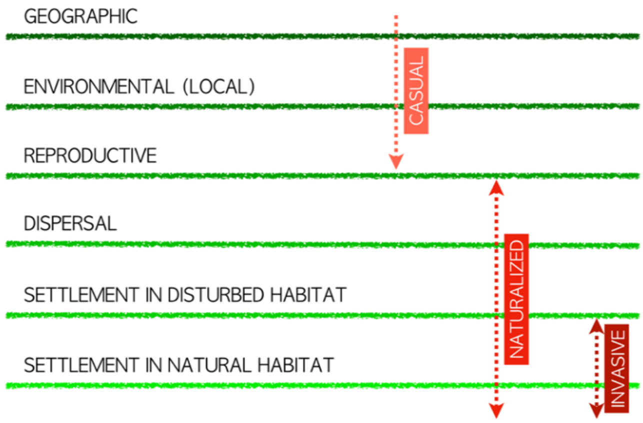

Fig. 1 G.I. Schematic representation of the main barriers limiting the spread of introduced species, which are: major geographical barrier (usually on intercontinental scale); environmental barriers (abiotic and biotic) at the site of introduction; reproduction barriers; local dispersal barriers; environmental barrier in anthropologically disturbed habitat; environmental barriers in natural or seminatural habitat. Adapted from Richardson et al. (2000)

A taxon that overcomes a major geographical distance due to human intervention is then defined as either introduced, non-native, non-indigenous or alien (1st barrier in Fig. 1 G.I.). To settle in an area, a species has to cope with the environmental conditions present in the point of introduction (2nd barrier in Fig. 1 G.I.); these conditions can be abiotic (climate, presence of refuge, etc.) or biotic (presence of prey/predators/symbionts, etc.). Once a taxon can reproduce regularly in the new range (3rd barrier in Fig. 1 G.I.), it is considered as successfully naturalized. Not all naturalized species become invasive; predicting which species will become invasive still represents an important objective for invasion ecologists (Richardson and Pyšek 2008). So far, species' traits, residence time, climate/habitat match and propagule pressure have been identified of important determinants of the success of an invasion (Pyšek et al. 2015). The rate of species' introduction rapidly increased during the last 200 years and especially during the second half of the 20th century and the beginning of the 21st (Seebens et al. 2017).

However, many introductions are not recorded at all, and most countries still lack an inventory of the invasive species present in their territory. For the case of Brazil, Zenni & Ziller's research (2011) aims at filling part of this knowledge gap and has identified an elevated number of invasive plants in the Atlantic Forest biome (129 species). The Atlantic forest biome extends on the Atlantic coast of Brazil from approximately 8°S to 28°S (Muylaert et al. 2018) and is one of the world's hotspots for biodiversity (Mittermeier et al. 2004); although reduced and fragmented, the forest exerts a direct influence on the lives of about 80% of Brazil's population by regulating watercourses, soil fertility, erosion and climate. Changes in a forest landscape can have consequences for the health of watercourses that run through it. The plant community on the banks of rivers is defined as riparian vegetation and it plays a fundamental role in regulating the interactions between land and water (Naiman et al. 1998). The geomorphology of a watershed regulates hydrological regimes (Bendix and Stella 2013), which in turn creates a filter for the establishment of plant species that have to cope with the type and intensity of disturbance in the area (Naiman et al. 1998).

The environmental heterogeneity of the riverine area – due to frequent natural disturbances such as flood events – increases its susceptibility to invasion by non-natives (Naiman and Décamps 1997). Natural routes like rivers are important channels for invasive plant species, many of which can disperse trough hydrochory and therefore can carry forward the invasion process even many kilometers downstream of the initial point (Richardson et al. 2007). In addition, numerous studies have shown that habitat fragmentation and human disturbance can facilitate the establishment and spread of invasive plants in a region (Planty-Tabacchi et al. 1996; Hierro et al. 2006).

One of the most common non-native plants in Brazil is *Hedychium coronarium* Koenig (Zenni and Ziller 2011), commonly known as white ginger lily or lírio-do-brejo. Originally from the Himalayas, the ginger lily was probably introduced in Brazil during colonial times (CABI 2019). It is a rhizomatous plant with fast growth that thrives in humid habitats such as marshes and stream banks (CABI 2019). Its reproduction is both sexual – with the production of white beautiful flowers (Fig. 2a G.I.) – and asexual – via rhizomatic propagation (Fig. 2b G.I.) (De Souza and Correia 2007).

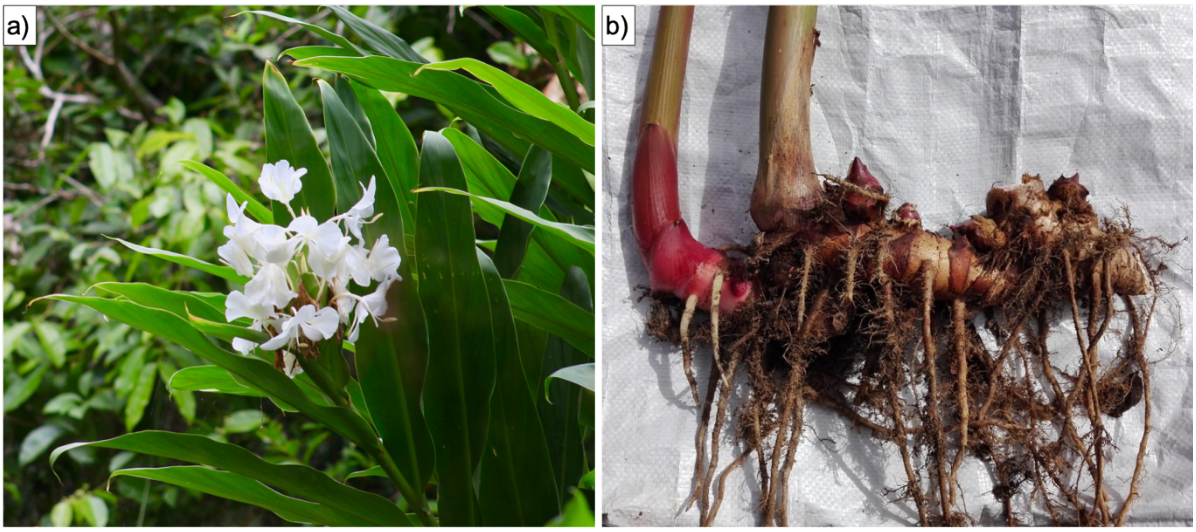

Fig. 2 G.I. a) Aboveground biomass of an *H. coronarium* individual, with leaves and inflorescence **b)** Fragment of belowground biomass of an *H. coronarium* clonal stand. Photos by Ginevra Bellini

This species is quite profitable when cultivated, because its components can be implemented in medicine, aesthetic, food and paper production (Corrêa 1984; Facundo and Moreira 2005; Joy et al. 2007). Perhaps for this reason, it has been introduced in 58 countries all over the world (Lim 2014); however, currently there is no global-level distribution map of the white ginger lily. At the present moment, *H. coronarium* is present in all of Brazil's biomes but it's mostly concentrated on the littoral area and in the Atlantic forest biome (Fig. 3 G.I.).

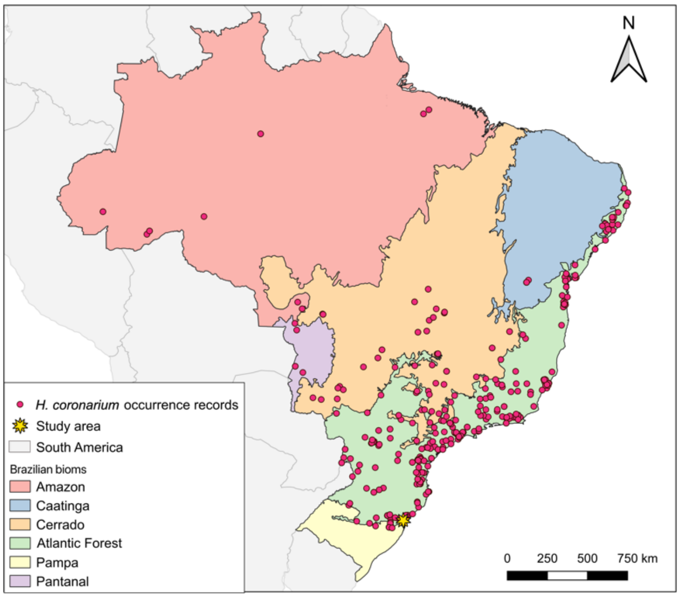

Fig. 3 G.I. Records of presence of *H. coronarium* in Brazil. The map was created by the authors with data retrieved from SpeciesLink.org.br, Reflora.org.br e Jabot.com.br

Even though the biology of the white ginger lily has received quite a lot of attention (especially regarding its medicinal properties), the ecology of this species is still quite understudied, both in its native and introduced range. Due to its widespread presence in the Atlantic forest biome and its potential negative effects on local flora, fauna, and ecosystem functions, we believe it is important to investigate which factors (natural and anthropogenic) facilitate the establishment of *H. coronarium* in riparian corridors.

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Article

Natural and anthropogenic factors facilitate invasion of riparian corridors by *Hedychium coronarium*

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Keywords: Non-native species, Atlantic Forest, Subtropical basin, GLMM

Introduction

Due to an historic human presence, riparian forests are often subject to anthropogenic influence (Connolly and Pearson 2005); the main threats for these ecosystems are land conversion, pollution and species' introductions (Lord and Clay 2006; Wahyuni 2016). In fact, several studies have shown that the anthropogenic alteration of landscapes causes the introduction of exotic plant species that can become invaders of riparian areas (Planty-Tabacchi et al. 1996; Hierro et al. 2006). Human land-conversion can have an effect on an ecosystem invasibility even after some time: forest clearing and subsequent abandonment can lead to grassland environments that are highly prone to invasions (Carboni et al. 2016; Haider et al. 2016). In addition, the environmental heterogeneity of the riverine area – due to frequent natural disturbances such as floods – increases its susceptibility to invasion by non-natives (Naiman and Décamps 1997). Natural routes like rivers are important channels for invasive plant species, many of which can disperse through hydrochory and therefore can carry the invasion process downstream (Richardson et al. 2007).

Riverine plants' invasions can have a negative effect on local fauna and flora (Powell et al. 2011) but also alter ecosystem's properties and processes (Gordon 1998). Riparian forests perform 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). In Brazil, for example, 120 million inhabitants depend on the water supply that is regulated by the riparian corridors of the Atlantic Forest (Fundação SOS Mata Atlântica 2018) but this ecosystem service is put at risk by the progressive loss and transformation of riverine vegetation. In fact, this area is the Brazilian biome that contains the highest number of invasive plants (129) (Zenni & Ziller, 2011).

One of the most common invasive plants in Brazil's marshes and riparian areas is *Hedychium coronarium* Koenig, also known as white ginger lily (English) or lírio-do-brejo (Portuguese) (Zenni and Ziller 2011); native of the Himalayan region, it is a rhizomatous plant belonging to the Zingiberaceae family. Its reproduction is both sexual – with the production of white zygomorphic flowers – and asexual – via rhizomatic propagation (De Souza and Correia 2007). It usually occupies shaded or semi-shaded areas (CABI 2019). The white ginger lily has a recognized commercial value in different fields: its rhizome's essential oil has antimicrobial properties (Joy et al. 2007), while its beautiful flowers can be used for aesthetic purposes or to produce perfume (Verma and Bansal 2010). The white ginger lily has been introduced to 58 countries all over the world, in many of which it is considered as a very invasive weed (Lim 2014). Even though the biology of the white ginger lily has received quite a lot of attention, its ecology is still quite understudied: it seems to have a negative effect on local plants (Instituto Horus - I3N 2019) and on local fauna too (Del-Rio et al. 2017).

Here we investigated the factors associated with the occurrence of *H. coronarium* in 296 plots along riparian corridors in the Maquiné watershed, at southernmost limit of the Atlantic Forest, in the Brazilian state of Rio Grande do Sul. In this area, the white ginger lily has been introduced a long time ago, possibly more than hundred years; the oldest record in the region is from 1934 (PACA-AGP 1351, Herbário Anchieta - Unisinos, Brazil), but it has been previously recorded in eastern Brazil starting from the XIX century (von Martius et al. 2005) and possibly before. This species is heterogeneously spread in riparian forests of the Maquiné river basin, ranging from sites where the species is absent to sites of high plant density. Different studies have shown that the longer is an invasive plant's residence time in a range, the higher is the number of habitats that the non-native plant can occupy and therefore stronger its invasion potential (Pyšek et al. 2015; Feng et al. 2016). Since *H. coronarium* has been long established in the region, we suggest its heterogeneous occurrence is less likely due to dispersal limitation rather than to favorability of local environmental conditions to establishment and persistence. Additionally, we wanted to test the hypothesis that disturbance, either natural or anthropic, should favor *H. coronarium* along riparian corridors. Disturbance is often related to susceptibility to plant invasion (Naiman and Décamps 1997) and streams in the study area are characterized by hydrological and geomorphic fluvial processes that represent natural processes that can constrain the establishment and persistence of plants in the riparian areas (Bendix and Hupp 2000). The Maquiné river's tributaries have marked longitudinal profiles, flowing from elevations of *ca.* 800 m down to 50 m a.s.l. in only 5-10 km, forming constrained valleys where high energy flows and flash floods are common. In this situation, stream banks and the riparian area are frequently subject to cut-and-fill alluviation, which is an erosional-depositional fluvial process that can produce new environments for plant succession (Lorang and Hauer 2017). We hypothesized that local variation in the intensity of this fluvial geomorphic process could affect occurrence of *H. coronarium*.

Specifically, we hypothesized that four mechanisms would increase the probability of the plant's presence in a plot: 1) propagule dispersal via hydrochory (possible thanks to the downstream position in hydrographic network and the presence of sediment deposition's areas, where rhizome fragments can settle); 2) dispersal facilitation by humans (represented by proximity to urban centers); 3) local natural disturbance (elevated stream slope and large stream substrate size as proxies for strong fluvial disturbance); 4) local anthropogenic disturbance (represented by low ecological integrity of riparian sites and presence of introduced tree species, agriculture, and buildings).

Materials and methods

Study area

This study focuses on the distribution of *H. coronarium* in the Maquiné river basin (Fig. 1), which is set in the state of Rio Grande do Sul, Brazil. The region's climate is humid subtropical with high annual rainfall (1400-1800 mm) (Moreno 1961). At the beginning of the 19th century, the area witnessed a massive conversion of forest to agricultural lands (Custodio 2004), but in the last 50 years there has been a decrease of the land use and a regeneration of native vegetation (Becker et al. 2005; Pasquetti et al. 2009).

Data collection

In situ

We registered the occurrence of *H. coronarium* along six tributaries of the Maquiné river (Água Parada, Encantado, Forqueta, Garapiá, Ouro, and Pinheiro), representing also a distance gradient from urban centers (Barra do Ouro e Maquiné, Fig. 1). We selected 148 random sites across the different streams, with a minimum spacing of 100m between sites (Fig. 1).

For each site, we set up on both stream banks a 10x5 m plot adjacent to the water on its longer side (Fig. 2), with the random coordinate as the midpoint; in total, we sampled 296 plots. In each plot, we recorded the presence or absence of *H. coronarium* and ten other local variables, listed in Table 1. For the variables Perturbation of understory vegetation, Intensity of local area's degradation, Intensity of livestock's disturbance, Intensity of agriculture and Abundance of non-native trees, levels (0 to 3) were defined considering Karr's scheme of ecosystem's integrity (1999 – Fig. 3) which takes into account both the gradient of biological condition and the gradient of human disturbance.

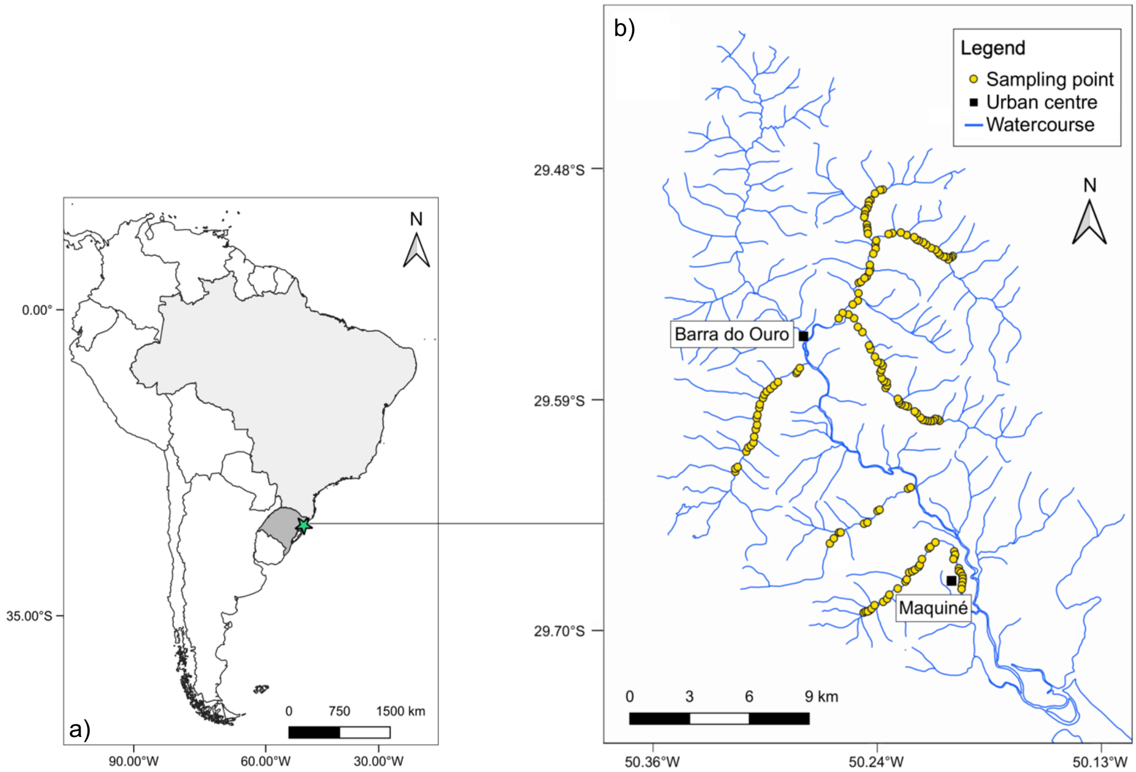

Fig. 1 a) Localization of our study area (green star) in the north coast of the Brazilian state of Rio Grande do Sul (dark grey) **b)** Study area in the Maquiné watershed. Yellow dots represent sampled sites, black squares stand for urban centers and blue lines represent watercourses

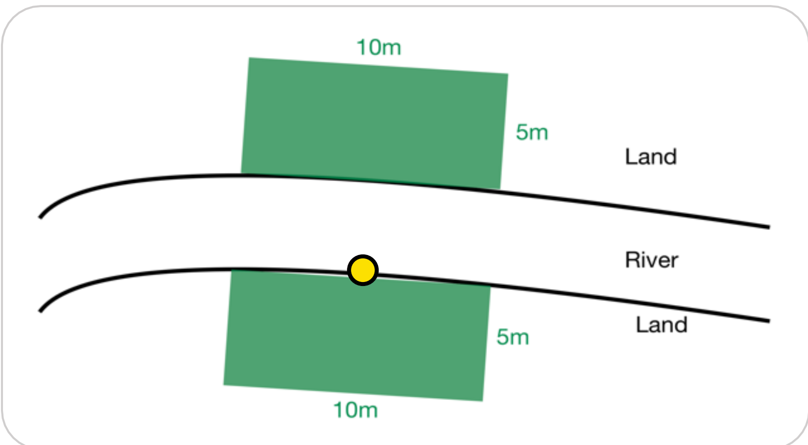

Fig. 2 Sampling scheme for each random GPS point (yellow dot). Two 10x5m plots (green rectangles) are set up, one centered on the GPS point and the other one in parallel position on the opposite bank. Both plots have their longer side adjacent to the bank

Table 1 Independent variables collected via software and in the field. For each variable we present the name, the way it was measured or quantified, the source it came from, what it represents and how it affects invasion

Variable	Measurement	Source	Indicating	How it affects the invasion process
House density	Percentage of area occupied by buildings in a 100m radius buffer	Satellite images and GIS software, as explained in Methods	Human presence	Human disturbance can facilitate invasive plants' establishment
Proximity to nearest urban center	Kilometers along river course	GIS software, as explained in Methods	Human presence	Human disturbance can facilitate invasive plants' establishment
Elevation	Meters above sea level (ma.s.l.)	GIS software, as explained in Methods	Human presence; elevated sites usually don't have a strong human presence	Human disturbance can facilitate invasive plants' establishment
Stream's slope	Angular degrees (°)	GIS software, as explained in Methods	Flood's disruptive power; the more inclined, the higher the energy	Intermediate slopes can facilitate establishment since their floods are strong enough to remove competitors' plantlets but still allowing propagules' arrival
Strahler's stream order	Integer numbers ≥1	GIS software, as explained in Methods	Propagules' supply	If low-order streams are invaded, high-order rivers can receive propagules from multiple sources
Dominant stream's substrate size	Seven size classes: <0.2cm; 0.2-1.6cm; 1.6-6.4cm;6.4-25cm; 25-50cm; 50-100cm; >100cm	Visually assessed in field	Flood's disruptive power; the bigger the substrate size, the higher the energy	Larger substrates can remove competitors' plantlets and create new niches
Erosional/ depositional channel patches	Erosion; deposition; transition area.	Visually assessed in field	Propagules' supply	Deposition can facilitate propagules' supply
Surrounding vegetation type	None; Grass; Shrubs; Trees	Visually assessed in field	Local integrity. High-integrity sites should have trees as dominant vegetation type	Human disturbance can facilitate invasive plants' establishment
Canopy cover	0% to 100%	Visually assessed in field	Local integrity; high-integrity sites should have almost full canopy cover	Human disturbance can facilitate invasive plants' establishment; patterns of sunlight availability can influence establishment success

Perturbation of understory vegetation	0 (absent) to 3 (high)	Visually assessed in the field	Local integrity; high-integrity sites should have an undisturbed understory	Human disturbance can facilitate invasive plants' establishment
Intensity of local area's degradation	0 (absent) to 3 (high)	Visually assessed in the field	Local integrity; high-integrity sites should not have traces of human presence such as trash, water pipes, fire remains or man-made structures	Human disturbance can facilitate invasive plants' establishment
Intensity of livestock's disturbance	0 (absent) to 3 (high)	Visually assessed in the field	Local integrity; high-integrity sites should have little to no signs of livestock presence	Livestock can remove competitors' plantlets and spread propagules
Intensity of agriculture	0 (absent) to 3 (high)	Visually assessed in the field	Human presence	Human disturbance can facilitate invasive plants' establishment and the use of herbicides can remove competitors
Abundance of non-native trees	0 (absent) to 3 (high)	Visually assessed in the field	Local integrity; high-integrity sites should have no exotic trees	Presence of non-native species can facilitate the arrival of others

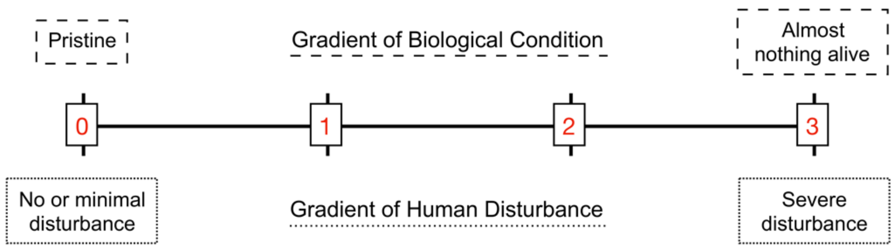

Fig. 3 Scheme representing how ecosystem's integrity is defined both by a biological and an anthropogenic gradient. Numbers in red indicate the levels we implemented to assess Abundance of non-native trees and intensity of Degradation, Livestock's disturbance and Agriculture. Adapted from Karr (1999)

GIS analysis

We used tools in ArcGIS 10.5.1 (ESRI 2011) to generate random sampling points for *H. coronarium* along the stream network and extract the values corresponding to Strahler stream order (1-4), elevation (meters a.s.l.), stream slope (degrees), distance to nearest urban center (km). Strahler order determination along the stream network was based on a modelled stream network (SEMA 2018, 1:25.000 scale), using the Rivex v.10.25 tool (Hornby 2017). Distance to the nearest downstream urban center was measured along the stream network instead of the road network because roads 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 to the main streams. We used the Network Analyst extension in ArcGIS to calculate distance to nearest urban center values. Density of buildings in a 100m 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 10x10m cells on the area occupied by the 100m-radius buffer and counted the number of cells where buildings were present. Stream slope was calculated as the mean slope along a 100 m stream reach centered on the sampling site location.

Statistical analysis

We performed all statistical analyses using the software R (Version 3.5.3 - R Core Team, 2019). Being the presence/absence of *H. coronarium* a binary response variable, we created a Generalized Linear Mixed Model (GLMM) (McCulloch and Neuhaus 2005) with binomial distribution and link function logit, using the library “lme4” (Version 1.1 - Bates, Mächler, Bolker, & Walker, 2015). Maximum Likelihood was estimated using the Laplace approximation (Liu 1993) and the significance of fixed effects was checked with a Wald test (Kenward and Roger 1997). Collinearity between variables was tested assessing the VIF of the model with the “car” package (Version 3.0 - Fox & Weisberg, 2019) using a threshold of 3, as recommended by Hair et al. (2019). The sampling stream of each site was included as a random independent variable with six levels (one per stream). Different models were formulated according to the literature and then selected via comparison of AIC (Akaike 1998); they are presented in Online Resource 1. The final model included the following variables as fixed independent factors: intensity of general degradation, abundance of exotic trees, vegetation type, distance to the nearest urban center, stream's slope, channel substrate size and Strahler's stream order. Since the estimate coefficients of the model are in terms of log(odds) of *H. coronarium*'s occurrence, for an easier comprehension we visualized the results using the "effects" package (Version 4.1 - Fox & 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 checked the simulated residuals for normality with a one-sample Kolmogorov-Smirnov test (Kolmogorov 1956) in the "DHARMa" package and we checked overdispersion using the package "blmeco" (Version 1.3 - Korner-Nievergelt et al., 2015), using 1.4 as threshold as suggested by the author.

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's goodness: the closer to 1 is the value, the more valid is the model. Using the package "cvAUC" (Version 1.1.0 - LeDell, Petersen, & van der Laan, 2014), we calculated a cross-validated AUC estimate and confidence interval.

Results

Hedychium coronarium was found in 205 out of 296 sampling plots (69.3%).

The model's residuals met the assumptions of normality (one-sample Kolmogorov-Smirnov test, D = 0.05, p-value = 0.37) and there was no overdispersion (dispersion=0.89); residual's graphs obtained with the DHARMa package are available in Online Resource 2. There was no collinearity among the variables. The variance of the random effect was 0.186. The cross-validated AUC had a value of 0.877 (lower c.i.=0.836, higher c.i.= 0.919), indicating that the model has a good predictive ability even on unseen data. All the model's variables proved significant in determining the presence/absence of the white ginger lily, except for stream slope. Estimated coefficients from the model are available in Online Resource 3.

Strahler stream order exerted a positive effect on the presence of the ginger lily (Fig. 4a), with riparian corridors of high-order rivers being more likely to host the plant. The distance to the nearest downstream town has a strong negative effect on the occurrence probability of *H. coronarium* (Fig. 4b); the further from an urban center, the more unlikely it is to find the plant.

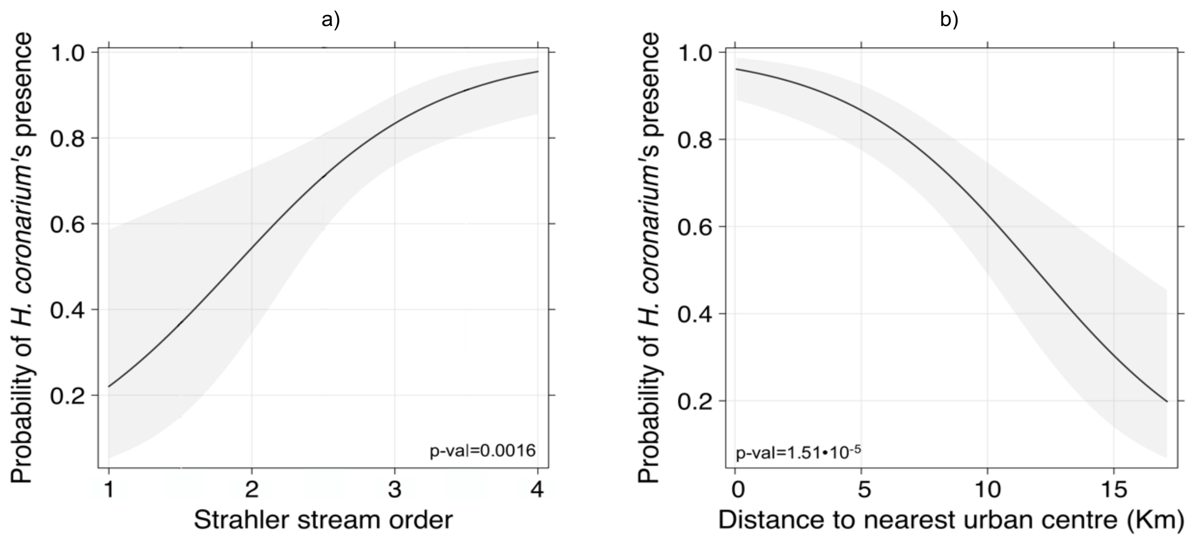

Fig. 4 a) Graphical visualization of the effect of Strahler's stream order on the occurrence probability of *H. coronarium* **b)** Graphical visualization of the effect of distance to nearest downstream urban center on the detection probability of *H. coronarium*

Regarding river substrate size classes, it seems that the higher the size of rocks in the riverbed, the higher is the chance of finding *H. coronarium* (Fig. 5a); small-intermediate sizes of substrate don't fit well in this pattern, but they are also associated with some uncertainty.

The type of local vegetation also proved important in explaining the presence/absence of *H. coronarium*: None and Grass were associated with a lower detection probability than Shrubs and Trees (Fig. 5b).

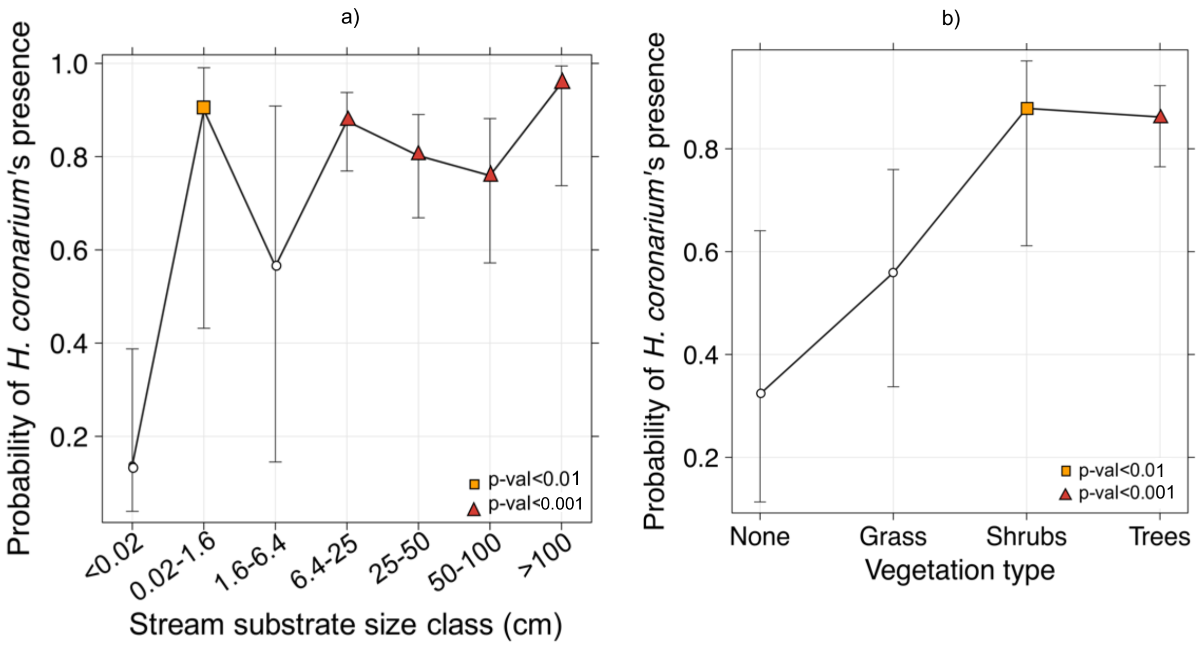

Fig. 5 a) Graphical visualization of the effect of river substrate size classes on the detection probability of *H. coronarium*; significance values are according to the reference level (Size: <0.02) **b)** Graphical visualization of the effect of local vegetation type on the detection probability of *H. coronarium*; significance values are according to the reference level (None)

On a more local scale, the presence of general degradation has a positive strong effect on the detection probability (Fig. 6a), showing a similar pattern to that of abundance of non-native trees (Fig. 6b).

Stream slope has a small negative effect on the probability of detecting *H. coronarium*: the more inclined the stream reach is, the less likely the plant is present; however, this is the only non-significant variable in the model, due to a quite elevated uncertainty for higher values of slope.

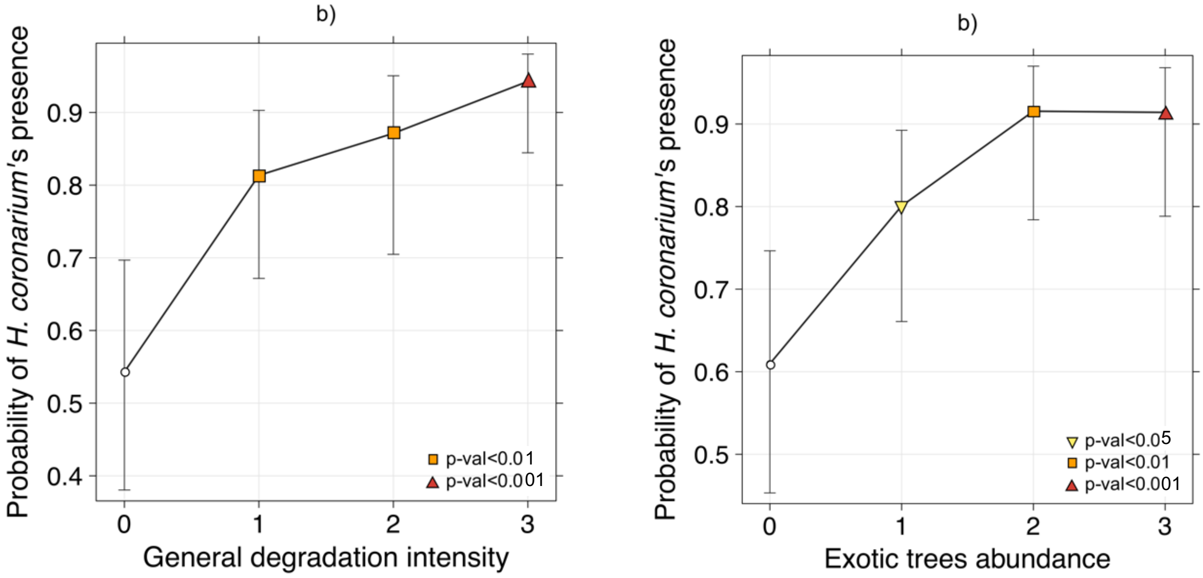

Fig. 6 a) Graphical visualization of the effect of general degradation on the detection probability of *H. coronarium*; significance values are according to the reference level (Degradation=0) **b)** Graphical visualization of the effect of exotic forest abundance on the detection probability of *H. coronarium*; significance values are according to the reference level (Abundance: 0)

Discussion

Our results suggest that the occurrence of *H. coronarium* in riparian areas is influenced not only by dispersal facilitation by humans (distance to urban center) but also by local anthropogenic disturbance (general degradation intensity and exotic tree species abundance). The influence of natural fluvial geomorphic processes was less clear, since only two variables had some effect on *H. coronarium* occurrence (stream substrate size and stream slope). So, although the species has been introduced and spread in the region a long time ago, its present pattern of occurrence still carries the sign of human facilitation of dispersal. Notably, local disturbance, particularly anthropogenic disturbance, was also an important factor for the species' occurrence, supporting the idea that disturbance is an ecologically determinant factor for this plant to establish in riparian areas.

For riverine plants that are able to reproduce asexually via fragmentation, watercourses can act as vehicles for hydrochoric dispersal, for example, by transportation of rhizome fragments to downstream sites, as our results regarding Strahler stream order seem to point out (the probability of white ginger lily presence is greater in streams with higher order number). This could suggest a downstream, "small-to-larger reach", dispersal pattern, and provides support for our first hypothesis which concerns the importance of natural propagule dispersal for the establishment of *H. coronarium*. Furthermore, according to Richardson et al. (2007), high-order streams usually present riparian plant assemblages that change continuously, possibly favoring this way the entrance of non-natives. The presence of erosional/depositional channel patches was not a meaningful variable for our model, possibly because both deposition and erosion have a small positive effect thanks to, respectively, propagules' deposition and competitors' removal.

However, in invasion ecology, a watercourse should not be seen exclusively as a dispersal medium, since its geomorphologic and hydrologic processes can have an effect on local establishment and persistence of plants. For example, the disruptive action of the stream substrate during high-energy flash floods can uproot the vegetation present on the shore (Naiman et al. 1998) and create openings for the arrival of non-natives; following this logic, it is understandable why our results point to larger substrate sizes causing an increase in the presence probability of *H. coronarium*. This is consistent with our third hypothesis, according to which natural disturbance favors the establishment of the invasive plant. Possibly, *H. coronarium* rhizome fragments are not only able to colonize these sites cleared by fluvial disturbance but may be also capable of occupying them faster than native species after disturbance events.

When determining priority areas for invasive species management, it is important to consider both the regional and the local scale of human presence. The results provide support for the second hypothesis we formulated, as proximity to an urban areas resulted in a higher chance of finding *H. coronarium*. In fact, areas closer to urban centers have a greater human presence than remote areas, and they usually undergo many processes of anthropogenic transformation (such as forest clearing) that create openings for the arrival of non-natives; in addition, closer to urban centers there is usually a higher movement of vehicles that might favor the plant's spread. In addition, in areas where human settlements were established quite recently, it is important to consider the history of the region's development. The white ginger lily was probably brought to the Maquiné watershed by the European colonizers that settled in the area from 1840 onwards (Pasquetti et al. 2009); the colonization proceeded from the highlands to the littoral along the course of the Ouro river, which – not surprisingly – is the only stream that doesn't present a clear pattern of association between *H. coronarium*'s presence and distance to an urban center. Knowledge of historic land-use can shine a light onto contemporary invasion patterns that are otherwise harder to explain (Mattingly and Orrock 2013).

When possible, however, an *in loco* measure of degradation might provide a clearer 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 novel 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 the study of Haider et al. (2016) on *H. coronarium*, the species was strongly associated with herbaceous patches, while in our research the white ginger lily was rather linked with shrub and tree vegetation, as is to be expected – being the species a forest-dwelling plant. This difference might also be ascribed to the different landscape evolution of the study area of Haider et al. (2016) (mostly converted to grassland in the 1950s) and ours, where the herbaceous patches were much younger and often inside of residential properties; therefore, perhaps the ginger lily wasn't present in our grassland plots because of the frequent maintenance of the area by the residents. Moreover, the strong positive effect of tree vegetation on the detection of *H. coronarium* might be due to the provisioning of partial shadow, which is ideal for the optimal growth of this species (CABI 2019). In addition, Santos et al. (2005) noticed a strong influence of partial shade on *H. coronarium*'s 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 can favor both growth and reproduction of this species.

A significant presence of non-native trees in the area increases, even more, the presence probability of the white ginger lily. This relationship is in agreement with the Invasional Meltdown hypothesis of Simberloff and Von Holle (1999), according to which the presence of a non-native species can facilitate invasion from others by increasing both its likelihood of survival and its possible ecological impact. Introduced pine trees (*Pinus* sp), for example, are known to make the soil pH more acid (Amiotti et al. 2000), which might be unfavorable for local plant species but does not constitute an obstacle for *H. coronarium* (Gilman 2014).

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, both natural and anthropogenic factors proved important to facilitate the establishment of *H. coronarium*. Our results shed light on the fact that local area degradation, along with the presence of exotic tree species and proximity to urban areas increases the probability of finding the white ginger lily in riparian corridors due to propagule supply, reduction of competition and high levels of disturbance. Riverine forests are ecotones between land and water and therefore it is understandable that both terrestrial and hydrologic factors have an effect on the establishment of *H. coronarium* in these ecosystems. Streams can transport propagules downstream but also create available niches for the plant, thanks to the disruptive action of sediments during floods. The type of surrounding vegetation can have an effect on the plant's growth and reproduction, which are optimal in partial shade conditions.

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Online Resource 1

Table 1 O.R.1 Different model combinations tested and their AIC values. Model 14 (highlighted in green) resulted as the best-fitting model

Model N°	House density	Proximity to nearest urban center	Elevation	Stream's slope	Strahler's stream order	Dominant stream's substrate size	Erosional/ depositional channel patches	Surrounding vegetation type	Canopy cover	Perturbation of understory vegetation	Intensity of local area's degradation	Intensity of agriculture	Abundance of non-native trees	AIC
1											•			339.8
2									•		•	•	•	334.1
3				•		•	•							341.9
4			•			•	•							316.8
5		•			•					•	•		•	318.2
6	•	•								•				350.9
7				•		•	•	•			•			313.4
8						•		•			•		•	310.7
9			•			•	•				•			304.9
10				•			•	•						352.3
11			•				•	•						337.7
12			•	•		•								316.5
13			•						•	•		•		354.1
14		•		•	•	•		•			•		•	279.9
15						•		•			•		•	310.1
Null														358.2
Full	•	•	•	•	•	•	•	•	•	•	•	•	•	284.3

Online Resource 2

The DHARMa package (Hartig 2016), creates residual graphs for generalized linear mixed models that can be interpreted as intuitively as the ones of linear models. Residuals are obtained via a simulation-based approach, similar to the Bayesian p-value or the parametric bootstrap, that transforms the residuals to a standardized scale between 0 and 1.

In the QQ plot (Fig. 1 of Online Resource 2) residuals should be aligned. In the Standardized VS predicted residuals plot (Fig. 2 of Online Resource 2) quantile lines should start at y-values of 0.25, 0.5 and 0.75 and be horizontal; however, that some deviations from this are to be expected by chance (Hartig 2016).

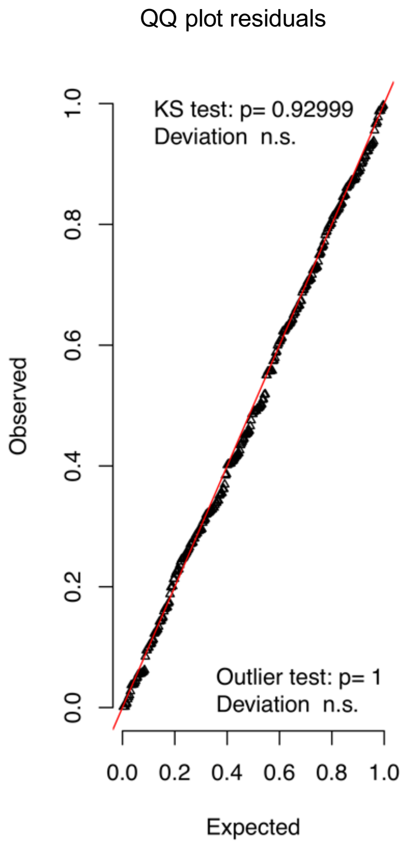

Fig. 1, O.R.2 QQ plot of simulated residuals for the final model

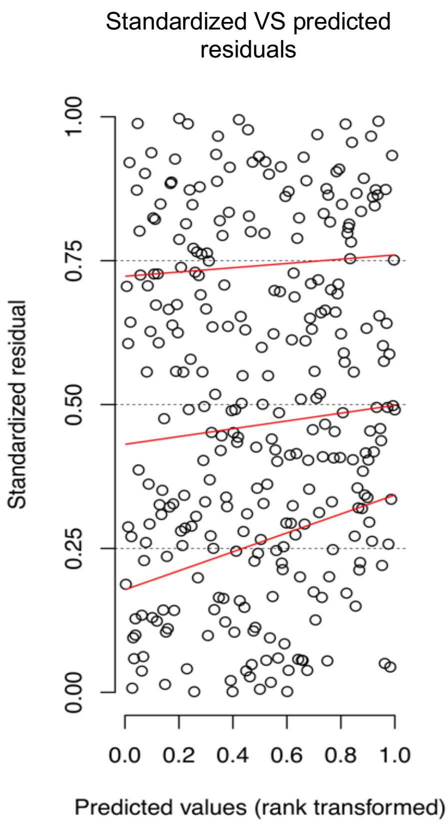

Fig. 2, O.R.2 Standardized VS predicted residuals' plot

Online Resource 3

Table 1, O.R.3 Coefficent Estimate and Standard Error for the intercept and for each variable of the final model. For categorical variables, coefficients are shown for each level except for the "Level 0", which is used as reference. Coefficients are in terms of change in the log(odds) of *H. coronarium*'s occurrence

Variable	Coefficient Estimate	Std. Error
(Intercept)	-7.69102	1.59263
Local area's degradation – 1st level (low intensity)	1.30037	0.4256
Local area's degradation – 2nd level (medium intensity)	1.74033	0.58954
Local area's degradation – 3rd level (high intensity)	2.62964	0.64449
Type of vegetation - Grass	0.97721	0.7446
Type of vegetation - Shrubs	2.71897	1.00332
Type of vegetation - Trees	2.57064	0.74673
Stream substrate size – 0.02-1.6cm	4.02573	1.46577
Stream substrate size – 1.6-6.4cm	2.08934	1.21967
Stream substrate size – 6.4-25cm	3.78476	0.79896
Stream substrate size – 25-50cm	3.2268	0.76026
Stream substrate size – 50-100cm	2.97748	0.80422
Stream substrate size – >100cm	4.94974	1.29274
Abundance of non-native trees – 1st level (low intensity)	0.94519	0.42028
Abundance of non-native trees – 2nd level (medium intensity)	1.93729	0.59927
Abundance of non-native trees – 3rd level (high intensity)	1.91856	0.56322
Strahler's stream order	1.43846	0.45635
Distance to nearest urban center	-0.27002	0.06241
Stream's slope	-0.06072	0.02919

<u>~ End of article ~</u>

General conclusion

Even though not all introduced species have negative consequences on local biodiversity and ecosystem processes, a few factors suggest that *Hedychium coronarium* might deserve attention in this sense. Thanks to its fast growth and clonal reproduction, this plant is able to rapidly colonize large areas and might have negative effects on local vegetation. For example, Haider et al. (2016) argue that in the long run *H. coronarium* might exert a negative influence on tree species by inhibiting the germination of their seedlings, as has been proven for the closely related *Hedychium gardnerianum* (Minden et al. 2010).

The spread of this invader at the expense of local plants can also affect animal species: according to Del-Rio et al. (2017), areas invaded by the ginger lily are avoided by the endemic and vulnerable bird São Paulo Marsh Antwren (*Formicivora paludicola*), and a further increase in occupied areas poses a serious threat to the remaining populations of this bird. Since it often grows on river's and lake's banks, the white ginger lily can affect also aquatic species: two studies showed that the presence of *H. coronarium* decreases dissimilarity of freshwater insect assemblages (Saulino and Trivinho-Strixino 2017a) as well as it simplifies their trait composition (Saulino and Trivinho-Strixino 2017b). The white ginger lily has also proven to have the capacity of altering the ecosystem's characteristics: in a subtropical reservoir, the littoral zone near banks fully occupied by *H. coronarium* was deeper than banks partially invaded or with native vegetation, due to the plant's vegetative growth into open areas of the reservoir; water near these invaded strands also had a lower pH (Saulino and Trivinho-Strixino 2017a).

Considering all these mentioned aspects, it is of fundamental importance to find and implement efficient control to the spread of *H. coronarium*. In addition, according to Costa et al. (2017,) anthropic climate change is likely to cause an increase in the suitable area for this invasive species in South America, and especially in the Atlantic Forest biome.

However, when formulating restoration plans, it is important to try and disentangle the relationship between human disturbance, presence of invasive species and changes in ecosystem processes; in fact, physical environmental changes could be due to either dominance from a non-native species or to the perturbation that initially allowed the invader to establish, or to an interaction of the two. The question "Are invasive species the drivers or passengers of change in degraded ecosystems?" (MacDougall and Turkington 2005) is an issue that merits careful thought in the context of ecosystems' restoration after invasion.

To prevent a further spread of *H. coronarium* in the Maquiné watershed it is fundamental to establish a dialogue with the local population and develop a management plan involving all stakeholders. The species' intentional planting in residential yards should be avoided at all costs, as riparian invaders are more likely to escape gardens and horticultural activities than other types of invaders (Catford and Jansson 2014).

At the moment, an optimal solution for the control of *H. coronarium* still hasn't been found. The clear-cutting of the plant's stem has been shown to actually promote biomass production (Maciel 2011), and if performed in riparian stands it can cause the input of rhizome fragments in the water current and thus their dispersal. Rhizome eradication is the method that leads to the highest reduction in this plant's biomass (Maciel 2011) and ideally it should be performed before the winter period to avoid the dispersal of their fragments by hydrochory (Santos et al. 2005); however, this method is very costly and hard to perform due to the rigidness of the roots. The usage of herbicides is also impractical as well as illegal in riparian areas of Brazil. Biological control through the usage of fungal pathogens has been proposed by Ellison and Barreto (2004) and Soares and Barreto (2008) identified five potential microorganisms for the control of *H. coronarium* in Brazil; yet, this method still hasn't been implemented in any management plan.