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RESEARCH ARTICLE

Integrating management techniques to restore subtropical forests invaded by *Hedychium coronarium* J. Köenig (Zingiberaceae) in a biodiversity hotspot

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The restoration of areas invaded by non-native plants is challenging as invasive plants may affect both biotic and abiotic components of ecosystems, leading to impacts that constrain recolonization by native species after invaders are eliminated. In such a scenario, restoration techniques as topsoil transposition might accelerate colonization by native species in forests. *Hedychium coronarium* J. Koenig (Zingiberaceae) is a Himalayan herbaceous rhizomatous plant recognized as invasive in several countries. This study aimed to experimentally evaluate the response of plant assemblages to topsoil transposition on a site invaded by *H. coronarium* after chemical control. Four treatments were applied: chemical control integrated with topsoil transposition, chemical control of *H. coronarium* alone, topsoil transposition alone, and no intervention (control). Plots were evaluated prior to the application of treatments and then monthly for 11 months after treatments. Parameters were measured for *H. coronarium* (number of ramets, ramet height, and cover) and other species (species richness, abundance, and cover). Plots treated with chemical control (regardless of topsoil transposition) were similar in terms of all parameters measured and species composition, with dominance of herbs and shrubs. Plots managed solely with topsoil transposition had lower species richness, abundance, and cover, but more diverse life-forms, being equally rich in climbers, trees, and herbs. Chemical control was effective to control invasion by *H. coronarium* and increase species richness and abundance on the managed site. Topsoil transposition promoted colonization by species that might accelerate restoration.

Key words: chemical control, forest succession, invasive non-native plant, regeneration, restoration, topsoil transposition

Implications for Practice

- Chemical control is an efficient management technique for *Hedychium coronarium* as well as to allow regeneration by native species from the surrounding vegetation.
- Topsoil transposition alone is not recommended for the restoration of forests invaded by *H. coronarium*. This technique did not eliminate the invader, but resulted in the establishment of native tree species in more advanced successional stages.
- Topsoil transposition associated to herbicide application might accelerate forest succession as the integration of techniques enables seedlings of later successional species to establish.

Introduction

The new geological era named Anthropocene is marked by a dramatic increase in human activity around the globe (Steffen et al. 2011, 2018). The transposition of biogeographical barriers associated with human activities leads to intentional and unintentional introductions of species, with no sign of saturation in the accumulation of introductions over time (Capinha et al. 2015; Seebens et al. 2017). Invasive species are those introduced species that overcome biotic and abiotic barriers and establish populations beyond the point of introduction (Richardson et al. 2000; Blackburn et al. 2011). The introduction and establishment of non-native species combined with the increase in the rate of extinction of native species contribute to biotic homogenization (McKinney & Lockwood 1999; Olden et al. 2004). As a consequence, biological invasions are a major global threat to biodiversity and to nature's contribution to people (Diaz et al. 2019).

Although the control of invasive non-native plants is one of the fundamental elements for ecological restoration

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(D'Antonio & Meyerson 2002), plant invasions hinder restoration achievements around the globe (Gaertner et al. 2012a; Prior et al. 2018). The magnitude of impacts caused by invasive plants is context-dependent and may vary with time, invader density and traits, and characteristics of the recipient community (Catford et al. 2019; Sapsford et al. 2020). Depending on the magnitude of impact, different measures for the restoration of invaded areas are necessary (Gaertner et al. 2012b). In addition, legacy effects of invasive non-native species in invaded ecosystems may pose difficulties to restoration efforts after invaders are eliminated (Gaertner et al. 2012a; Sapsford et al. 2020). For instance, the recovery potential of indigenous plants in South African *fynbos* after the exclusion of invasive non-native plants varied with time since invasion and the identity of the invasive species. Control efforts in areas previously occupied by *Acacia saligna* resulted in higher cover by invasive non-native species than those previously invaded by *Pinus radiata* (Mostert et al. 2017). Legacy effects may also generate changes in the local seed bank in invaded sites (Gioria & Pyšek 2016). These effects may be persistent, as shown for areas invaded by *Rhododendron ponticum* in Scotland after the invasion was eliminated (Maclean et al. 2018). Therefore, natural regeneration of native species in invaded areas must not be assumed as certain after invasive species are controlled (Sapsford et al. 2020). Complementary efforts are often required for effective ecological restoration (Maclean et al. 2018).

Restoration techniques that promote natural succession may accelerate the occupation of restoration sites by native species. One of these techniques is the transposition of topsoil, which implies the removal of a layer of soil from a local plant community in a more advanced successional stage and its transfer to the area to be restored. This technique can help overcome environmental conditions that may lead to dispersal limitation and constrain natural regeneration in degraded ecosystems (Pilon et al. 2019). Topsoil transposition is intended to increase the probability of soil recolonization by microorganisms and to introduce propagules such as root fragments and seeds (Siminski & Tres 2014; Ferreira et al. 2015). Topsoil transposition may also increase species richness in managed areas (Silva et al. 2015; Piaia et al. 2017; Pilon et al. 2019). The successful use of this technique in areas previously occupied by invasive species has also been documented. Areas of Brazilian savannas (Cerrado) invaded by *Urochloa decumbens* (an African grass) where topsoil was transposed resulted in increased species richness and cover of native grasses (Pilon et al. 2018). Topsoil transposition and seed rain were the techniques resulting in the highest density of native plants in a study that compared six restoration techniques in a riparian forest previously invaded by *Pinus elliottii* (Schorn et al. 2010).

Around the world, riparian forests, wetlands, and disturbed areas are being invaded by *Hedychium coronarium* J. Koenig (white ginger, Zingiberaceae), a pervasive invasive plant in several countries (ISSG 2007; Motooka et al. 2002; Sampaio & Schmidt 2013; Witt et al. 2018). This invasive species reproduces vegetatively by rhizomes, forming dense thickets (Kissmann & Groth 1997; Manish 2013). There is evidence that the shade originated by dense stands is a barrier to the establishment of saplings of native species (Haider et al. 2016). Although information about the control of *H. coronarium* is available (Dechoum & Ziller 2013), studies focused on methods to restore the degraded habitat after invasion control are still missing. Additionally, topsoil transposition has not been as commonly used for restoration as other techniques, such as seedling planting in the Atlantic Rainforest (Guerra et al. 2020).

The present study was aimed at experimentally assessing the potential of using chemical control on *H. coronarium* integrated with topsoil transposition for restoration in a degraded riparian forest. We compared the number and height of *H. coronarium* ramets as well as regenerating plant species richness, cover, and abundance in plots subjected to four treatments: (1) chemical control integrated with topsoil transposition, (2) chemical control of *H. coronarium* alone, (3) topsoil transposition alone, and (4) no intervention (control). Our first prediction was that experimental plots managed with chemical control integrated with topsoil transposition would result in lower number and height of ramets and higher plant species richness, cover, and abundance compared with plots managed with other treatments. Our second prediction was that plant composition in plots where topsoil transposition was applied would become more heterogeneous than in plots managed with other treatments. This prediction is based on the premise that topsoil transposition enables the arrival of propagules of a more variable set of plant species from surrounding forest fragments from which dispersal might be limited due to environmental barriers.

Methods

Study System

The study site is located in the Ibirama National Forest, a federal protected area established in 1988 that covers approximately 520 ha in southern Brazil (geographic coordinates −27,039573°S, −49,471,389°W). According to the Köppen–Geiger classification, the climate is subtropical, humid mesothermic with hot summers (Cfa) for the region (Instituto Chico Mendes de Conservação da Biodiversidade 2008). Elevation varies from 250 to 580 m a.s.l. The total average annual rainfall varies between 1,400 and 1,600 mm, and the annual average temperature varies between 18 and 20°C (INMET 2018).

About 460 ha of the protected area is covered by native vegetation (Atlantic Rainforest, average height 25–30 m), mostly secondary forest in an advanced stage of succession. Part of the primary forest was felled in the 1950s and 1960s, when a sawmill was established as part of the state policy for wood exploitation (Instituto Chico Mendes de Conservação da Biodiversidade 2008). The remaining area is represented by fragments of primary forest and forests in early and intermediate successional stages surrounded by degraded or converted areas (rural roads, cultivation areas, and pastures in neighboring properties). There are six invasive non-native species documented for the area, including *Hedychium coronarium* (Instituto Chico Mendes de Conservação da Biodiversidade 2008).

Hedychium coronarium is a perennial herb native to areas in Nepal and India, in the region near the Himalayas, up to altitudes of 1,900 m. Pseudostems (also called ramets) about 2 m tall develop from rhizomes. Fruits are ellipsoid to oblong, measuring 22–25 mm, and contain numerous orange-reddish seeds of about 5 mm in length (Chiba 2014).

The species was disseminated by human activities and is established in different biomes in Brazil, including the Cerrado, Caatinga, and Atlantic Forest (Zenni & Ziller 2011). Impacts include obstruction of water flow in channels, streams, and wetlands, and the displacement of native species as a consequence of fast vegetative growth (CABI 2014; Haider et al. 2016). There are records of invasion for *Hedychium* species in pristine forests in Hawaii and the Reunion Islands, where seeds are dispersed by birds (Rejmánek 1996) that feed on the red aril. Establishment of new invasion *foci* is therefore unpredictable and increases the difficulty of control. The invasiveness of *H. coronarium* is partially attributed to phenotypic plasticity—a larger quantity of amyloplasts accumulate in the rhizomes of plants invading non-flooded areas, which is an adaptation to less favorable conditions that facilitate the occupation of a wide range of environments (Almeida 2015). The species is also able to sprout from small rhizome fragments, a fact that needs to be taken into account in order to prevent further spread due to management techniques (Almeida 2015). Dechoum and Ziller (2013) verified that foliar spray using glyphosate in a 3% dilution is efficient to control *H. coronarium*. Around 95% of the ramets (including leaves and root systems) were dry at the end of the experiment (after 20 months since the first herbicide application). The herbicide was reapplied every 3 months during the experiment.

Hedychium coronarium is commonly observed in riparian areas in the Ribeirão do Coxo basin where the studied National Forest is located, both in forests and open areas along watercourses and wetlands in the protected area. The experiment was conducted in a riparian forest impacted by siltation due to a reservoir built downstream in Ribeirão do Coxo in the 1980s. Sand banks were formed on one side of the stream. This area would most likely have evolved into native forest in due course, as on the opposite side (Supporting Information, Table S1–Table S26 and Figure S1–S2.). Over time, the sand banks were invaded by *H. coronarium* which covers approximately 0.64 ha of the study area (27,038368°S, −49,470,281°W).

Experimental Design and Data Collection

An experiment with 12 randomized blocks was established between 18 and 22 July, 2017. Each block included four 1 m^2 plots, with 48 plots in total. The plots were set up at 1 m distance in order to prevent the interference of treatments on ramets from neighboring plots, as rhizomes can grow to 60 cm in length according to measurements taken from the study site. Plots were delimited with wooden poles. The vegetation in the space between plots was regularly mown as necessary to keep ramets lower than 15 cm in height. The minimum distance between blocks was f4 m.

Each plot inside each block was selected at random to receive one of the following treatments: "Soil"—cutting and topsoil transposition; "Herb"—cutting and foliar application of glyphosate herbicide at a 3% dilution on *H. coronarium* sprouts; "Soil +Herb"—cutting, foliar application of glyphosate herbicide at a 3% dilution on *H. coronarium* sprouts and topsoil transposition; and "Control"—no intervention. Only ramets of *H. coronarium* were cut in the plots subjected to treatments "Soil," "Herb," and "Soil+Herb." *Hedychium coronarium* ramets were cut only once, when the experiment was established.

Before treatments were applied, number of *H. coronarium* ramets, mean height of ramets (mean of 10 ramets selected at random), percentage of cover by *H. coronarium* and by other species (native and non-native), plant species richness (all except *H. coronarium*), and abundance of individuals per species (all except *H. coronarium*) were recorded for all plots. Percentages of cover by *H. coronarium* and by other species were visually estimated and classified as: Class 1: 0–5% cover (median: 3%); Class 2: 5–25% (median: 15%); Class 3: 25–50% (median: 37.5%); Class 4: 50–75% (median: 62.5%); Class 5: 75–95% (median: 85%); Class 6: 95–100% (median: 97.5%), as in Daubenmire (1959). Median values were used in statistical analyses. Ramets subjected to treatments "Soil," "Herb," and "Soil+Herb" were cut with a machete close to ground level in July, 2017.

Approximately 1 month later (16 August, 2017), sprouts were treated with punctual herbicide application once they reached about 15 cm in height (Dechoum & Ziller 2013). Punctual spraying on low sprouts generated good results with a low volume herbicide application in comparison with spraying ramets at their top height without former cutting (Dechoum & Ziller 2013). Foliar spray was conducted with a 1.25 L hand sprayer in the plots subjected to treatments Herb and Soil+Herb. The herbicide used (Nortox 480 BR) has glyphosate as active ingredient and was applied at a 3% dilution with a dye used to mark treated plants, according to the method described by Dechoum and Ziller (2013). Safety measures were adopted for application, such as the use of personal protection equipment to minimize exposure to the herbicide.

Topsoil was transposed 2 days after chemical control in the plots subjected to treatments Soil and Soil+Herb. The topsoil used was collected from two nearby areas inside the Ibirama National Forest (geographic coordinates: −27.044764°S, −49.458728°W, and − 27.037943°S, −49.461157°W) with native forest cover in advanced successional stages. A layer of about 5 cm of soil plus litter were collected. After collection, the soil from each area was revolved to ensure homogenization, then transported for application on the plots forming a layer approximately 5 cm thick.

The first of 11 monthly evaluations of the experiment after treatment implementation was conducted approximately 1 month later, on 19 September , 2017. The same parameters considered in the initial evaluation were observed. Complementary applications of chemical control were conducted in September, 2017, January and March, 2018, always following monthly evaluations, when ramets reached 15 cm in height. Herbicide was applied individually on each ramet to prevent affecting neighboring individuals.

Each plant present in the plots was tagged, taxonomically identified, and classified by life-form (e.g. tree, shrub, subshrub, climber, or herb [Klein 1979; Reflora 2018]) and origin (native or non-native) (Reflora 2018; Tropicos 2018).

Statistical Analyses

The data collected during the initial evaluation of the experiment (July, 2017), before treatments, were analyzed using generalized linear mixed models (GLMM) to detect differences in response variables between treatments. In each model run for each response variable (number of ramets of *H. coronarium*; abundance, cover, and richness of regenerating plant species), treatments were considered fixed effects while blocks were considered random effects for the evaluation of uniformity of the study site.

The differences between the values obtained for the parameters observed in the last evaluation of the experiment and those in the initial evaluation (before treatments) were used as response variables. Treatments were inserted in models as fixed effects, and blocks as random effects. Linear mixed models (LMM) were adjusted for the relation between part of the response variables (number of ramets that sprouted and percentage of cover by *H. coronarium*) and the explanatory variable (treatment). GLMM were adjusted for the remaining response variables. The validation of models was conducted from a graphic analysis of residues. Contrasts between the factors of the explanatory variable were established for each model, and *p* values were adjusted for multiple comparisons using the HolmBonferroni method (Holm 1979).

In order to test the second prediction, matrices of dissimilarity in species composition were generated from these data based on the Bray–Curtis index and used for the graphic representation of the PCoA and for comparison by means of permutational multivariate analysis of variance (PERMANOVA). Abundance matrices per plot and per treatment were built for the months of January and July, 2018. Data of the initial evaluation (July, 2017) were not used in this analysis because there were very few individuals of other species at the time, which made any comparison impossible.

All analyses were conducted in RStudio environment version 1.0.153 (R Core Team 2017) using the *car* (Fox & Weisberg 2011), *ggplot2* (Wickham 2009), *lme4* (Bates et al. 2015), *MASS* (Venables & Ripley 2002), *multcomp* (Hothorn et al. 2008), *sciplot* (Morales 2017), and *vegan* (Oksanen et al. 2017) packages.

Results

Initial Evaluation

Only differences in the number of ramets (Fig. 1A) were observed during the initial evaluation (before treatments) between plots subjected to different treatments in the study site: plots subjected to treatment Herb had more ramets than treatments Soil and Control (Supporting Information, Tables S1 and S2). Ramet mean height (Fig. 1B; Supporting Information, Tables S3 and S4) and percentage of cover by *H. coronarium* (Fig. 1C; Supporting Information, Tables S5 and S6) did not differ between treatments.

Very few individuals of other species were observed during the initial evaluation. Therefore, no difference in richness (Fig. 1D), abundance (Fig. 1E), or percentage of cover by regenerating species (Fig. 1F) was observed between plots subjected to the different treatments (Supporting Information, Tables S7 to S12). Three species were registered: *Cyperus* sp. (Cyperaceae), *Sphagneticola trilobata* (Asteraceae), and *Brugmansia suaveolens* (Solanaceae), the latter a non-native species.

Evaluation of Cover, Richness, and Abundance of Regenerating Species

When comparing the difference between the data collected in the beginning and at the end of the experiment, the number, height, and cover of ramets increased in Control and Soil treatments and decreased in Herb and Soil+Herb treatments (Figs. 2A–C; Supporting Information, Tables S13–S18). Conversely, the increase was approximately double for plant species richness, three times for abundance,and more than seven times for cover of regenerating species per plot in treatments Herb and Soil+Herb than in treatments Soil and Control (Figs. 2D–F; Supporting Information, Tables S19 and S24). Variation in the number of ramets, height of ramets, percentage of cover by *H. coronarium*, and cover, abundance, and species richness over time are shown in Figure S2 (Supporting Information).

Evaluation of Species Composition

A total of 109 species were registered throughout the months of the experiment, 76 of which identified to the level of species, 23 to the level of genus, eight to the level of family, and two were not identified (Supporting Information, Table S25). In the last evaluation, herbs predominated in plots in Control and treatments Herb and Soil+Herb, while in plots subjected to treatment Soil an even number of trees, climbers, and herbs was observed, with higher abundance of tree species (Tables 1 and 2).

Nine (8.26%) of the 109 species registered were observed in all treatments throughout the experiment (Supporting Information, Tables S25 and S26). The occurrence of 11 non-native species was also registered (10.1%) — two of which (*Eucalyptus* sp. and *Solanum lycopersicum*) were only represented by one individual that, in both cases, died before the end of the experiment.

Species composition in plots in the sixth month (January, 2018) and at the end of the experiment (July, 2018) differed between treatments (Fig. 3A,B, respectively). In both cases, there was no superposition between Control, Soil, and Herb. Treatment Soil+Herb was more variable in composition and was partially superposed with all other treatments (Fig. 3A,B).

There were no species in common between plots in treatment Soil and other treatments in terms of the most abundant regenerating species, and two native species predominated: *Euterpe edulis* and *Trema micrantha* (Table 2). Individuals of these species were also observed during monthly evaluations in plots in treatment Soil+Herb, but few saplings survived until the last month (Supporting Information, Table S26). The presence of non-native plants among the five most abundant species was only observed in plots treated with herbicide (Herb and Soil+Herb).

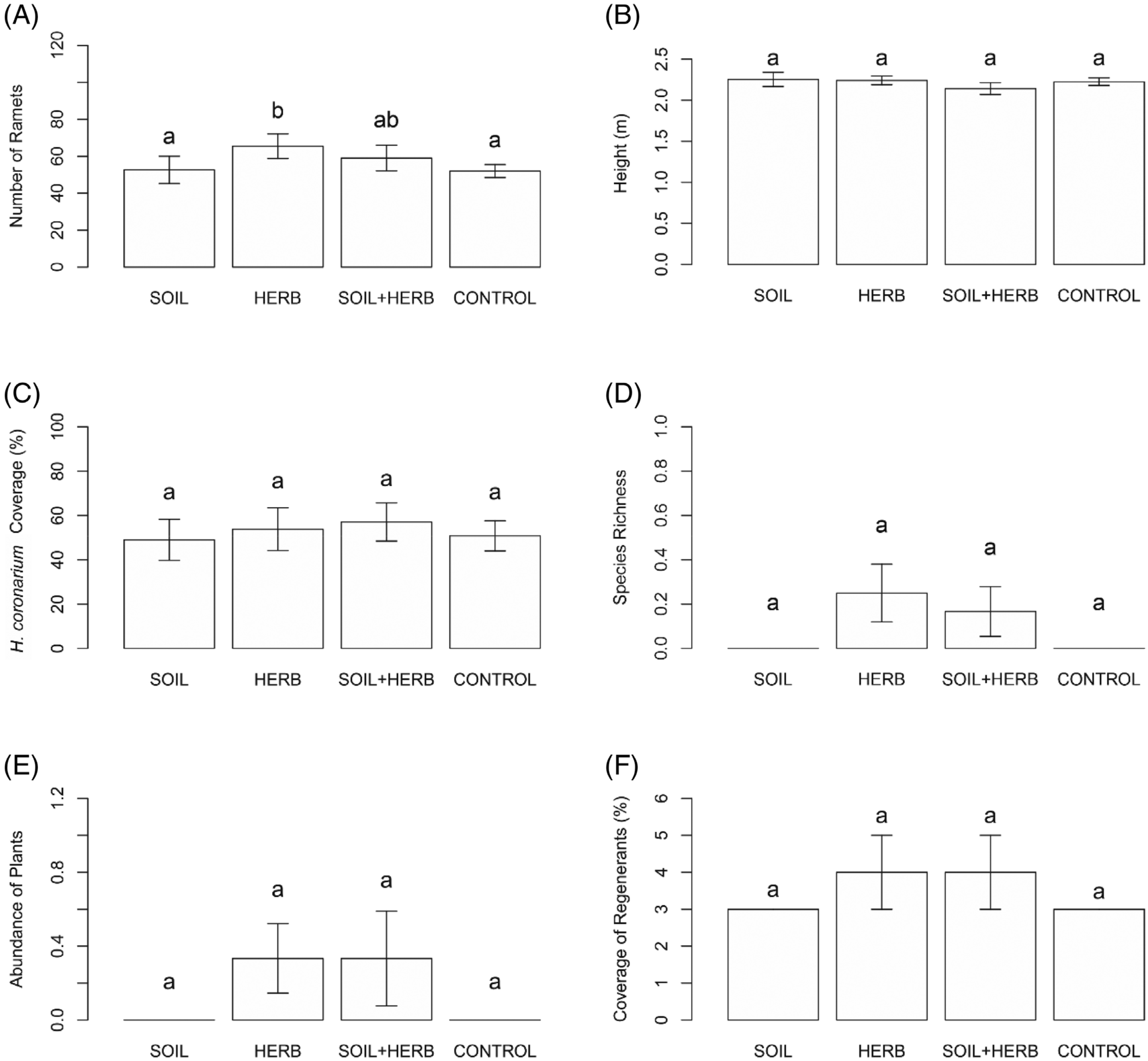

Figure 1 Mean (±SE) of variables calculated per plot using data from the initial evaluation of plots subjected to different treatments, conducted in July,2017 in the study site located in the Ibirama National Forest (Ibirama, SC, Brazil). The *x*-axis corresponds to treatments Soil (cutting and topsoil transposition), Herb (cutting and herbicide application), Soil+Herb (cutting, herbicide application and topsoil transposition), and Control (no intervention). In the *y*-axis: a, number of *Hedychium coronarium* ramets; b, mean ramet height; c, cover by *H. coronarium*; d, regenerating species richness; e, abundance of regenerating species; f, cover by regenerating species. Different letters indicate significant differences between results detected in contrasts a posteriori, with adjusted *p* values.

Discussion

While herbicide application was effective to control *H. coronarium*, topsoil transposition enabled seedlings of later successional species to establish, accelerating forest succession. The integration of these techniques is therefore effective for forest restoration. Our first prediction that the association between topsoil transposition and chemical control of *H. coronarium* (treatment Soil+Herb) would result in higher regenerating plant species richness, cover, and abundance was not corroborated. These response variables (regenerating plant species richness, cover, and abundance) were similar in Herb and Soil+Herb treatments, and higher than those observed in Soil and Control treatments. On the other hand, the prediction that species composition in plots subjected to topsoil transposition would be more heterogeneous than in plots subjected to other treatments was corroborated: the Soil+Herb treatment resulted in a larger variation in species composition. From a functional perspective, trees were the predominant life-form in the treatment Soil, whereas herbs were predominant in treatments Soil+Herb and Herb.

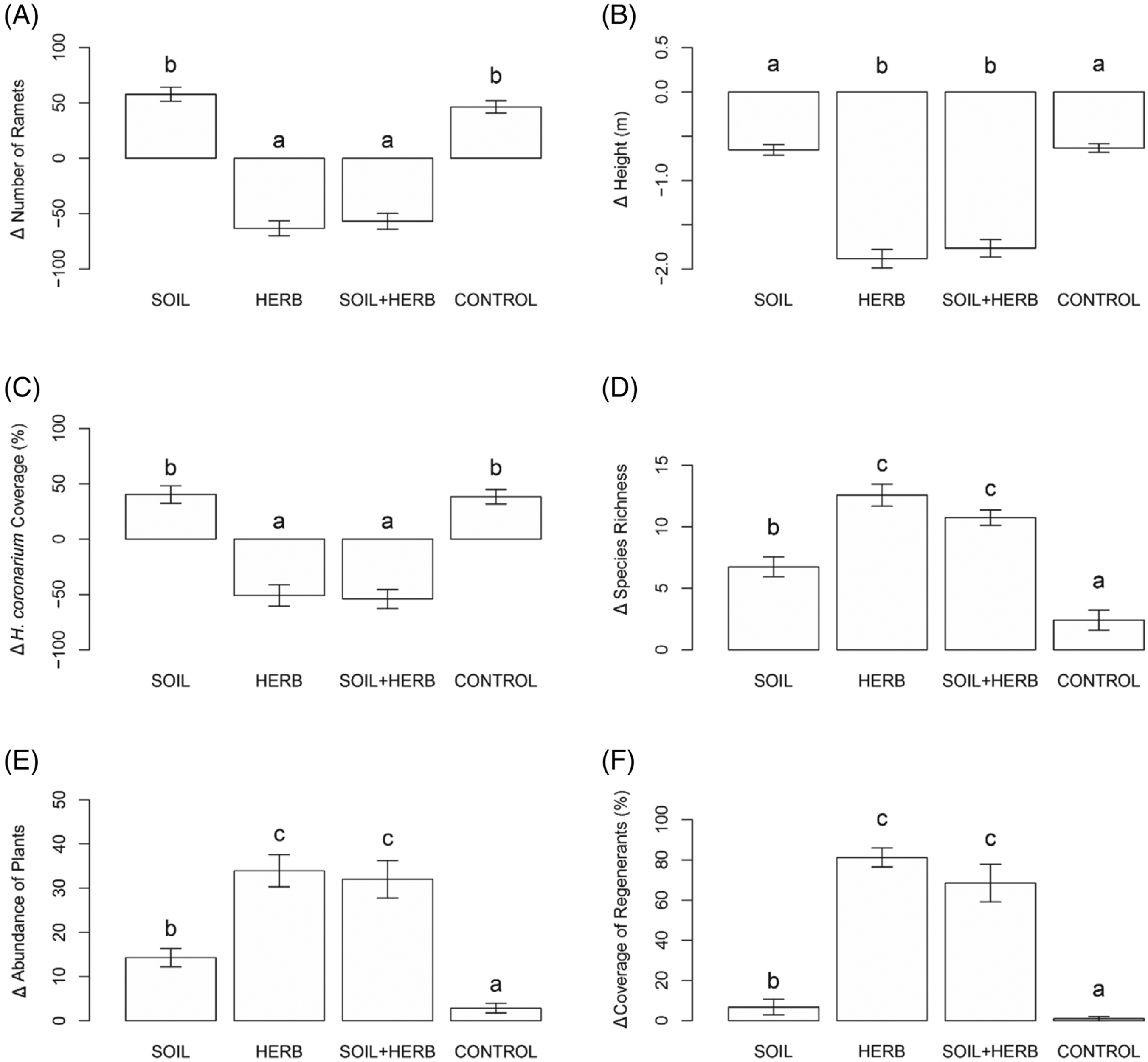

Figure 2 Mean (±SE) of the difference (Δ) between the values obtained from the final (July,2018) and initial evaluations (July,2017) in the study site located in the Ibirama National Forest (Ibirama, SC, Brazil). The *x*-axis corresponds to treatments Soil (cutting and topsoil transposition), Herb (cutting and herbicide application), Soil+Herb (cutting, herbicide application, and topsoil transposition), and Control (no intervention). In the *y*-axis: a, number of *Hedychium coronarium* ramets; b, mean height of ramets; c, cover by *H. coronarium*; d, regenerating species richness; e, abundance of regenerating species; f, cover by regenerating species. Different letters indicate significant differences between results detected in contrasts a posteriori, with adjusted *p* values.

The success of ramet control in the plots treated with chemical control agrees with the results obtained by Dechoum and Ziller (2013). In the plots treated with topsoil transposition without chemical control, however, no effect of the transposition on *H. coronarium* was observed. Resprouting and ramet growth was fast, as in about 3 months the ramets reached the height at which they remained until the final evaluation. When evaluating the regeneration of plots managed by cutting *H. coronarium*, Chiba et al. (2016) observed that the species tends to develop a large number of ramets and invest less in height after such intervention, a fact also observed in this experiment. The increase in density and decrease in ramet height in conditions of less intraspecific competition agrees with reports on the occurrence of phenotypic plasticity for the species, which indicate a trade-off between number and height of ramets under different conditions of competition and humidity (Chiba et al. 2016; Costa et al. 2016).

An increase in richness, abundance, and cover by regenerating species was observed in Herb and Herb+Soil treatments,

Table 1 Total number of species and abundance (in brackets) of regenerating species per treatment registered in the final evaluation of the experiment established in the Ibirama National Forest (Ibirama, SC, Brazil), classified by habit. Both native and non-native species were considered. Treatments were: Soil (cutting and topsoil transposition), Herb (cutting and herbicide application), Soil+Herb (cutting, herbicide application, and soil transposition), and Control (no intervention).

Treatment	*Tree*	*Shrub*	*Subshrub*	*Climber*	*Herb*	*Total*
Control	1 (1)	2 (4)	1 (5)	2 (9)	11 (15)	17 (34)
Herb	0	2 (81)	4 (25)	3 (7)	43 (298)	52 (411)
Soil	11 (117)	1 (2)	3 (5)	10 (22)	9 (23)	34 (169)
Soil+Herb	4 (10)	3 (73)	1 (14)	3 (12)	39 (273)	50 (382)

Table 2 Total number of regenerating individuals (*n*) of the five most abundant native and non-native species in each treatment in the final evaluation of the experiment established in the Ibirama National Forest (Ibirama, SC, Brazil). Non-native species are marked with an asterisk. Treatments were: Soil (cutting and topsoil transposition), Herb (cutting and herbicide application), Soil+Herb (cutting, herbicide application, and soil transposition), and Control (no intervention).

Control	n	*Herb*	n	*Soil+Herb*	n	*Soil*	n
Mikania cordifolia	6	*Boehmeria caudata*	80	*Cardamine bonariensis**	104	*Euterpe edulis*	52
Ludwigia peruviana	5	*Cardamine bonariensis**	57	*Boehmeria caudata*	68	*Trema micrantha*	45
Boehmeria caudata	3	*Ageratum conyzoides*	31	*Ageratum conyzoides*	30	*Chusquea* sp	9
Borreria palustris	3	*Borreria palustris*	25	*Drymaria cordata**	16	*Jacaranda puberula*	5
Ipomoea cairica	3	*Ludwigia peruviana*	22	*Amaranthus blitum**	15	*Mikania cordifolia*	5

especially due to ruderal species. The early colonization of managed plots by ruderal species may have been influenced by the characteristics of the areas near the study site. It is well known that the occurrence of disturbance incurs in the selection of plants of fast-growth, high fecundity, short life cycles, and colonizing ability, defined as ruderal (Chiuffo et al. 2018). Therefore, higher availability of resources in the areas managed with chemical control (with and without topsoil transposition) may have favored colonization by ruderal species present in the surroundings. This may have created difficulties for the establishment of native tree species in plots subjected to treatment Soil +Herb, in which a higher abundance of tree species was expected due to the presence of propagules in the transposed soil. Transposition of topsoil accelerates recolonization not only by trees, but also by other life-forms such as climbers (Ferreira & Vieira 2017). This corroborated the results of the treatment with topsoil transposition without chemical control.

Life-form composition was more variable, dominated by trees and climbers in treatment Soil and by herbs in plots managed with chemical control (treatments Herb and Soil+Herb). There are two other possible explanations for the scarce presence of trees in treatment Soil+Herb compared with Soil treatment. The first is the accidental application of herbicide on leaves of regenerating plants—despite the fact that herbicide was applied individually on each *H. coronarium* ramet and no side effects were detected on regenerating plants (e.g. yellowing and drying of leaves) during the experiment. Another factor that may have affected the results is that the effects of soil runoff due to seasonal floods were probably stronger in the plot of the treatments Soil+Herb and Herb than in the treatment Soil. We observed that the ramets of *H. coronarium* in the Soil treatment were functioning as physical barriers for soil runoff during flooding events. These factors, combined or not, may have influenced the result of only a few tree species colonizing the plots of Soil+Herb treatment. In order to avoid the accidental application of herbicide on regenerating plants, further experimental studies should focus on applying restoration techniques in two phases, starting with control using herbicides, then moving on to topsoil transposition after a larger proportion of the invader population is controlled.

The response to topsoil transposition may occur late in the managed area, once the germination of seeds from the transposed soil can take place for an extended period of time. In a review of 162 tree species native to the Atlantic Rainforest, approximately 40% of the species considered had dormant seeds, which helps conserve them longer in the soil (Souza et al. 2015). From these examples, it is clear that topsoil transposition may have mid-term effects in the managed plots. A longer monitoring period of the experiment would therefore be interesting to accompany the evolution of the floristic composition in these plots after the development of shrubs, as tree species may establish then.

Two tree species predominated in plots managed only with topsoil transposition, *Trema micrantha* and *Euterpe edulis*. The latter is a palm that offers resources to animals up to 10 months in the year, with peak fructification in winter, when there is lower availability of other food sources. Fruits are consumed by a large diversity of birds and mammals, and dispersal of other tree species upon visits to the fruit bunches have been recorded (Silva 2011; Silva et al. 2017). Pioneer species such as *Trema micrantha*, which grow fast and produce fruits dispersed by animals, can not only improve conditions for the establishment of secondary species, but also increase the

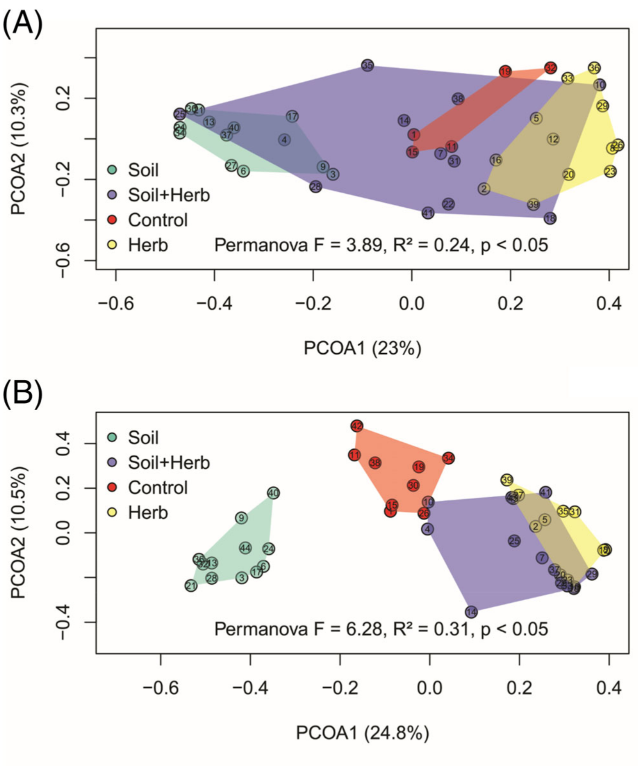

Figure 3 Graphic representation of the principal component analysis (PCoA) of the floristic composition of plots in different treatments in the study site located in the Ibirama National Forest (Ibirama, SC, Brazil) in the months: (A) January,2018; (B) July,2018. Treatments: Soil (cutting and topsoil transposition); Herb (cutting and herbicide application); Soil+Herb (cutting, herbicide application, and topsoil transposition); Control (no intervention).

diversity and density of such species in restoration areas (Vázquez-Yanez 1998; Viani et al. 2015). Due to the characteristics of *Trema micrantha* and *Euterpe edulis*, it must be noted that, despite lower richness, abundance, and cover of regenerating species in the treatment with topsoil transposition without chemical control, this treatment facilitated the establishment of species that may have a significant role for restoration in the mid and long terms.

When conducted individually, management interventions are often inefficient because they do not consider all the factors that prevent restoration (Nsikani et al. 2018). Therefore, the combination of techniques with integrated management practices seems to be the best strategy to restore areas invaded by non-native plants. In this aericle, we provide strong evidence that the integration of topsoil transposition from forests in advanced successional stages associated with chemical control of populations of *H. coronarium* is an effective method to restore and accelerate succession in degraded riverine forests. Although almost all *H. coronarium* ramets were eliminated by chemical control, it is noteworthy that some ramets were still present at the end of the experiment. This highlights the need for constant monitoring and, if necessary, reapplication of chemical control in order to avoid reinvasion of restauration sites.

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Supporting Information

The following information may be found in the online version of this article:

Table S1: GLMM statistics adjusted to the number of Hedychium coronarium ramets per treatment in the initial evaluation of the study site (Ibirama National Forest – Ibirama, SC, Brazil) conducted in July, 2017.

Table S2: Paired comparisons between factors of the explanatory variable conducted after GLMM adjustment to the data on number of Hedychium coronarium ramets per treatment in the initial evaluation of the study site (Ibirama National Forest – Ibirama, SC, Brazil) conducted in July, 2017, with p values adjusted by the Holm-Bonferroni method.

Table S3: GLMM statistics adjusted to the height of Hedychium coronarium ramets per treatment in the initial evaluation of the study site (Ibirama National Forest – Ibirama, SC, Brazil) conducted in July, 2017.

Table S4: Paired comparisons between factors of the explanatory variable conducted after GLMM adjustment to the data on height of Hedychium coronarium ramets per treatment in the initial evaluation of the study site (Ibirama National Forest – Ibirama, SC, Brazil) conducted in July, 2017, with p values adjusted by the Holm-Bonferroni method.

Table S5: GLMM statistics adjusted to the percentage of cover of Hedychium coronarium ramets per treatment in the initial evaluation of the study site (Ibirama National Forest – Ibirama, SC, Brazil) conducted in July, 2017.

Table S6: Paired comparisons between factors of the explanatory variable conducted after GLMM adjustment to the data on percentage of cover of Hedychium coronarium ramets per treatment in the initial evaluation of the study site (Ibirama National Forest – Ibirama, SC, Brazil) conducted in July, 2017, with p values adjusted by the Holm-Bonferroni method.

Table S7: GLMM statistics adjusted to species richness per treatment in the initial evaluation of the study site (Ibirama National Forest – Ibirama, SC, Brazil) conducted in July, 2017.

Table S8: Paired comparisons between factors of the explanatory variable conducted after GLMM adjustment to the data on species richness per treatment in the initial evaluation of the study site (Ibirama National Forest – Ibirama, SC, Brazil) conducted in July, 2017, with p values adjusted by the Holm-Bonferroni method.

Table S9: GLMM statistics adjusted to abundance of regenerant species per treatment in the initial evaluation of the study site (Ibirama National Forest – Ibirama, SC, Brazil) conducted in July, 2017.

Table S10: Paired comparisons between factors of the explanatory variable conducted after GLMM adjustment to the data on abundance of regenerant species per treatment in the initial evaluation of the study site (Ibirama National Forest – Ibirama, SC, Brazil) conducted in July, 2017, with p values adjusted by the Holm-Bonferroni method.

Table S11: GLMM statistics adjusted to regenerant species percentage of cover per treatment in the initial evaluation of the study site (Ibirama National Forest – Ibirama, SC, Brazil) conducted in July, 2017.

Table S12: Paired comparisons between factors of the explanatory variable conducted after GLMM adjustment to the data on regenerant species percentage of cover per treatment in the initial evaluation of the study site (Ibirama National Forest – Ibirama, SC, Brazil) conducted in July, 2017, with p values adjusted by the Holm-Bonferroni method.

Table S13: LMM statistics adjusted to the difference between final and initial number of Hedychium coronarium ramets per treatment on the experiment conducted from July, 2017 to July, 2018 on Ibirama National Forest (Ibirama, SC, Brazil).

Table S14: Paired comparisons between factors of the explanatory variable conducted after LMM adjustment to the data on difference between final and initial number of Hedychium coronarium ramets per treatment on the experiment conducted from July, 2017 to July, 2018 on Ibirama National Forest (Ibirama, SC, Brazil).

Table S15: GLMM statistics adjusted to the difference between final and initial height of Hedychium coronarium ramets per treatment on the experiment conducted from July, 2017 to July, 2018 on Ibirama National Forest (Ibirama, SC, Brazil).

Table S16: Paired comparisons between factors of the explanatory variable conducted after GLMM adjustment to the data on difference between final and initial height of Hedychium coronarium ramets per treatment on the experiment conducted from July, 2017 to July, 2018 on Ibirama National Forest (Ibirama, SC, Brazil).

Table S17: LMM statistics adjusted to the difference between final and initial percentage of cover of Hedychium coronarium per treatment on the experiment conducted from July, 2017 to July, 2018 on Ibirama National Forest (Ibirama, SC, Brazil).

Table S18: Paired comparisons between factors of the explanatory variable conducted after LMM adjustment to the data on difference between final and initial percentage of cover of Hedychium coronarium per treatment on the experiment conducted from July, 2017 to July, 2018 on Ibirama National Forest (Ibirama, SC, Brazil).

Table S19: GLMM statistics adjusted to the increment on species richness per treatment on the experiment conducted from July, 2017 to July, 2018 on Ibirama National Forest (Ibirama, SC, Brazil).

Table S20: Paired comparisons between factors of the explanatory variable conducted after GLMM adjustment to the data on increment on species richness per treatment on the experiment conducted from July, 2017 to July, 2018 on Ibirama National Forest (Ibirama, SC, Brazil). The p values were adjusted by the Holm-Bonferroni method.

Table S21: GLMM statistics adjusted to the increment on abundance of regenerant species per treatment on the experiment conducted from July, 2017 to July, 2018 on Ibirama National Forest (Ibirama, SC, Brazil).

Table S22: Paired comparisons between factors of the explanatory variable conducted after GLMM adjustment to the data on increment on abundance of regenerant species per treatment on the experiment conducted from July, 2017 to July, 2018 on Ibirama National Forest (Ibirama, SC, Brazil). The p values were adjusted by the Holm-Bonferroni method.

Table S23: GLMM statistics adjusted to the increment on regenerant species percentage of cover per treatment on the experiment conducted from July, 2017 to July, 2018 on Ibirama National Forest (Ibirama, SC, Brazil).

Table S24: Paired comparisons between factors of the explanatory variable conducted after GLMM adjustment to the data on increment on regenerant species percentage of cover per treatment on the experiment conducted from July, 2017 to July, 2018 on Ibirama National Forest (Ibirama, SC, Brazil). The p values were adjusted by the Holm-Bonferroni method.

Table S25: List of species observed during evaluations of the experiment conducted in the Ibirama National Forest (Ibirama, SC, Brazil), by family.

Table S26: Abundance of native and non-native regenerating species per treatment observed between January and July, 2018, in the experiment established in the Ibirama National Forest (Ibirama, SC, Brazil), categorized by habit.

Figure S1: Study area in the Ibirama National Forest.

Figure S2: Mean (±SE) throughout the months (x axis) of variables.

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