Research Article

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Push-pull to manage leaf-cutting ants: an effective strategy in forestry plantations

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Abstract

BACKGROUND: Leaf-cutting ants (LCAs) are amongst the most important forestry pests in South America. Currently, their control is carried out almost exclusively through the application of toxic baits of restricted use. Here we evaluate a push-pull strategy (*i.e.*, the simultaneous use of attractant and repellent stimuli in order to divert pests) to manage LCAs *Acromyrmex* spp. in young willow plantations in the area of Delta of the Parana River, Argentina, a wetland ecosystem. First, we surveyed ants' selection of farmland vegetation during one year. Then, we estimated ants' preferences between the willow *Salix babylonica* and a subsample of plant species from farmland vegetation under laboratory conditions. Finally, we designed and performed a fully crossed experimental field assay to evaluate a push-pull strategy by using farmland vegetation as pull stimulus.

RESULTS: We surveyed 39 plant species in the area, 19 of which had been foraged by LCAs along the year. Plants were selected by species, not by abundance. In the lab, ants showed similar preference for the cultivated willow and the subsample of plant species. *Push-pull* was the only treatment that maintained willow remaining vegetation above 60–80% at the end of the growing season.

CONCLUSIONS: For the first time the push-pull strategy was evaluated in social insects. We demonstrated that it can be successfully used to manage LCAs in young willow plantations. Our strategy generates biodiversity, which can improve the ecosystem functioning, and it can be easily implemented by producers since its design is based on regular willow plantations.

Supporting information may be found in the online version of this article.

Keywords: push-pull; leaf-cutting ants; forestry plantations; farmland vegetation; wetland

1 INTRODUCTION

Leaf-cutting ants (LCAs) have the ability to cut and process fresh vegetation to use it as the nutritional substrate for their fungal symbiont.[1–3] Regarding the variety of plants, these insects may be considered polyphagous or generalist herbivores.[4–6] Nevertheless, foragers show marked preferences for leaves of certain plant species,[7–9] which result in a range of host plant use, from high acceptance to complete avoidance.

In a forestry production, with minimum plant biodiversity, LCAs have few alternatives for harvesting, so they become a problem for producers. Being recognized as serious pests in the Neotropics,[10] they are amongst the most important forestry pests in South America, affecting tree establishment, while reducing wood production.[11–13]

Until now, the control of LCAs in the tropics and subtropics has been carried out, almost exclusively, through toxic baits derived from conventional insecticides or fungicides. Most of them contain sulfluramid (fluoro aliphatic sulfonamide) and fipronil (phenylpyrazole) as active principles. Both compounds are dangerous for non-targeted animals, the environment, and human health.[14–19] In addition, the use of these compounds has been restricted by governments and forest product certification agencies, like the Forest Stewardship Council (FSC), deriving in an urgent need for a sustainable alternative.

Push-pull is a strategy of integrated pest management, which involves the behavioral manipulation of insect pests, integrating

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stimuli that turn the protected resource unattractive or unsuitable to insect pests (push), while luring them towards an attractive source (pull), from where the pests are subsequently removed.[20] This strategy has been successfully used in several farming systems, *e.g.*, to control *Striga* sp. in sub-Saharan cereal production[20–23], *Helicoverpa* sp. in cotton crops[24,25], and the *Rhagoletis cerasi* fly in the cherry fruit.[26] It has been also used in forestry systems to control the mountain pine beetle *Dendroctonus ponderosae* in *Pinus contorta*. [27–29] However, it has never been evaluated in LCAs or any other social insect species.

There is strong evidence indicating that increasing plant diversity in some crop systems raises abundance and, in most cases, richness of birds, predatory insects, and soil organisms, while non-predatory insects and pests respond negatively.[30] Evidence reports an increase of 44% of natural enemies, 54% herbivore death, and 23% reduction of crop damage in crop systems with high plant biodiversity in comparison with monocultures or agronomic systems with few vegetable species.[31] Essentially, biodiversity in crop fields disrupts the herbivore capacity to locate a suitable host plant, through a variety of strategies: the use of visual or chemical stimuli that may act by repelling pests from a crop, or trapping herbivores on a plant other than the crop, or blocking movement of herbivores with tall vegetation, or altering the volatile profile of crop plants.[32] Thus, the farmland vegetation growing in the area could be used as a deterrent resource for LCAs. In addition, the increase of plant diversity brings further benefits to the agroecosystem, since plants respond positively to diversified productions (*i.e.*, crop and forage yield, wood production, yield stability, and pollination services).[33]

This study was performed in the Delta of Parana River in Buenos Aires, Argentina. This area is part of one of the most important wetland ecosystems in South America due to its location and extent. Wetlands are among the most productive ecosystems in the world, providing critical habitat for flora and fauna, and often representing highly diverse ecosystems.[34] The Lower Delta of Parana River is being rapidly modified: approximately 83 000 ha of the original plant cover have been replaced by Salicaceae plantations including willows (*Salix* spp.) and poplars (*Populus* spp.),[35] and the amount of cattle has increased by an order of magnitude along a decade.[34] In this region, LCA species *Acromyrmex ambiguus* and *A. lundii*, are considered to be the most important pests affecting young forestry plantations.[36]

The aim of this study was to evaluate a push-pull strategy for management of LCAs in young willow plantations in the Delta of Parana River. In order to estimate the possibility of using farmland vegetation as a cutting alternative for LCAs, we assessed its availability and palatability around the cultivated area, and its selection for consumption by foragers of *A. ambiguus* in comparison with the most common cultivated willow, under field and lab conditions. Then, we designed and performed a fully crossed experimental field assay, using a combined mechanical and chemical barrier as push stimulus, and farmland vegetation as pull stimulus. Field assays were performed in young willow plantations on two representative farms, presenting the typical environmental conditions found there: Natural and Modified.

2 MATERIALS AND METHODS

2.1 Vegetation availability and ants' preference

2.1.1 Field survey of farmland vegetation and ants' selection

Relative plant abundance and richness were surveyed for an entire year (from August 2015 to July 2016), in an area of Salicaceae plantations at the Delta of Parana River Experimental Station of the National Institute of Agricultural Technology (INTA), Campana, Buenos Aires Province, Argentina (34°10'S 58°51'W). Each month, species richness and relative biomass were evaluated. A 50 cm × 50 cm wire frame was used, and nine samples were taken randomly in the field. All plant material inside the squares was removed by shears, stored in paper bags and transported from the field to the laboratory, where it was identified, oven-dried at 70 °C during 24 h, and then weighed (dry mass). Relative species abundance was calculated monthly, dividing dry mass of each plant by total dry mass.

To evaluate ants' selection simultaneously with the field survey, three colonies of *A. ambiguus* were identified in the same area. Considering each nest as the center, a circle of a 6 m perimeter was delimited, and every plant species cut by worker ants *in situ* was identified by direct observation. Ants' selection was recorded as a binary response (cut/no cut) every month for each plant species.

2.1.2 Ants' preferences

Laboratory assays were performed with *A. ambiguus* colonies collected at the Delta of Parana River Experimental Station, INTA. Ants were collected and placed inside a plastic container (30 cm × 44 cm × 30 cm) acting as the foraging arena. The upper portion of the foraging arena was coated with Vaseline to prevent ants from escaping. The fungus was placed separately in a rectangular plastic container (23 cm × 14 cm × 7 cm) inside the foraging arena, acting as the fungus chamber. Colonies were maintained in a room under a photoperiod of L12:D12 h, 23–25 °C temperature, and approximately 60% relative humidity. Ants were fed three times a week with either fresh ash leaves (*Fraxinus* spp.) or poplar (*Populus* spp.) during spring and summer, or primrose jasmine (*Jasminum meznyi*) during autumn and winter. Additionally, apple, oat flakes, corn flour, and rice were offered throughout the year.

Dual choice assays were performed among all possible combinations of seven selected plant species. The following species were tested: *Ligustrum sinense*, *Amorpha fructicosa*, *Monteiroa glomerata*, *Lonicera japonica*, *Phytolacca americana*, *Iris pseudacorus*, and *Salix babylonica*. Plant species were chosen based on the results obtained in the field survey, except in the case of *Monteiroa glomerata*, which was included because it is a native species that spontaneously grows in the area and it is cut by ants (September 2015 pers. obs.). *Salix babylonica was* also included to perform the comparisons, because it is one of the most abundant willow genotypes planted in the area.

Assays were carried out on five independent colonies. Each colony was connected to the experimental arena (33 cm × 46 cm × 12 cm plastic box) by a wooden bridge, where the ants were offered leaves of two different plant species of similar size, 30 cm apart from each other, and were allowed to forage for 45 min. Thereafter, plant leaves were removed. Leaves were scanned before and after being offered to the ants to evaluate the area consumed (cm^2). A total number of 105 preference assays (21 pairs of plant species ×5 ants' colonies) were performed.

2.2 Use of farmland vegetation in a push-pull strategy

2.2.1 Field sites

Two field assays were replicated in the surroundings of the Delta of Parana River Experimental Station, on farmlands with different contrasting environmental conditions. in site A, the land was modified by levees and polders, so water irrigation was scarce. Four ants' nests were found in this site. Whereas in site B, land was not modified, water was flowing in and out of the plantation as a natural flooding movement in a wetland ecosystem. Only one ant nest was found in site B, probably due to the environmental characteristics (Supporting Information, Table S1). The size of the experimental area in each site was approximately 100 m^2, which falls within a foraging distance for *Acromyrmex* spp. individuals from a nest.[37]

2.2.2 *Treatments*

As a *push* (*i.e.*, repellent) stimulus, a commercial mechanical barrier, commonly used by producers,[37] was placed around the twig in order to protect plant material. Additionally, farnesol (SIGMA Aldrich), a LCA repellent sesquiterpene, was applied (100 mg in 100 mg lanoline) below the mechanical barrier forming a 2 cm band around the twig.[38] As a *pull* stimulus, spontaneous farmland vegetation was allowed to grow in between young willow trees. The assay consisted of four experimental plots in a split plot design in each field site. Each plot comprised 12 young willow trees (*i.e.*, 3 months old) (*Salix babylonica var sacramenta*) arranged in two rows separated by 1.5 m. In this area, producers initiate willow plantations by planting portions of willow branches called 'cuttings' (50–70 cm length) or 'bare (unrooted) pole cuttings' (2–3 m length), and these cuttings regrow in a few weeks. In our experiment, each plot was planted by using these two different plant materials (subplots): six willow plants originated from 'cuttings' (50 cm length), and six willow plants originated from bare pole cuttings (2 m length), hereafter called 'pole cuttings' (Supporting Information, Figure S1). The *push* stimulus was placed around the twig, approximately at 15 cm from the ground in the case of cuttings, and 1.2 m from the ground in the case of pole cuttings. Experimental plots were separated from each other by approximately 10 m. The fully crossed design included the following four experimental treatments, one in each plot: 1-*Push-pull*: plants were protected by the repellent stimulus (farnesol + mechanical barrier), and farmland vegetation was kept around the trees. 2-*Push*: the repellent stimulus (same as above) was used, but farmland vegetation was mechanically removed as it was growing. 3-*Pull*: farmland vegetation was kept, but young willow trees were not protected. 4-*Control*: farmland vegetation was continuously removed as it was growing, and young willow trees were not protected. The distribution of the treatments is shown in Supporting Information, Figure S1.

Individual young willow trees were photographed against a light grey background along the growing season, starting in November 2017, for 5 months until March 2018. The percent remaining vegetation was estimated starting with 100% foliation in all plants for the first measurement (if the vegetation percentage was higher than 100% because of growth, it was still considered to be 100%).

2.3 Data analysis

2.3.1 *Vegetation availability and ants' preference*

To evaluate if relative species abundance was associated to ants' selection (binary response as dependent variable), we performed a generalized linear mixed effect model (GLMM) with repeated measures design. The model consisted of a binary logistic regression with logit link function using the lme4[39] package in R statistical software.[40] Relative species abundance variable was taken as the fixed part of the model. And random variables were month of the measurements, due to repeated measures, and plant species identity, for making inferences about population of farmland vegetation. Pseudo R squared were calculated for GLMM using the MuMIn package.[41]

In ants' preference assays, in order to calculate the area cut by ants, leaf area (in cm^2) was estimated by ImageJ as described in Guerrero Rincón and collaborators.[42] All possible combinations of plant species were compared by pairs, once in each colony (N = 5). Comparison matrices of 7×7 (the seven plant species tested) for each colony were built with the 21 preference tests performed, each cell *ij* representing a pair of plant species, and its value, the result of the trial where *i* species (row) was preferred or not, to a *j* one (column). Differences in cut area were tested by using Chi-square test ($P < 0.05$). In case of significant differences, the value assigned to an *ij* cell was 1 for the most cut area and 0 for the least cut one. For combinations in which preference was non-significant ($P > 0.05$), a value of 0.5 was assigned to both plant species, because this situation was considered a tie.[43] Hierarchy in each colony and, in a matrix built by adding the results of the five colonies, was verified by Modified Landau's linearity index, h′,[44] because it considers interactions where relationships are unknown. The Landau's index ranges from 0 to 1, where 1 indicates complete linearity and 0 indicates that all species are equally preferred. The analysis of matrices for each colony was performed to evaluate if there were differences in the ants' preference related to the colony identity. Plant preferences were ranked by cutting preference by David's score, a dominance ranking index, which takes into account the importance of each item into the matrix.[45] Normalized David's score was used, because it varies between 0 and N-1, where N is the number of compared species, with higher values indicating higher preference levels. The values for each plant species were compared with an analysis of variance (ANOVA) followed by a Tukey's multiple comparison test in R.[40]

2.3.2 *Use of farmland vegetation in a push-pull strategy*

Percent remaining vegetation at the end of the growing season (5 months after starting the assay) in both field sites was analyzed with a GLMM, fitted using maximum likelihood with a Gamma distribution and inverse link function, using the lme4 package[39] in R.[40] The fixed part of the model included the categorical variables Plant Material (*cuttings* and *pole cuttings*) and Treatment (*push-pull*, *push*, *pull*, and *control*), and the random part included nested variables: Field, Plot, and Subplot.

This assay was conducted in two field sites with contrasting environmental conditions. Our sample size was six plants per Plant Material and Treatment.

This assay was designed with two predictor variables (Treatment and Plant Material), but we cannot overview the environmental conditions and how they affected the response variable (Percent remaining vegetation) in both field sites. So, to evaluate the effect of treatments under each different environmental condition, sites A and B were analyzed separately with a generalized linear mixed-effects model (lme4 package in R). The categorical variables Plant Material and Treatment were the fixed part of the model. As the random part, Plot and Subplot were the nested variables.

3 RESULTS

3.1 Vegetation availability and ants' preference

3.1.1 *Field survey of farmland vegetation and ants' selection*

Thirty-nine plant species were recorded in the area along the year. Vegetation available to *A. ambiguus* was diverse throughout the year, especially from October to March, which corresponds to spring and summer seasons in the Southern Hemisphere (up to 18 species) (Fig. 1). Among the 39 plant species recorded, 19 were foraged by LCAs (black dots, Fig. 1). The GLMM analysis determined that relative species abundance was not related to ants' selection (P = 0.85). In order to achieve a better understanding of ants' selection, the proportion of variance explained by GLMM model was measured as conditional and marginal R^2_{GLMM}. The analysis showed a higher proportion of variance explained by random variables than relative abundance as fixed variable ($R^2_{GLMM(c)}$ = 75.9%, $R^2_{GLMM(m)}$ = 0.036%, respectively). This may be due to the very large effect of month and plant species in ants' selection. To determine how much variability was explained by each random variable, the estimated variances were compared. The results showed that plant species variance was higher than that accounted for by month (9.78, 0.87 both in link scale, respectively). This suggests that plant species identity may be the main effect explaining variability in ants' selection. For example, *Lonicera japonica* and *Iris pseudacorus* were foraged by *A. ambiguus* during the whole year, even during months with low abundance (*e.g.*, in May). *Sonchus oleraceus*, *Amorpha fructicosa* and *Ligustrum sinense*, were always foraged when available, although their abundance was low. The woody species *Populus* spp., *Gleditsia triacanthos* and *Fraxinus* spp. were also highly foraged by ants when they were present.

3.1.2 Ants' preference

Landau's Linearity Index value for each colony matrix was not significant ($P > 0.1$), except for colony 2 ($P = 0.03$). The results of the five colonies together (*h-modified* = 0.62, P = 0.11) indicates that preferences across options are not linear (Supporting Information, Figure S2), without a perfect hierarchical organization between plant options. In order to show a quantitative analysis for each plant species preference, we calculated the normalized David's score (N = 5). Results showed that *L. sinense* was significantly more preferred than *Phytolacca americana* and *I. pseudacorus*. Interestingly *S. babylonica*, the willow plant, ranked between preferred plant species of the farmland vegetation (Fig. 2).

3.2 Use of farmland vegetation in a push-pull strategy

Percent remaining vegetation in both field sites was the highest for the *push-pull* treatment (above 60%), and dropped to 40% or less for *control*, *pull*, and *push* treatments (Fig. 3). GLMM was significant for Treatment (P = 0.001) and the Tukey test indicated *push-pull* as the treatment with significant differences ($P < 0.01$). The analysis was non-significant for Plant material or interaction between variables (P = 0.08 and P = 0.09, respectively).

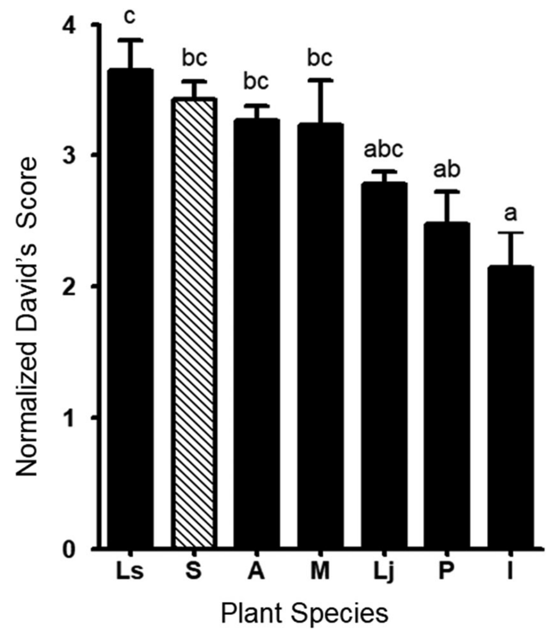

Figure 2. Mean (+SE) of the normalized David´s Score values representing preferences of *Acromyrmex ambiguus* for seven plant species calculated from dual choice assays in the laboratory. *Ligustrum sinense* (Ls), *Salix babyonica* (S), Amorpha fructicosa (A), *Monteiroa glomerata* (M), *Lonicera japonica* (Lj), and *Iris pseudacorus* (I). Different letters indicate statistical differences across species calculated by Tukey test ($P < 0.05$).

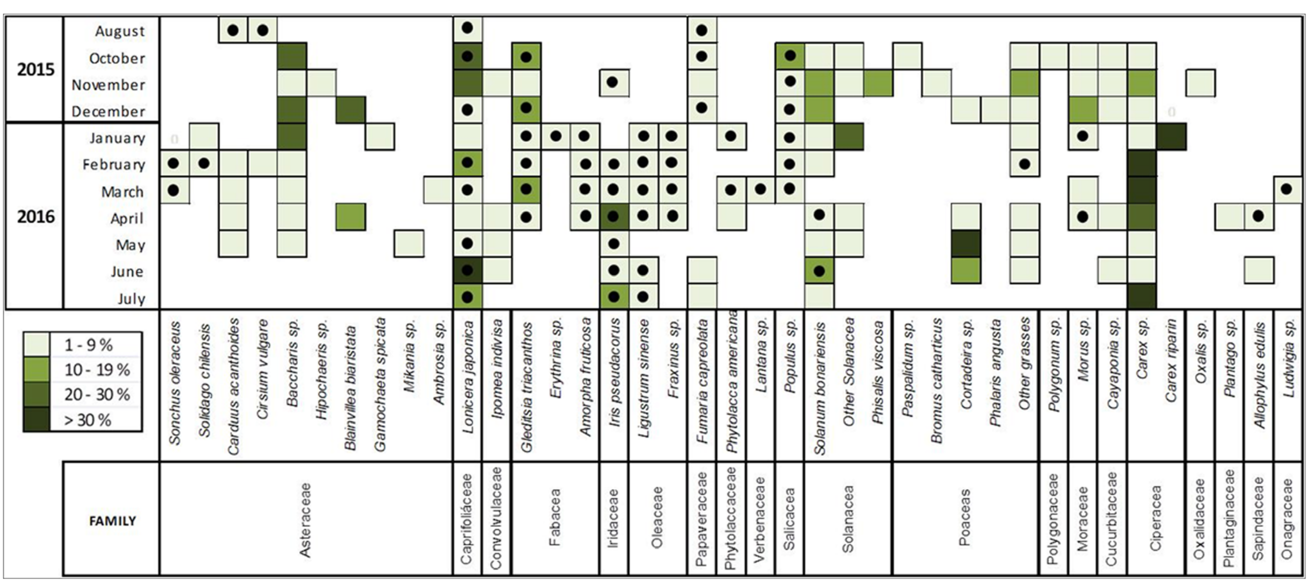

Figure 1. Plant families and species richness surveyed during a year. Green color intensity indicates abundance of each species per month (% of dry weight, see inset). Black dots indicate ants cutting activity within a month.

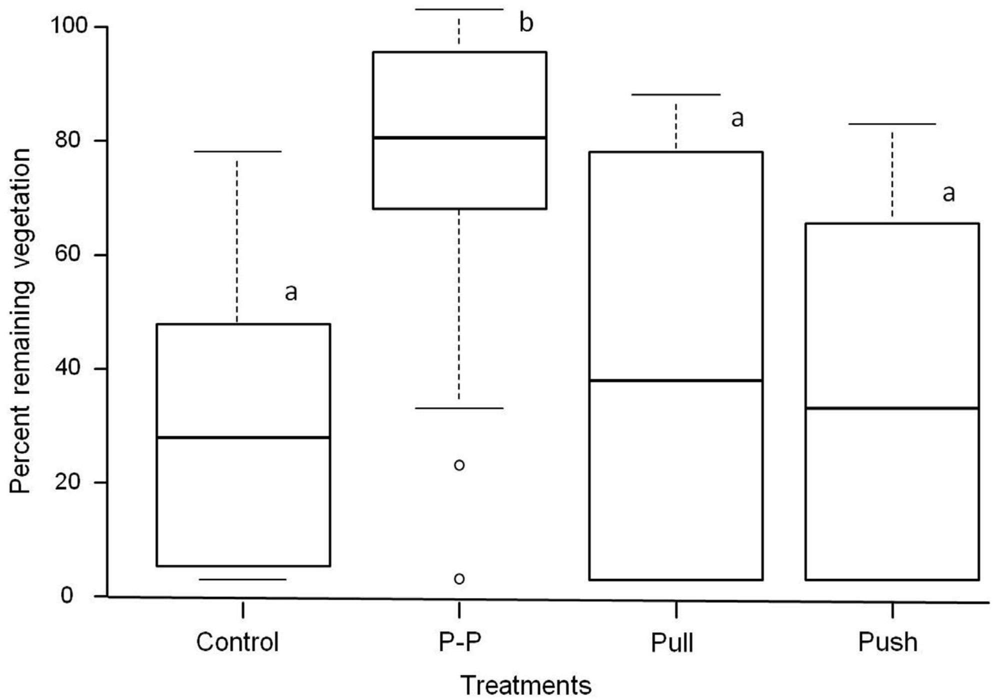

Figure 3. Percent remaining vegetation for the four treatments: Control, Push-pull (P—P), Pull and Push. Boxes indicate the first to third quartile range with the median indicated by a line across the box, whiskers represent the range. The circles denote outliers. Different letters indicate significant differences calculated by Tukey test ($P < 0.05$, N = 6).

When study sites were analyzed separately, both also showed significant differences in the treatment variable ($P = 0.01$ for site A, and $P = 0.04$ for site B, Fig. 4), and non-significant for the interaction between variables ($P = 0.31$ for Site A, $P = 0.14$ for Site B). in site A, the *push-pull* treatment showed the highest values for percent remaining vegetation (over 60%) and no willow death. Plants growing under the treatment *control*, *push*, and *pull* were highly attacked (below 30% of remaining vegetation) and there was 53% of willow mortality. in site B, percent remaining vegetation was high (around 80%) in both *push-pull* and pull treatments, while it dropped in *control* and *push* treatments, and there was only 8% of willow mortality. In this field, the Plant Material variable showed highly significant differences ($P = 0.009$).

A qualitative temporal analysis from each field site is shown as Supporting Information (Figure S3). In all cases, including cuttings and pole cuttings at both sites, percent remaining vegetation in the *push-pull* treatment was maintained at the highest levels along the whole growing season. Noteworthy, in site A, the one with levees and polders, plants from the other treatments got less than 10% of remaining vegetation (in some cases dropped to 0%), while in site B, with natural flooding movement, the minimum percent remaining vegetation was approximately 40%.

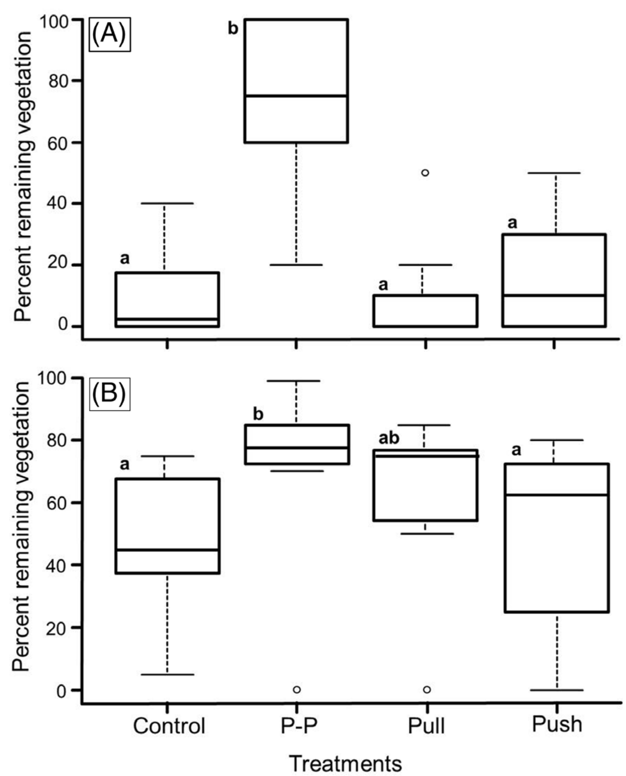

Figure 4. Percent remaining vegetation at the end of the growing season for each Treatment on each field site: (a) Site A, land modified and (b) Site B, land with natural flooding. Boxes indicate the first to third quartile range with the median indicated by a line across the box, whiskers represent the range. Circles denote outliers. Different letters indicate significant differences calculated by Tukey test ($P < 0.05$, N = 6).

4 DISCUSSION

This study demonstrated, for the first time, that the push-pull strategy can be successfully used to manage leaf-cutting ants. We also showed that the farmland vegetation growing spontaneously in a forestry plantation can be used as a pull stimulus, diverting LCAs activity from protected plants. Our field assays have been designed by using the producers' regular plantations. Thus, these results encourage the field implementation of this strategy and the experimentation with other commercial tree species.

Our push-pull strategy was based on a broad knowledge of ant biology. We used stimuli with different ranges of action: A *push* stimulus (farnesol plus mechanical barrier) acting as a short-range repellent: Ants must climb the twigs and get close to the barrier (few millimeters) to be repelled. And a *pull* stimulus (farmland vegetation), acting at long-range (meters) by diverting ants to forage on other plants. The joint use of short-range push and long-range pull stimuli conforms a type III push-pull strategy in the framework presented by Eigenbrode *et al.*[46] This is one of the least used combinations of stimuli for pest management, which appears to be an optimal option for LCAs. While protecting cuttings with a push barrier, we are blocking one of the foraging options. At the same time, since LCAs largely rely on chemical cues for orientation,[47] the diversity of odors and complexity offered by the farmland vegetation can 'mask' the finding of the willow.[33]

The highest levels of willow percent remaining vegetation (*i.e.*, less attacked plants) were obtained under the *push-pull* treatment. Bare pole cuttings are used to initiate the willow plantation by some producers who are interested in silvopastoral systems. The use of taller plant material to initiate the plantation allows farmers to introduce cattle sooner into the forestry. Our results in site B showed that this material could constitute an advantage in the case of LCAs management, since the length of the pole cuttings can facilitate the placement of the barrier and prevent ants from using farmland vegetation as a bridge to climb up and pass over the mechanical barrier. The mechanical barrier we used as part of the *push* stimulus is already being used by several local producers. The addition of farnesol as a chemical barrier could help to improve the *push* stimulus, because LCAs have to face two obstacles while trying to get the willow foliage. However, the efficacy of mechanical *vs* mechanical + chemical barrier needs further investigation.

Even when the push-pull strategy was successful in both experimental field sites, the characteristics of the area should be considered during the implementation of this type of integrated pest management. Water availability is the most important factor, because it has implications for LCAs colonization, and also determines the type of vegetation present in the field site. in site A, water was scarce due to land systematization by means of polders and four ant nests were present along the season, turning foraging pressure on cultivated plants high. Farmland vegetation included a low number of plant species, some of which were non-selected by *A. ambiguus* (*e.g.*, *Carduus acanthoides*, *Baccharis* sp., *Carex* sp., *Sonchus oleracerus)*. As a consequence, ants had far fewer options to cut, increasing the foraging pressure on the willow plants. Under these conditions, more than 50% of the young willow plants died in *control*, *push*, and *pull* treatments. On the other hand, in site B, water had the normal flooding movement of a wetland, limiting LCAs colonization, and only one ant nest was present throughout the season. In addition, plant species available were among those most selected by ants (*e.g.*, *Lonicera japonica*, *Ipomea indivisa*, *Amorpha fructicosa*, *Iris pseudacorus*, *Ligustrum sinense*, *Fumaria capreolata*, *Phytolacca americana*, *Morus nigra, and Oxalis* sp., among others, see Fig. 1), lowering the foraging pressure on young willow plants. This could explain why under the *pull* treatment the percent remaining vegetation in willow plants was the highest (80%). Only 8% of the young willow plants died in *control*, *push*, and *pull* treatments, and young willow plants remained almost intact in the *push-pull* treatment, showing maximum synergy between stimuli.

Another factor to be considered when implementing this type of integrated pest management is the variability of plant preferences among the colonies or populations of LCAs. Ants' foraging decision is complex. Plant species are accepted or avoided depending on environmental conditions,[9] ant species,[47,48] colony and symbiotic fungus needs,[49] colony age or size[50] or certain foliage mechanical and chemical characteristics.[4,51] In our study, throughout the year, LCAs used many or most of the locally available plants. Thus, before adopting this strategy, a preliminary survey to acknowledge the presence of palatable local plant species within the farmland vegetation should be performed, in order to account for such variability.

Currently, the most common method to control LCAs is the use of toxic baits, but it is the least suitable method for our study site. The Delta of the Parana River, has a permanent presence of water, and high soil humidity. Under these conditions, baits swell in a single day, making them unattractive to ants. These wet baits stay in the field, and their toxic components drain into the river.[16,18] Moreover, LCAs learn to avoid toxic baits once they realize that they are toxic to the fungus.[52] The push-pull strategy was designed as an alternative, toxic free and environmentally safe local option to manage LCAs. Using a mechanical and chemical barrier as *push* stimulus, we generate a behavioral change in ants; as a generalist herbivore, they will cut alternative vegetation instead of the protected willow plants. Using farmland vegetation as *pull* stimulus gives ants other options to cut. As demonstrated, ants select some species above others, without preference between the willow and these selected plants. In our study site there were plants species selected and non-selected by LCAs. Both types of vegetation grow spontaneously in the field. On the one hand, ants' selected vegetation gives farmers the advantage of having alternative resources to manage LCAs without doing sow labor. On the other hand, the presence of unselected vegetation will increase biodiversity improving some ecosystem services, promoting production resilience, and consequently reducing the need for outside inputs.

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SUPPORTING INFORMATION

Supporting information may be found in the online version of this article.

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