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Know thy enemy: interspecific differences of pine consumption among leafcutter ants in a plantation

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Abstract The damage to plantations by pests is often determined by perceptions rather than objective data, resulting in excessive use of pesticides. Leafcutter ants are considered important pests to plantations in America. We evaluated the difference in *Pinus taeda* biomass consumption by four *Acromyrmex* leafcutter ant species which co-inhabit plantations of this pine species. These ants exhibit morphological and behavioral differences, i.e., *Ac. heyeri* has mandibles adapted to cut monocots, while the other species cut dicots, which may result in differences in their consumption of pine. We collected the plant biomass that ants carried into their nests and recorded the foraging activity in different seasons throughout a year. The *P. taeda* biomass carried into leafcutter nests was less than 20 % compared to total plant biomass. Colonies with greater foraging activity carried a greater amount of total biomass, but they did not carry more pine biomass. The leafcutter ant species studied differed in their use of pine biomass, but not of total biomass. *Acromyrmex ambiguus* and *Ac. crassispinus* were the species carrying the greatest amount of pine biomass and with more colonies using pine, whereas very little amounts of pine were carried by *Ac. heyeri* and by very few colonies. Thus, leafcutter ant species do not cause the same damage to pine plantations. Our results also highlight the importance of pest management strategies based on a thorough knowledge of the biology of the species, including those characteristics which can predict the use that each species will make of the plantation.

Keywords *Acromyrmex* · *Pinus taeda* · Forestation · Species traits · Pest species

Key message

- Leafcutter ants in Argentina are generally treated with chemical pesticides without damage quantification.
- There is a pressing need to increase the estimations of leafcutter ants' damage to plantations by the more than 35 *Acromyrmex* and 10 *Atta* species.
- Differences in pine biomass consumption among four leafcutter ant species that co-inhabit a forestation were found.
- A behavioral trait and a lower flexibility in resource selection seem to be the factors involved in the observed differences.
- These results aid in building predictive tools for the potential impact of these species as pests, as well as to reduce pesticides in the environment by limiting its use to real pest species.

Introduction

The damage to a plantation inflicted by a certain species, and therefore its pest status, is often assessed through perception rather than objective data (Hill 1983). This may lead to the excessive use of pesticides, with the negative consequences to the environment associated to such

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practices, including the loss of non-target and benefic organisms (Newsom 1967; Pimentel et al. 1992).

The leafcutter ants in the genera *Acromyrmex* and *Atta* are considered among the main herbivores in the Neotropics, because they cut great amounts of leaves from different plants in order to culture a symbiotic fungus with which they feed their larvae (Hölldobler and Wilson 1990). These ants usually attack several plantations in their habitat (Montoya-Lerma et al. 2012; Della Lucia et al. 2014). In such situations, most producers turn to chemical control methods in order to reduce the impact of ants on their plantations (Montoya-Lerma et al. 2012). These agrochemicals are usually applied incorrectly, either because they are used in excess or because there is no proper knowledge regarding how each control method affects ants [Della Lucia et al. 2014; but see Zanetti et al. (2014) and reference therein for exceptions in Brazil], and have been shown to affect their natural enemies (Guillade and Folgarait 2014a). Most importantly, these control methods are not specific to the leafcutter ant species which are pests, but are used indiscriminately against all the leafcutter ant species present (Della Lucia et al. 2014). However, not every leafcutter ant species using the plantation as a resource causes an economically significant damage (Fowler et al. 1989; Della Lucia et al. 2014; Guillade and Folgarait 2014b), and there is a pressing need to increase the estimations of the resource utilization by the more than 35 *Acromyrmex* and 10 *Atta* species (Della Lucia et al. 2014).

We assessed the differences in *Pinus taeda* biomass intake by four leafcutter ant species in the genus *Acromyrmex* inhabiting a pine plantation: *Acromyrmex ambiguus*, *Ac. crassispinus*, *Ac. heyeri*, and *Ac. lundii*. They share the general characteristics of the leafcutter ants, with colonies comprising hundreds of thousands individuals, physically and chemically marked foraging trails extending from the nest, and foragers which cut leaves from several plants in order to maintain their fungus garden (Hölldobler and Wilson 1990). Nonetheless, there are important differences in morphology and behavior among these species which may influence the level of injury they exert on a plantation.

One such difference is that *Ac. heyeri* cuts mostly monocotyledon leaves, specifically grasses, whereas the other species mostly focus on several dicotyledon plants (Fowler 1988). These differences in the use of plant species are correlated to morphological differences in the ants' heads. Grass leaves offer greater resistance to cutting than most dicotyledon leaves, and thus, *Ac. heyeri* heads are bigger in proportion to their bodies, which allows for larger mandibular muscles and therefore greater mandibular strength (Fowler 1988). Furthermore, their mandibles are shorter and stouter than those of dicotyledon-cutter ants (Fowler 1988). Pine needles exhibit similar morphology and toughness to monocotyledon leaves (Bernays et al. 1991; Zovi et al. 2008), suggesting that *Ac. heyeri* should be better pre-adapted to use this resource.

Considering these factors, our hypothesis is that the leafcutter ant species differ in their use of pine as a resource. If ants are limited in their use of pine because of the greater toughness of pine needles, *Ac. heyeri* can be expected to be the species using greater amounts of pine needles as a resource. Since there are no comparative studies on the damage inflicted by these four different leafcutter ant species to the same plantation, we described the pine biomass carried by these ants compared to the total plant biomass carried, and we discuss our results in terms of the potential damage to the plantation.

Materials and methods

Study site

Data collection was conducted in an 1000-ha pine plantation in Entre Ríos, Argentina (31.66°S, 58.02°W), where *Pinus taeda* is the most abundant species planted, followed in importance by other pine species such as *P. eliotti*, as well as *Eucalyptus*. The space between rows of trees is occupied by native grasses and bushes typical of this ecoregion, belonging to the families Asteraceae, such as *Baccharis cordifolia*, *Bidens subalternans*, *Gamochaeta pensylvanica*, *Senecio pinnatus*, and *Solidago chilensis*; Boraginaceae like *Echium plantagineum*; Brassicaceae like *Raphanus sativus*; and Celastraceae such as *Maytenus ilicifolia*, which ants also use as a resource. Ants are controlled using agrochemicals (granulated baits containing sulfluramid, fipronil, chlorpyrifos and diflubenzuron, as well as insufflation with dry deltamethrin powder) mainly when pine saplings are planted. Afterwards, in plots older than 1 year, only focalized treatments on nests are performed. Due to this intensive ant control, there were hardly any ant nests in plots planted with pine less than 2 years before the beginning of our study. Thus, sampling was carried out in 3-year-old plots planted exclusively with *P. taeda,* with enough ant nests to carry out our samplings (see Sect. "Data collection"). These pines had an average height of 4.5 m. Although damage in pines older than 1 year was reported to be minimal (Cantarelli et al. 2008; Nickele et al. 2012), producers continue to control ants, regardless of their abundance, during the first 3 years of the plantation. On the other hand, it has been shown that leafcutter ant damage in older pines can be potentially harmful both directly by the damage through defoliation and indirectly, via higher colonization of aphids and other pests after leafcutter defoliation (Cantarelli et al. 2008).

Nonetheless, our aim was to compare the abilities and relative importance of the ant species as pine consumers, rather than to estimate the damage or economic injury level that they may inflict on the plantation.

Data collection

We performed an extensive search for leafcutter ant nests throughout the plantation. Due to chemical control methods of ants, only plots older than 2 years had leafcutter ant nests. Thus, we thoroughly inspected 2-ha areas in sixteen 3-years *P. taeda* plots, and geo-referenced every leafcutter nest found, identifying them to the species level. These areas were established in order to determine nest density of each ant species. In the five plots with higher nest density, that were at least 100 m to 2 km apart from each other, we selected the colonies with the largest nest mounds (for those species that build such structures, i.e., *Ac. ambiguus*, *Ac. crassispinus*, and *Ac. heyeri*) and those that exhibited great activity on their foraging trails. In those plots where we selected ant nests to work with, there was no insecticide application for the duration of our essays. Each of the nests selected was occupied by an ant colony, and therefore, each nest could be considered a replicate. We selected at least five nests per species. However, at the next sampling season, several nests were inactive (see Sect. "Results"), and although we searched for new nests, it was impossible to find as many as five nests in some seasons for ant species with low nest density. Thus, our sample sizes varied from 3 to 20 nests per species, depending on the season (see Table 1 for sample sizes). In order to assure independence among replicates, we used nests that were at least 30 m apart. Although leafcutter ant foraging trails are reported to be several meters long, our field measurements of distances from colony to focal tree (5.5 m mean, 3.7 m SD, 20 m max) indicate that in the site this distance is enough to avoid colony interference. In fact, we never observed interactions among workers or crossing of foraging trails of different colonies. Whenever a nest had more than one active foraging trail, one was randomly selected, whereas those with very little activity were excluded. We quantified the activity of both laden and unladen ants returning to the nest during 1 min, counted at a point close to where the trail enters the nest. These measurements, taken during the times when ant activity was at least higher than five ants returning to the nest/min, were repeated three times, with 1-min pauses between records, so that the activity measurement lasted 5 min in total. Immediately afterwards, we collected the loads from all the ants returning to the nest for 15 min. We recorded at each nest the number of active trails and whether pine was being carried on trails other than the one sampled.

Table 1 Relationships between pine dry biomass or total vegetation dry biomass, carried by four leafcutter species from a pine plantation, with ant activity (average laden plus unladen ants returning to the nest per minute)

	Pine biomass (g)			Total biomass (g)			N
	β	R^2/ρ	p	β	R^2/ρ	p	
Ac. ambiguus							
Pooled seasons	0.004	0.03	0.25	0.03	0.22	*<0.001*	41
Early spring		0.12	0.74		0.87	*<0.001*	10
Late spring		1.00	0.33		1.00	0.33	3
Summer		0.37	0.49		0.42	0.43	6
Autumn		0.26	0.31		0.73	*0.003*	15
Winter		0.49	0.26		0.68	0.11	7
Ac. crassispinus							
Pooled seasons	0.006	0.19	*<0.001*	0.04	0.32	*<0.001*	65
Early spring		0.34	0.17		0.44	*0.05*	18
Late spring		−0.03	0.92		0.09	0.75	13
Summer		−0.25	0.48		0.43	0.21	10
Autumn		0.77	*<0.001*		0.62	*0.01*	15
Winter		0.29	0.45		0.91	*0.001*	9
Ac. heyeri							
Pooled seasons	0.001	0.01	0.36	0.02	0.29	*<0.001*	75
Early spring		–	–		0.54	*0.04*	17
Late spring		0.48	0.10		0.69	*0.001*	20
Summer		0.31	0.24		0.35	0.17	16
Autumn		–	–		0.68	*<0.001*	15
Winter		–	–		0.68	0.09	7
Ac. lundii							
Pooled seasons	0.001	0.09	0.07	0.02	0.41	*<0.001*	39
Early spring		–	–		0.37	0.49	6
Late spring		0.17	0.75		0.88	*0.03*	6
Summer		0.30	0.47		0.67	0.08	8
Autumn		−0.02	0.93		0.76	*<0.001*	11
Winter		−0.08	0.84		0.51	0.18	8

Pooled data across seasons were analyzed with a linear regression, and the regression coefficient (β), the R^2, the probability value (p), and sampling size (N) are shown in the columns. For each season, the correlation between pine dry biomass or total vegetation dry biomass carried by the ants with ant activity was analyzed with Spearman correlations. Spearman's coefficients (ρ) and p values are shown in columns. Significant p values are highlighted in italics

Whenever a colony was foraging pine, we followed the trail to those trees from which ants were cutting to determine if it had been planted or if it was a natural regeneration. The behaviors of ants cutting pine were also recorded, i.e., if they established a trail up the trunk or if ants were cutting needles on the ground. The plant material collected was taken to the lab, where they were sorted into monocotyledons, dicotyledons, and pine. Items were then dried at 60 °C to constant weight using a precision scale (Metller AJ150).

Samplings were repeated five times between October 2013 and August 2014, in order to include possible temporal variations in the use of resources by the ant species studied. These sampling times corresponded to early spring (October), late spring (November), summer (December), autumn (April), and winter (August) in the Southern hemisphere.

Data analyses

In order to obtain a measurement of biomass carried per colony, we multiplied the measurements taken at each foraging trail by the number of active trails. When a colony was foraging pine, we multiplied the pine biomass only by the number of trails where ants were carrying pine. We thus obtained a measure of the biomass intake per colony during 15 min. This is important because leafcutter ant species can differ in the number of foraging trails. However, except for those ant species not active in a particular season, the rest of the ants maintained a similar circadian activity between species (according to our daily and random visits to nests from all species), although it varied according to the season: c. 9 h in early, late spring and autumn, 10 h in summer, and 8 h in winter, with foraging starting and finishing at similar hours. Therefore, we did not need to correct for differences in the foraging time across species.

We averaged the three 1-min measurements of ants returning to the nest (pooling laden and unladen ants) for each nest at each season to obtain a measure of ant activity. Ant activity was compared across species using ANOVA; whenever results were significant, we employed the Tukey test for a posteriori comparisons to evaluate differences between *Ac. heyeri* and the other ant species. Total biomass carried, pine biomass carried, and percentage of pine biomass were compared using the Kruskal–Wallis test, with species identity as the independent factor, given that the ANOVA residuals were not normal. Whenever the differences were significant, we compared medians using the Mann–Whitney tests, with the Holm correction to maintain $\alpha = 0.05$. We used linear regressions to evaluate the relation between both pine and total biomass carried and ant activity for data pooled for all seasons; and for each season, we used Spearman rank correlations due to low data points in some combinations. The proportion of colonies cutting pine per species and seasons was assessed using a logistic model (Crawley 2007). All statistical analyses and graphs were carried out using the R environment (R Development Core Team 2013).

Results

The most abundant species at our study site were *Acromyrmex crassispinus* and *Ac. heyeri* (4.5 ± 5.0 and 4.5 ± 3.4 nests/ha, mean ± SD, respectively), followed by *Ac. ambiguus* and *Ac. lundii* (1.2 ± 0.4 and 1.2 ± 0.9, respectively). Most of the nests that we geo-referenced in a sampling season were inactive the following season. We even observed many colonies in the process of moving, with workers carrying pieces of the fungal garden and brood to a new site.

Total biomass (i.e., pine + non-pine) carried by the ants into the nests during 15 min did not differ across species (Kruskal–Wallis $p > 0.1$ for all samplings); however, we found significant differences in pine biomass carried (Fig. 1). Nonetheless, there was a great variation in the use of pine by the different colonies within a species, and as a result, the differences across species were not significant in late spring ($H = 5.4$, $df = 3$, $p = 0.14$), when only one *Ac. heyeri* colony carried great amounts of pine (0.53 g, Fig. 1). However, that amount did not represent more than 30 % of the pine biomass carried by other species. Moreover, during the rest of the seasons, this species did not carry pine, or carried it in very small amounts (Fig. 1).

The pine biomass transported into the nests was a small fraction of the total biomass carried, only occasionally surpassing 20 % (Fig. 2, except *Ac. ambiguus* in late spring and autumn). In fact, in very few colonies, the pine biomass carried represented more than half of the total biomass (only 17, 10, 5, and 1 % of the nests of *Ac. crassispinus*, *Ac. ambiguus*, *Ac. lundii*, and *Ac. heyeri*, respectively). Colonies with greater foraging activity did not carry more pine biomass (Table 1, except for *Ac. crassispinus*), whereas the total plant biomass carried increased with greater foraging activity (Table 1). Foraging activity did not differ across species (early spring $F_{3,47} = 2.5$, $p = 0.07$; late spring $F_{3,38} = 1.9$, $p = 0.14$; autumn $F_{3,53} = 1.1$, $p = 0.34$; winter $F_{3,27} = 0.2$, $p = 0.90$) except in summer, when *Ac. lundii* was more active than *Ac. crassispinus* and *Ac. heyeri* (Fig. 3, $F_{3,36} = 4.6$, $p = 0.008$, Tukey contrasts between *Ac. lundii*, *Ac. crassispinus*, and *Ac. heyeri* $p < 0.05$).

The percentage of colonies carrying pine varied across species and seasons (logistic model: ant species $p < 0.001$, season $p = 0.02$; Fig. 3), and the species with more colonies carrying pine also varied according to the season (interaction between species and season $p < 0.001$; Fig. 3). *Acromyrmex heyeri* was the species with the smallest proportion of colonies cutting pine, whereas *Ac. ambiguus* and *Ac. crassispinus* had the greatest proportion of colonies attacking pines, and *Ac. lundii* was intermediate (Fig. 3).

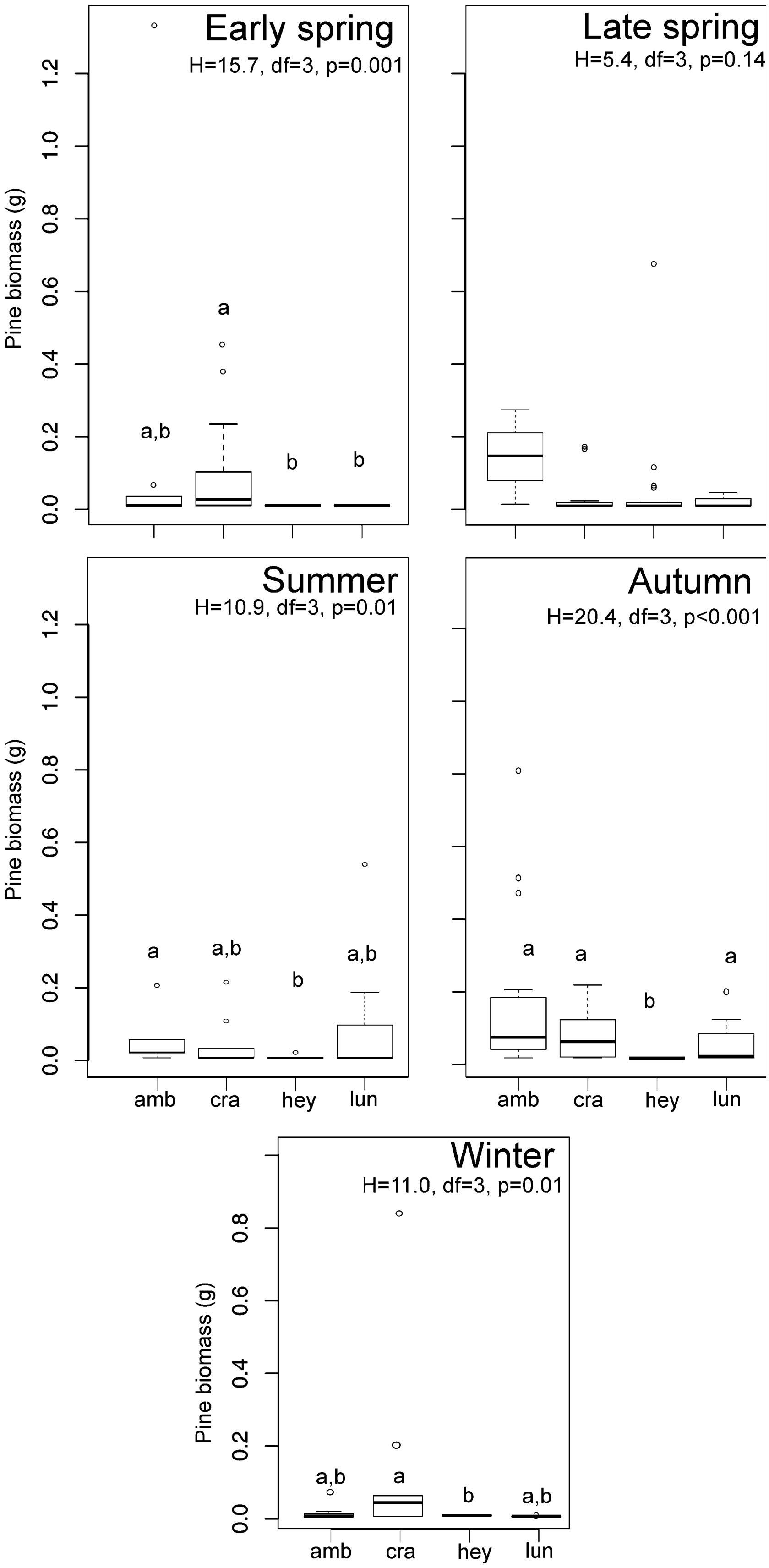

Fig. 1 Dry weight of pine biomass (g) carried by the leafcutter ants *Acromyrmex ambiguus* (amb)*, Ac. crassispinus* (cra)*, Ac. heyeri* (hey), and *Ac. lundii* (lun) in different seasons throughout a year in a pine plantation. The statistics shown are Kruskal–Wallis tests, and *same letters above boxes* represent species that did not differ according to multiple comparisons corrected by the Holm method. The *thick line* represents the median, and upper and lower limits in *boxes* represent the 1st and 3rd percentiles, respectively; the edges of the *broken lines* are approximations to the 95 % confidence interval, and the *dots* are outlier values

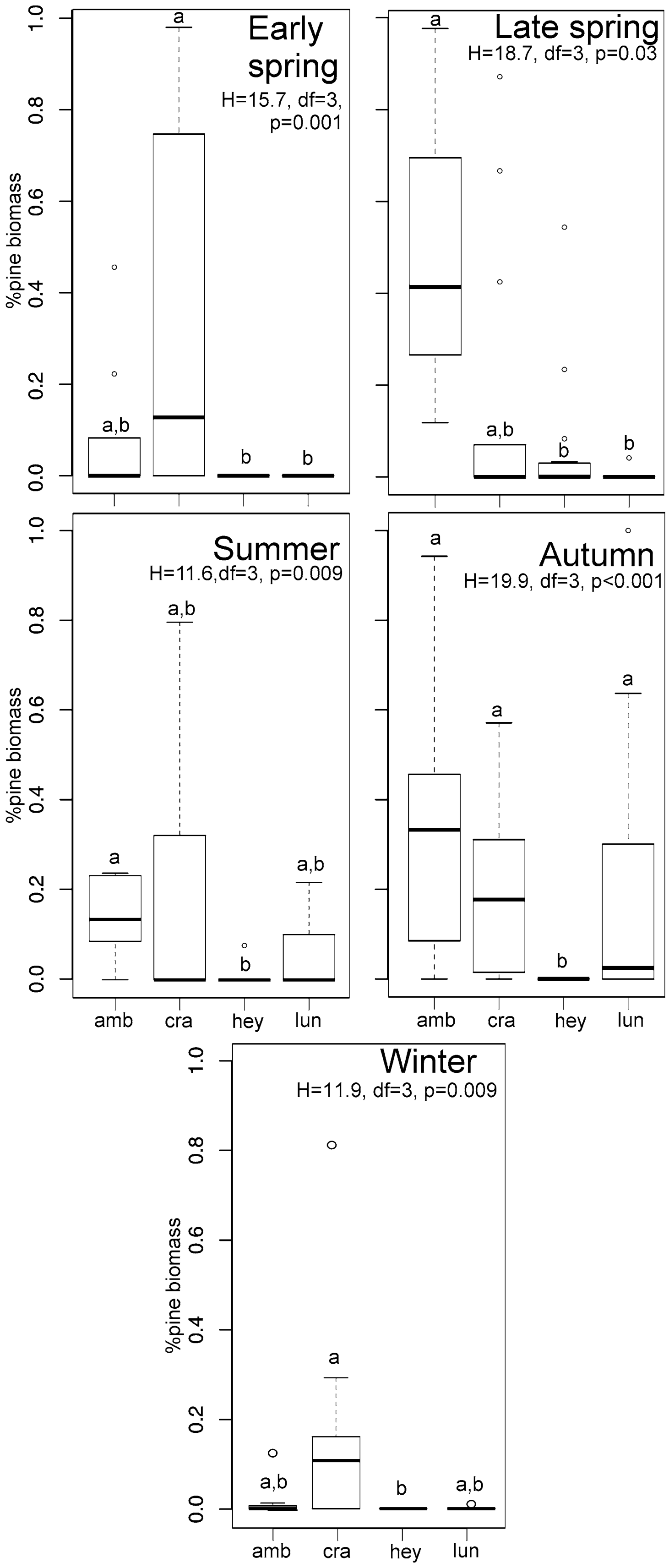

Fig. 2 Percentage of pine biomass in relation to total biomass carried by the leafcutter ants *Acromyrmex ambiguus* (amb)*, Ac. crassispinus* (cra)*, Ac. heyeri* (hey), and *Ac. lundii* (lun) in different seasons throughout a year in a pine plantation. The statistics shown are Kruskal–Wallis tests, and *same letters above axes* represent species that did not differ according to multiple comparisons corrected by the Holm method. The *thick line* represents the median, and upper and lower limits in *boxes* represent the 1st and 3rd percentiles, respectively; the edges of the *broken lines* are approximations to the 95 % CI, and the *dots* are outlier values

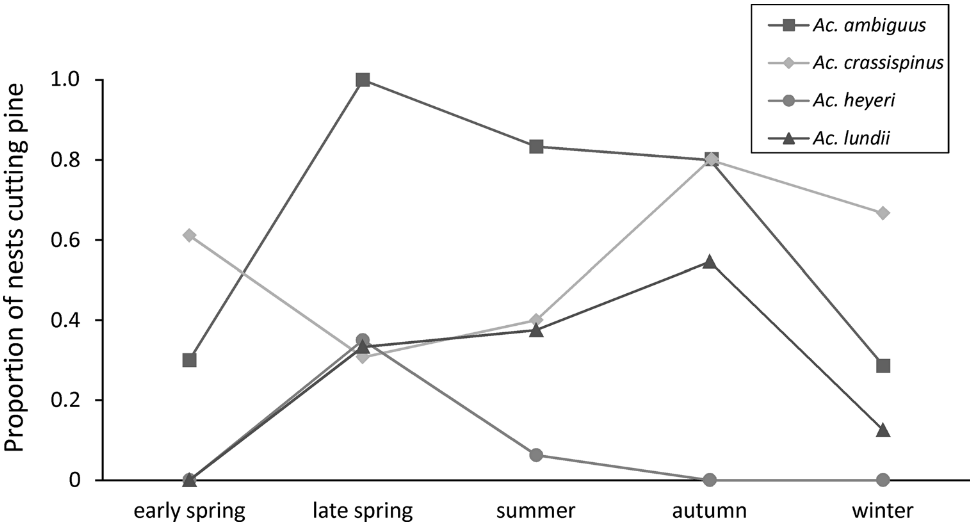

Fig. 3 Proportion of leafcutter ant colonies cutting pine trees at each season in a pine plantation, according to species: *Acromyrmex ambiguus* (amb), *Ac. crassispinus* (cra), *Ac. heyeri* (hey), and *Ac. lundii* (lun). The *number of nests* sampled at each time is given in Table 1

Of the species cutting pine, only *Ac. ambiguus* completely defoliated trees. Only *Ac. ambiguus* and *Ac. crassispinus* cut terminal buds as well as needles. Ants foraged both young needles from the sampling year and old needles from previous years. We also found ants foraging on natural regeneration trees, i.e., younger pines that originate naturally from the plantation. The three species that cut dicotyledons also carried monocotyledons (24, 26, and 38 % of the items carried by *Ac. ambiguus, Ac. crassispinus*, and *Ac. lundii,* respectively). *Acromyrmex heyeri*, on the other hand, only carried 7 % dicotyledons, mostly flowers.

Discussion

Acromyrmex ambiguus was the species with the greatest proportion of colonies cutting pine, and it carried the greatest amount of pine biomass. Furthermore, this was the only species that completely defoliated pines. Total defoliation is the greatest injury that leafcutter ants can inflict, usually resulting in the death of the tree (Cantarelli et al. 2008). Therefore, this species was the most harmful in our site, and this is the first study to report its potential as a pest species on a forestation or more generally on a plantation. On the other hand, and in contrast to our hypothesis, *Ac. heyeri* was the species that cut and carried significantly the least amount of pine biomass: only 13 % of the colonies carried pine, when pooling samplings across seasons, and the pine biomass carried represented at most 30 % of the pine biomass carried by the other three *Acromyrmex* species present at the site. Thus, although this species is capable of cutting pine, our results show that it does not prefer this resource.

Among the mechanisms that explain the little use of pine by *Ac. heyeri* that we found, the behavioral trend of these ants to not climb trees seems to be an important factor when choosing new resources to cut. Ant species cutting monocotyledons do not need to climb trees in search for leaves to cut, given that grasses rarely exceed 1 m height, whereas dicotyledon cutters often climb trees in search for leaves (Vasconcelos 1990). Given that the height of pines older than 1 yr usually exceeds 1 m, this behavioral difference in the search for resources may limit monocotyledon cutter ants in the use of pine trees. In fact, our field observations show that these ants carried mostly needles that had fallen to the ground because of the wind, and we rarely observed these ants forming a foraging trail up the tree trunk as the other species did. In fact, our results agree with the only other study available about *Ac. heyeri*, which reports that this species was nine times less damaging than *Ac. lobicornis* in 60-day-old pine seedlings (Cantarelli 2005). *Acromyrmex heyeri* attacked a significantly lower proportion of pine seedlings and removed less biomass than *Ac. lobicornis*, even when the latter had a much lower density (Cantarelli 2005). Although these results need to be confirmed due to the low number of nests sampled and small time frame of that study, this seems to indicate that this species is of no major concern to pine production.

It is also likely that factors related to less plasticity of this species to select resources may have influenced their lack of preference for pine. For example, our data show that this species only cut 7 % of plant material that was not monocotyledons, its resource of choice, whereas the other species, which prefer to cut dicotyledons, used 24–38 % monocotyledons, which speaks of a greater plasticity in the selection of plant material. Moreover, *Ac. lundii* carried a high percentage of grasses (38 %) and was intermediate regarding pine consumption, suggesting that in fact there might be a negative relationship between pine consumption and the tendency to forage on grasses. Finally, it is possible that *Ac. heyeri* is more susceptible to pine secondary compounds, which may be repellent to leafcutter ants (Barnola et al. 1994).

The unexpectedly high frequency of colony moving that we found can increase the foraging area of a colony in a plantation, but on the other hand, it can decrease the risk of a pine being attacked repeatedly over several months or years. Moreover, a marked tendency to move colonies may decrease the efficacy (at the plantation level) of certain insecticides that are applied over the nests. Although all four species had a high incidence of colony moving, almost all the *Ac. ambiguus* nests were abandoned and the colonies relocated to other sites. This is yet another relevant trait of this species that deserves further study when evaluating its pest potential and how to control it.

The pine biomass carried by the ants was little when compared to the total biomass employed by the colonies, even for those species that carried greater proportions of pine (*Ac. ambiguus* and *Ac. crassispinus*). Furthermore, a greater foraging activity did not imply a greater consumption of pine (with the exception of *Ac. crassispinus*), suggesting that ants preferred to forage on a variety of plant resources, even in a plantation where the cultivated resource is predominant. This should be taken into account when managing a plantation, because leaving patches of native vegetation among the pines might be a simple strategy to mitigate the attack of ants on the cultivated plants, as previously suggested for managing *Atta* herbivory in coffee plantations (Varón et al. 2007), and which also seems to be the case in pine plantations attacked by *Ac. crassispinus* in Brazil (Nickele et al. 2012).

In absolute terms, the pine biomass carried by leafcutter ants seems to be rather little. The maximum daily pine biomass intake was 47.8 g, recorded for an *Ac. ambiguus* colony in summer (calculated as the biomass carried in 15 min/colony multiplied by the average daily foraging hours). The biomass of *P. taeda* needles from 3-year-old trees has been estimated in 2000–3000 g per tree for this region (Fassola et al. 2010). Therefore, the colony that cut most pine during a year, belonging to the species that foraged the greatest proportion of pine, would need ca. 50 days to completely defoliate a pine. These estimations, which are in fact overestimations because we measured ant biomass carried when ant activity was not low, question the need to control leafcutter ants in pine plantations of this age.

Our work shows that, even when a priori leafcutter ants are all considered potential pests, not all species of leafcutter ants may cause the same damage to pine plantations. This knowledge, as well as detailed information on the biology of the species, should be employed when managing leafcutter ants in plantations, not only to save money by not controlling those species that do not cause significant damage, but also to reduce the use of pesticides in the environment. For example, there are several species that specialize in foraging on grasses (such as *Atta vollenweideri*, *Atta capiguara*, *Ac. landolti*, *Ac. fracticornis*, *Ac. balzani*; Fowler 1985), and although the consumption of pine by other grass-cutter species remains to be tested, we predict that they will not be harmful to pine plantations.

Author contribution

LE and PJF conceived and designed research. LE and MAF conducted field work. LE analyzed data. LE and ACG wrote the manuscript. PJF obtained funds for conducting this research. All authors read and approved the manuscript.

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