RESEARCH ARTICLE

Effect of intraspecific competition on the demography of leaf-cutting ants: a matrix model approach

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Abstract

Intraspecific competition is a pervasive phenomenon with important ecological and evolutionary consequences in ants. However, its effect at population level remains less known. We investigated the effect of intraspecific competition on the demography of the leaf-cutting ant *Acromyrmex lobicornis* using a stochastic matrix demographic model parameterized with 3 years of census data. Given that competition is a negative interaction with potential consequences on fitness, we expected that nests that share their foraging area with conspecific nests would have a lower population growth rate than nests that did not. The stochastic growth rate of all sampled nests showed positive values, but with differences according to their competitive condition. Nests that did not share their foraging area showed a 34% annual growth, while nests that shared their foraging area with another conspecific nest showed only 13%. This difference appears to be related to a reduced probability that small nests grow to medium size in the competitive condition, this transition being the one that contributes the most to the population growth rate. These results suggest that competitive interactions often restrict the growth of small nest sizes, supporting previous evidence that proposed young ant colonies as the most vulnerable demographic stage. The known pattern of low overlap in ant foraging areas could be a consequence of a lower population growth rate of nests under competitive conditions. This illustrates how selective pressures on individuals (e.g., ant nests) can influence demography, emphasizing the role of intraspecific competition at population level and the potential consequences for species density and geographical ranges.

Keywords *Acromyrmex lobicornis* · Aggressive behaviors · Ant nests · Foraging · Stochastic matrix model

Introduction

Competition has been proposed as one of the most important selective forces that structure ant assemblages. Ants possess many of the traits expected to generate competition, such as large, long-lived, and sessile colonies, well-defined foraging territories and aggressive behaviors. Because different species of ants often require similar resources for nest sites and food, they may be commonly observed to interact aggressively with one another (Fellers 1987; Savolainen et al.

1989; Andersen et al. 1991, Andersen and Patel 1994). As such, competition has been described as the 'hallmark of ant ecology' (Hölldobler and Wilson 1990; Cerda et al. 2013), and is considered to play a key role in structuring local ant assemblages. However, the overlap in preferences for food type, activity time, or habitat is stronger among colonies of the same species than among colonies of different species. Consequently, intraspecific competition is usually stronger than interspecific competition (Adler et al. 2018; Chen et al. 2018).

Despite that intraspecific competition is a pervasive phenomenon with important ecological and evolutionary consequences in ants, its effect at population level remains less known. The effect of intraspecific competition has been studied mainly by correlating density with nest distribution (Fowler 1977; Ryti and Case 1986; Cushman et al. 1988; Adams and Tschinkel 1995), analyzing aggressive behaviors among individuals from different colonies at lab and field conditions, and recording agonistic interactions at food baits (Boulay et al. 2010; Parr and Gibb 2010). However, fewer

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investigations have studied how competition influences ant demography, which is key to better understand competition as a selective force.

The leaf-cutting ant species *Acromyrmex lobicornis* Roger is a good system to study the effect of intraspecific competition on ant demography. First, their colonies are relatively large (~ 10,000 workers) and use well-defined trails to access the plants that they cut, allowing a proper delimitation of their foraging territory (Farji-Brener 2000; Höldobler and Wilson 2011). Second, colonies rarely move once established and nests are long-lived (Farji-Brener 2000; Jofré et al. 2018). Thus, it is plausible to speculate that nests with overlapping territories have been competing for plant resources. Third, like other leaf-cutting ant species, colonies exhibit intraspecific aggression to protect their territories (Hernandez et al. 2002; Ballari et al. 2007; Di Marco et al. 2010). Finally, this ant species has a number of traits that facilitate to conduct demographic studies. Individual demographic units (i.e., nests) are easily surveyed at field because of the presence of an external nest-mound and refuse dumps, their colonies are founded and maintained by a single queen meaning one can track the demographic history of individual 'propagules' from foundation forward, and ecologically relevant proxies for colony size (i.e., nest-mound dimension) are straightforward to define and measure, which simplifies the construction of demographic models (Fowler et al.1986; Farji-Brener 2000; Farji-Brener et al. 2003; Jofré et al. 2022). All these characteristics make this leaf-cutting ant species particularly adequate to study the effect of intraspecific competition at population level.

Here, we investigated the effect of intraspecific competition on the demography of the leaf-cutting ant *A. lobicornis*. To do that, we used a stochastic matrix demographic model parameterized with 3 years of census data from a number of ant nests with and without conspecific nests within their foraging area. Given that competition is a negative interaction with potential consequences on fitness, we expect that the set of nests that share their foraging area with conspecific nests will have a lower population growth rate than the set of nests that do not have conspecific nest within their foraging area.

Materials and methods

Study area and leaf-cutting ant species

Field work was performed in a natural reserve of San Luis ("La Florida"), Argentina (33° 07′ S y 66° 03′ W, Fig. 1A). The reserve covers 340 ha, with an average altitude of 850 m. The average annual temperature in January (summer) is 25 °C and 9 °C in July (winter); the mean annual rainfall is about 600 mm (Del Vitto et al. 1994). The vegetation is represented by species belonging to the Phytogeographic Province of Chaco, Chaqueño Serrano District. This nature reserve is occasionally affected by overgrazing, fire, and logging. Due to these disturbances, native plant species typical of Chaco Serrano as well as exotic species are common in the area (Del Vitto et al. 1994). The dominant native species are *Lithraea molleoides*, *Prosopis caldenia*, *Vachellia caven*, *Celtis ehrenbergiana*, *Briza subaristata*, *Eragrostis lugens*, *Bouteloua curtipendula*, *Schizachyrium plumigerum*, and *Bothriochloa springfieldii*, mixed with exotic species, such as *Rosa rubiginosa*, *Ulmus* sp., *Robinia pseudoacacia* and *Cynodon* sp. (Del Vitto et al. 1994).

We worked with *A. lobicornis* Roger, one of the most common leaf-cutting ant species in Argentina in general,

Fig. 1 A Location of the study area. **B** Photos show the natural reserve and a nest of the leaf-cutting ant *Acromyrmex lobicornis*

and in the study area in particular (Farji-Brener and Ruggiero 1994; Jofré et al. 2018, 2022). *A. lobicornis* nests reach depths of 1 m; on the soil surface, the ants construct a mound made of twigs, soil, and dried plant material, which may reach a height of 0.5 m and a diameter of 1 m. Inside this mound, ants tend a fungus on which larvae feed (Farji-Brener 2000; Bollazzi et al. 2008). This ant species has relatively large colonies (~ 10,000 workers) and they forages in columns along well-defined foraging trails, which allows to clearly define their foraging area (Farji-Brener 2000; Farji-Brener et al. 2003; Jofré et al. 2018, Fig. 1B).

Field methodology

In the spring of 2012, we randomly marked 30 nests of *A. lobicornis* within the natural reserve. We included a wide range of nest sizes to properly perform demographic analyses. Each nest was individually marked and annually censured during the peak of ant activity (spring and summer) in 2012, 2013, and 2014. At each visit, we determined the following demographic parameters: (a) whether the ant nest was active or inactive (i.e., dead), (b) the size of the nest, and (c) the presence or absence of neighboring nests of the same species within the foraging territory of the focal nest. Nests were considered dead if there was an excess of leaf-litter, spider webs or other debris in the entrances, if no sign of worker activity was detected after disturbing the nest; and if signs of foraging activity were absent (Farji-Brener et al. 2003; Veira-Neto et al. 2016). Nest size is considered a good estimator of colony growth in leaf-cutting ants (Fowler 1977, Fowler et al. 1986; Vieira-Neto et al. 2016). In the case of *A. lobicornis*, we measured nest size as the diameter of the nest-mound because mounds were almost circular in shape. In mound-building ant species, it is known that nest-mounds increase in size as the colony grows, and they also decrease in size as the colony size decreases (Farji-Brener 2000; Farji-Brener et al. 2003; Tadey and Farji-Brener 2007; Jofré et al. 2022). Mounds decrease in size because they need constant maintenance because are often subjected to disturbances and breaks that reduce their dimensions. When a colony of leaf-cutting ants decreases because of ant mortality or contamination of their fungus gardens, the number of ants that are working in the repair and maintenance of the mound is notably reduced, resulting in a reduction in mound-size dimensions. To delimit the foraging territory of each focal nest, we measured the length of all its foraging trails and calculated the mean trail length. This measure was considered as the radius of a circular foraging territory with the focal nest located at the center. Each nest was thus characterized with (+) or without (−) intraspecific competition depending the presence or absence of neighboring nests within its foraging territory, respectively. In our sampling, we never found nests that were sampled as a focal colony

and as well as a competitor. In sum, we determined for each sampling period (2012–13; 2013–14) whether each nest increased or decreased its mound-size, and whether was alive or not according their category regarding the presence/absence of neighboring nests. These measures were our data base to build the matrix models and the projection matrices.

Statistical analysis: population structure and projection matrices

General methods

Structured population demography refers to the study of population dynamics of species in which individuals (in a generic sense, nests in our case) differ substantially in demographic processes (i.e., vital rates) associated with age, size, developmental stage, social status, or any other attribute that affects their contributions to population growth (Caswell 2001). The population dynamics is based on two kinds of discretization. On the one hand, a population is subdivided into discrete categories. Based on eco-physiological criteria, the life cycle of individuals is divided into discrete classes (or categories), that differ in vital rates associated with survival and reproduction. On the other hand, its dynamics are described in terms of discrete-time, projecting the population condition from time t to a time $t+1$. For each time unit, a vector $n(t)$ (called state vector) represents the number or proportion of individuals in the population for each category at time t. The study of the population dynamics translates variables measured at individual level within each class into demographic parameters, as emergent attributes of the population. These matrix models are probably the most commonly used in structured population dynamics studies (Caswell 2001).

The principal tool for assessing the dynamics of structured populations are the population projection matrices, square matrices in which entries are based on demographical processes occurring among classes. Each entry m_{ij} in the projection matrix represents the contribution of class j to class i from time t to $t+1$. In the simplest case (deterministic), population dynamics is governed by the formula: $n(t+1) = M.n(t)$, i.e., the projection matrix M is post-multiplied by the vector $n(t)$ to obtain the state vector at time $t+1$. Under certain properties of the projection matrix (see Caswell 2001), if this multiplication is repeated over several time-steps, the population will grow, remain stable, or decline at a constant rate (i.e., finite rate of stochastic increase, λ, the dominant eigenvalue of the projection matrix), and the proportions of individuals belonging to different categories will become constant (i.e., stable size distribution, μ, the corresponding eigenvector) (see Caswell 2001).

When vital rates change depending on environmental conditions, population dynamics can be studied by means of stochastic matrix models, described by the equation $n(t+1) = M(t).n(t)$, that is similar to the deterministic case, except that the projection matrix changes in each time step. Stochasticity can be incorporated in the model in several ways. We choose to use random selection of projection matrices with constant entries. The model assumes that the environment changes from one year to the next, and that the particular characteristics of the environment affect the population. This implies that under the same environmental conditions, the response of the population will be the same, but it will change if environmental conditions change. Thus, to study population dynamics from this perspective, we need k (at least two) matrices M_1, M_2 … M_k being the projection matrices under each set of environmental conditions. In each time t, $M(t) = M_i$, where M_i is selected randomly from the matrices set. The value of stochastic models in population dynamics lies in providing valuable information to explore and compare the population response to different degrees of environmental variability, simulating different scenarios (real or of possible interest) that evaluate the response of populations to various sets of environmental conditions. The theory of stochastic matrix models has been extensively developed by Caswell (2001), and the bibliography abounds where these models are applied to population studies.

Estimating stochastic rate of population growth

For the stochastic matrix models (as in the deterministic case), several results can be obtained that describe the population dynamics through the stochastic selection of matrices or parameters. The main ones are: (a) the stochastic rate of population growth, usually denoted by λ_S. (b) a confidence interval for the estimator λ_S; (c) the sensitivities matrix and, (d) the elasticities matrix. These matrices are of the same order of the projection matrices $M(t)$. The stochastic population growth rate λ_S, is estimated by numerical simulation from log λ_S. As in the deterministic case, the comparison of log λ_S with zero is an indicator of the long-term population variation. If log $\lambda_S > 0$ the population has an increasing asymptotic dynamic, if log $\lambda_S < 0$ it has a decreasing dynamic and if log $\lambda_S = 0$ they are not expected changes in population numbers (or if λ_S is greater than, less than or equal to 1, respectively). This demographic parameter has the formula: log $\lambda_S = \text{Lim}_{t \to \infty}(1/t)(N(t)/N(0))$, where $N(t)$ is the total number of individuals at time t and $N(0)$ represents the initial population. The sensitivity analysis makes it possible to distinguish those demographical processes whose variation would affect the population growth rate largely, that is, at higher sensitivity values of an element of the projection matrix, at small disturbances in that parameter, greater variations in the population could be expected

in population growth rate. Sensitivity of λ_S to perturbations in m_{ij} entry of projection matrix $M(t)$ is defined as: $s_{ij} = \partial \lambda_S / \partial m_{ij} = \lambda_S \, \partial \log(\lambda_S) / \partial m_{ij}$. Analogous, the elasticity matrix (or proportional sensitivities), is a matrix where each element represents the relative contribution of each matrix entry to the constitution of the population growth rate λ_S. Thus, an elasticity of 0.6 indicates that 60% of λ_S is due to the process involved in the corresponding entry of the projection matrix. Because elasticities sum to 1, they can be interpreted individually or grouped according to a criterion of interest, for example, grouping all the elasticities that correspond to the contributions of one category to all the others, or those that correspond to a same demographic process. Elasticities are defined by the equation: $s_{ij} = \partial \log(\lambda_S) / \partial \log(m_{ij})$. In the present work, we evaluate by means of stochastic matrix models the demographic dynamics of *A. lobicornis* with and without intraspecific competition.

Using the field data for the analyses

To build the matrix model and to estimate the demographic parameters, sampled nests were separated in three discrete classes of size: small (1) medium (2) and large (3) following the criteria used in Farji-Brener et al. (2003) and Jofré et al. (2022). Small nests were those with a mound diameter < 70 cm (which are probably below the reproductive size), medium those between 71–99 cm, and large those > 100 cm in diameter. We defined the projection interval (one-time step) as 1 year. Matrix entries are constituted by two demographic processes: (1) recruitment (i.e., the number of new nests produced by a single queen produced in each nest between one census and the next, i.e., ν_1, ν_2, ν_3); and (2) transition between size classes. The latter includes stasis (the probability of remaining in a class from one census to the next. i.e., $\alpha_1, \alpha_2, \alpha_3$), growth (reaching another class from one census to the next, i.e., $\beta_{1 \to 2}, \beta_{1 \to 3}, \beta_{2 \to 3}$) and regression (i.e., moving to a smaller class from one census to the next, i.e., $\beta_{2 \to 1}, \beta_{3 \to 1}, \beta_{3 \to 2}$). These transitions involve survival and class changing.

We constructed two projection matrices based on field data corresponding to the periods of 2012–13 and 2013–14. Recruitment rate was estimated based on the existing information from leaf-cutting ants in general (Fowler et al. 1986; Farji-Brener et al. 2003; Holldobler and Wilson 2011), because there are no data available for *A. lobicornis*. This kind of estimation has been used in other demographic ant studies (Farji-Brener et al. 2003; Vieira-Neto et al. 2016; Jofré et al. 2022). Considering that (a) as the nest grows, the production of reproductive individual increases, (b) there are more predation events during nuptial flights, and (c) the survival rate of incipient nests is very low (Fowler 1977; Vasconcelos and Cherrett 1995; Farji-Brener et al. 2003; Vieira-Neto et al. 2016), we

determined a reproductive rate per nest as 100 queens in small nests, 200 in medium nests and 500 queens for large nests with a survival rate of 5%; and a 10% of survival of incipient nests. Therefore, the contributions of new successful nests from one year to the next were defined as 0.5 nests for each small nest, 1 nest for each medium nest, and 2.5 nests for each large nest (Farji-Brener et al. 2003; Jofré et al. 2022). Since the reproduction was estimated from references, it is important to assess the sensitivity of our results to avoid uncertainty in these estimates. We thus test the robustness of our results of the matrix model to the uncertainty of our reproductive estimates following the methodology proposed by Claessen et al. (2005). The results showed that the ranking of the most important vital rates did not depend on our estimates of reproductive values (see ESM Appendix 1). Stasis, growing and regression were calculated from the field data as the proportion of nests that remained in their class, or grew to a higher or decreased to a lower class, respectively.

Obtaining population projections from field data

After defining the projection matrices, an arbitrary initial population vector was projected and the stochastic population growth rate (λ_S) was calculated. This stochastic growth rate was obtained from numerical simulations that choose one of the matrices each year and multiply it by the most recent population vector. To perform the simulations, projection matrices for the periods 2012–13 and 2013–14 were entered into the simulation process with the same probability (0.5). The stochastic growth rate (λ_S) and its confidence interval were obtained for each competition condition; with or without conspecific nests inside the foraging area (+ COM and – COMP, respectively). Two further analyses in each competition condition were carried out to assess the impact that small changes in demographic processes (i.e., projection matrix entries) have on the stochastic population growth rate: sensitivity and elasticity. As explained before, sensitivity analysis measures the impact of absolute changes in vital rates of population growth rate (i.e., the absolute contribution), while elasticity analysis estimates the effect of a proportional change in the vital rates of population growth rate (i.e., a relative measure of that contribution) (Benton and Grant 1999). Because elasticities total one, they can be summed in subsets to provide a proportional measure of the importance of each demographic process for the population growth (Tuljapurkar et al. 2003). Definitions and calculation procedures can be found in Caswell (2001) and Stubben and Milligan (2007). All model calculations were performed by means of a programming code using GNU Octave, 4.0.0 (Eaton et al. 2019).

Results

Descriptive results: number of nests per size category and transitions among size classes

Of the 30 focal nests sampled, 17 had no nests within its foraging area (− COMP), and 13 had one nest, of medium size, within its foraging area (+ COMP). No nest showed more than one conspecific nest within its foraging area. The number of nests per size category varied between nests with or without competition. While nests with neighbors showed a larger proportion of nests of medium size and smaller proportion of initial nests, nests without neighbors showed a larger proportion of nests in initial and medium-size categories along the sampling years (Fig. 2). Regarding the transition among size classes, nests without neighbors showed a higher proportion of nests that reached medium-size class from small-size class, lower proportion of nests that reached large-size class from intermediate-size class, and a relative lower mortality in initial size classes than nests with neighbors (Table 1).

Population growth, elasticity and sensitivity

The calculations revealed that both sets of nests (with and without competition) showed intrinsic stochastic growth rate (λs) greater than one, but with differences regarding the competitive condition. The set of nests of *A. lobicornis*
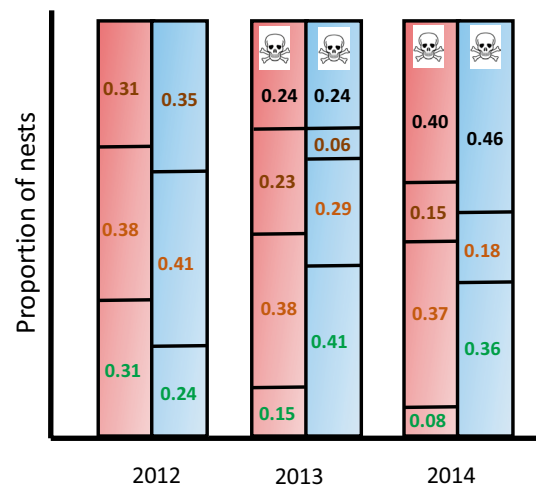

Fig. 2 Number of nests (proportion) per size class founded in the sampling years of 2012, 2013 and 2014. Red bars are nests that share their foraging area with other conspecific nest ($N = 13$ nests), and blue bars are nests that not share their foraging area with other conspecific nest ($N = 17$ nests). Numbers in green belong to the small class of nests, numbers in orange to the intermediate-size class, and numbers in brown to the larger-size class. Numbers in black represents dead nests

Table 1 Number of nests (in percent) that increase (e.g., $1 \rightarrow 2$), remain (e.g., $1 \rightarrow 1$) and decrease (e.g., $2 \rightarrow 1$) their size along the sampling period according to whether they share or not their foraging territory with another nest of the same species (+ and – competition, respectively)

	+ Competition		− Competition	
	2012–2013	2013–2014	2012–2013	2013–2014
$1 \rightarrow 2$	0	0	13	6
$2 \rightarrow 3$	15	8	0	0
$1 \rightarrow 3$	0	0	0	0
$1 \rightarrow 1$	15	8	12	18
$2 \rightarrow 2$	15	22	12	12
$3 \rightarrow 3$	8	8	5	0
$2 \rightarrow 1$	0	0	12	12
$3 \rightarrow 2$	24	15	5	0
$3 \rightarrow 1$	0	0	18	5
$1 \rightarrow X$	15	8	0	18
$2 \rightarrow X$	8	8	18	5
$3 \rightarrow X$	0	0	5	0
X	0	23	0	24
N	13	13	17	17

Death (X) of nests of each size class (e.g., $1 \rightarrow X$) are also described. Size classes: $1 =$ small nests, $2 =$ intermediate nests, and $3 =$ large nests (see text for further explanation). $N =$ number of total nests sampled per period

Fig. 3 Above, conceptual model for the life cycle of *A. lobicornis* colonies. Life cycle classes include Small (1), Medium (2) and Large (3) nests. Below, projection matrices for *Acromyrmex lobicornis* nests that share or not their foraging area with another conspecific nest (+COMP, left, and – COMP, right, respectively). The stochastic growth rate (λs) and its confidence interval for each condition are shown inside the box. In the matrix, ν_1, ν_2, ν_3 represent recruitment for each size category, α_1, α_2, α_3 represent stasis (i.e., permanence in each size category), $\beta_{1 \rightarrow 2}$, $\beta_{1 \rightarrow 3}$, $\beta_{2 \rightarrow 3}$ represent growth from one class to a larger one, and $\beta_{2 \rightarrow 1}$, $\beta_{3 \rightarrow 1}$, $\beta_{3 \rightarrow 2}$ represent regressions from one class to a smaller one (see text for a more detailed explanation)

($E_{1 \rightarrow 2} = 21\%$, Fig. 4). Finally, in all competitive conditions, the intrinsic population growth rate appears to be more sensitive to the transition of small to medium sized nests (i.e., $\beta_{1 \rightarrow 2}$), followed by the permanence in small nest sizes (i. e, stasis, $\beta_{1 \rightarrow 1}$), and, to a lesser extent, the growth of medium to large-size nests (i.e., $\beta_{2 \rightarrow 3}$) (Fig. 5). However, in comparative terms, the intrinsic population growth rate was more sensitive to the transition of small to medium nests in the case of nests that shared their foraging area compared with those not ($\beta_{1 \rightarrow 2}$ 3.82 versus 1, respectively, Fig. 5).

Discussion

Intraspecific competition in ants is a prevalent phenomenon with important ecological consequences, but its effect at the population level is usually less documented. This work contributes to better understand this phenomenon by providing evidence that intraspecific competition can limit population growth in leaf-cutting ants. As predicted, ant nests that share their foraging area with other conspecific nests show a lower intrinsic population growth rate than nests with no neighboring nests within their foraging area. This relatively low intrinsic population growth rate under a competitive context appears to be related to a reduced probability that small nests will grow to medium nest size, which is the most sensitive transition between class sizes. These results suggest

that did not share their foraging area with other conspecific nests showed a higher intrinsic stochastic growth rate than the set of nests that shared their foraging area with a conspecific nest (1.34 ± 0.01 versus 1.13 ± 0.01, respectively). Consequently, the population of *A. lobicornis* showed a 34% or 13% annual growth rate depending on the presence or absence of one conspecific nest within its foraging area, respectively. The higher λs of nests in (− COMP) condition appear to be related to a higher probability that small nests grow to medium size (i.e., $\beta_{1 \rightarrow 2}$). Whereas the set of nests that did not share their foraging area grew from small to medium size with a probability between 0.14 or 0.45 depending on the year, the set of nests that shared their foraging area showed almost null probability in this size transition (Fig. 3). Accordingly, elasticity analyses revealed that the small nest size is the stage that most contributed to the intrinsic population growth rate in all the cases, with slight differences among competitive situations (Fig. 4). In nests that shared their foraging area, almost all the contribution came from the permanence into the small nest stage ($E_{1 \rightarrow 1} = 84\%$). However, in the set of nests that did not share their foraging area, the contribution to the intrinsic population growth rate also came in part from the permanence into the small nest stage ($E_{1 \rightarrow 1} = 50\%$), however a significant percent came from the transition from small to medium size
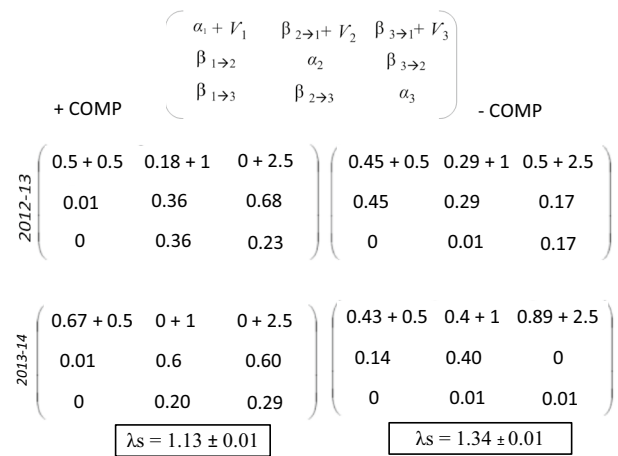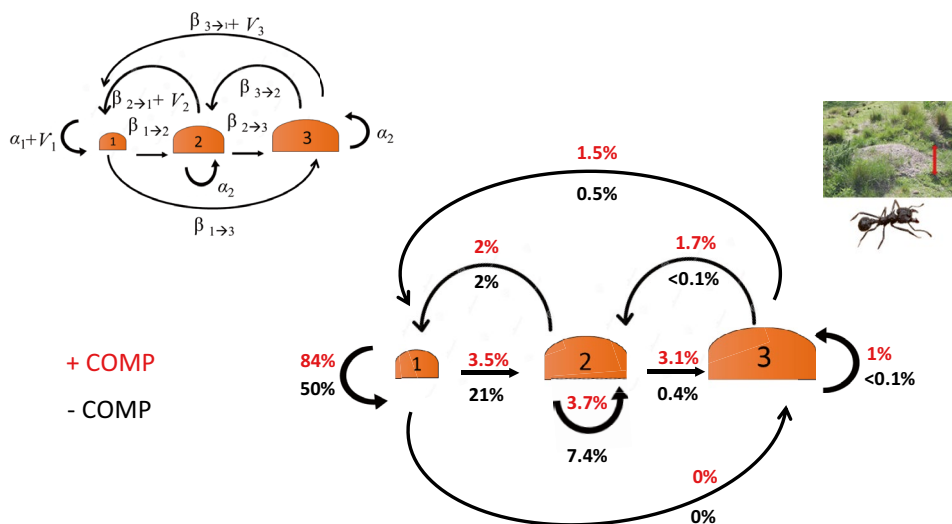
Fig. 4 Diagrams of the elasticity analysis for *Acromyrmex lobicornis* that share or not their foraging area with another conspecific nest (+COMP and – COMP, respectively). Life cycle classes include Small (1), Medium (2) and Large (3) nests. The values estimate, in percent, the contribution of the vital rates on population growth rate. The numbers in red correspond to the values in+COMP situation. Up to the left, we showed the conceptual model for its life cycle (see Fig. 2 for a detailed explanation)

Fig. 5 Sensitivity matrices for *Acromyrmex lobicornis* that shared or not their foraging area with another conspecific nest (+COMP and – COMP, respectively). On the left, we showed a small figure of the conceptual model for its life cycle (see Fig. 2 for a detailed explanation)
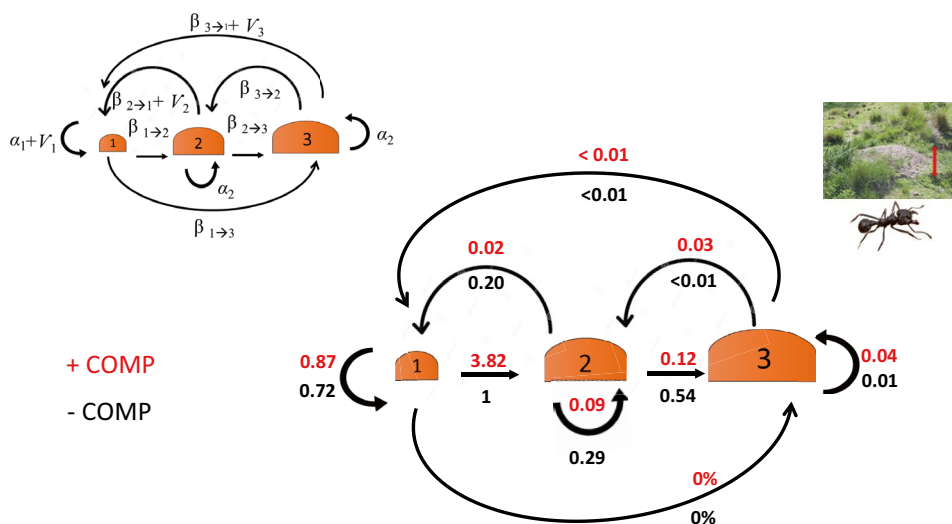
that competitive interactions strongly restrict the growth of young ant nests, confirming previous evidence which proposes small nests as the more vulnerable size class.

Small nests, that house incipient ant colonies, are especially vulnerable to environmental conditions and strongly dependent on the acquisition of resources (Fowler 1977; Fowler et al. 1984, 1986; Farji-Brener et al. 2003). First, small nests are more susceptible to changes in abiotic conditions than large nests, which affect both the ants themselves and the adequate growth of their fungus culture. Second, the relatively small number of foraging ants in the first developmental stage of the nest restricts the area of resource exploration and the amount and variety of plant fragments that enter the colony. Therefore, it seems logical that competition strongly restricts the growth of small nests more than the growth of larger nests.

The reduced intrinsic population growth rate in nests that share their foraging area with other nests can be a consequence of both direct and indirect interactions, i.e., competition by interference or exploitation, respectively. On the one hand, there is observational and experimental evidence of direct aggressive behaviors between ants of neighboring nests. Founding queens and workers from incipient nests can be executed by established colonies of leaf-cutting ants (Rockwood 1973; Fowler 1992; Fowler et al. 1984). Particularly, *A. lobicornis* ants of one nest can discriminate workers from another nest of the same species, exhibiting intraspecific aggression to protect their territories (Hernandez et al. 2002; Ballari et al. 2007; Di Marco et al. 2010). In our study area *A. lobicornis* harvest only 60% of the available plant species, with strong preferences to very few plant species that are in low abundance

(Jofré et al. 2018). This high degree of selectivity toward a few number of low abundant plant species may strengthen the competition between neighboring nests (Franzel and Farji-Brener 2000; Nobua-Bhermann 2014).

We found that nests that share their foraging area with another conspecific nest showed a lower rate of population growth than nests without neighbors, which suggests that resource competition negatively affects ant demography. However, in this study, we did not confirm whether the availability of palatable plants is limited, neither did we document whether nests that share foraging territories consume the same plant species. As stated, resource limitations are considered a pre-requisite for competitive interactions to occur (Keddy 1989). But as we mentioned earlier, in the study area, plant coverage is relatively scarce, and *A. lobicornis* shows selective foraging toward few plant species that are in low abundance, preferences that are consistent among nests of the same species (Jofré et al. 2018). This evidence, together with the fact that their long-lived colonies rarely move once established (Farji-Brener 2000; Jofré et al. 2018), strongly suggests that nests that show overlapped foraging areas compete for limited plant resources. In sum, since nests with and without neighbors were interspersed throughout the sampling area and shared similar environmental conditions, it's hard to believe that there is another reason besides competition that could be the cause of the low intrinsic population growth in nests that shared their foraging territory with another nest of the same species.

Using a stochastic matrix model approach, we showed that intraspecific competition results in a reduced rate of intrinsic population growth. However, we also found that the intrinsic population growth rate under a competitive condition, despite being lower than a non-competitive scenario, was still positive ($\lambda s > 1$). Interestingly, in the sampling area, we never found that a focal nest shared its foraging territory with more than one nest. This suggests that sharing a foraging area with more than one nest could cause a population decline, being selected negatively. The low overlap level in foraging ranges is common in leaf-cutting ants but also in other ant groups (Bernstein and Gobbel 1979; Levings and Traniello 1981; Acosta et al. 1995; Gordon and Kulig 1996; Solida et al. 2010). Our results suggest that the known general pattern of a low overlap level in ant foraging territories could be the consequence of a lower intrinsic population growth rate of populations that share their territories with other nests. This illustrates how selective pressures on individuals (i.e., on ant nests in our study case) can influence their demography, emphasizing the role of intraspecific competition at the population level and their potential consequences for species density and geographical ranges.

Declarations

Conflict of interest Not applicable.

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