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Unexpected costs of extended phenotypes: nest features determine the effect of fires on leaf cutter ant's demography

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Research

Cite this article: Jofré LE, de Torres Curth M, Farji-Brener AG. 2022 Unexpected costs of extended phenotypes: nest features determine the effect of fires on leaf cutter ant's demography. *Proc. R. Soc. B* **289**: 20212333. https://doi.org/10.1098/rspb.2021.2333

Received: 21 October 2021
Accepted: 25 January 2022

Subject Category:
Ecology

Subject Areas:
ecology, behaviour

Keywords:
Acromyrmex lobicornis, *Amoimyrmex striatus*, ant-nests, disturbances, population dynamics, stochastic matrix models

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Electronic supplementary material is available online at https://doi.org/10.6084/m9.figshare.c.5834309.

A key principle of the extended phenotype concept is that the benefit of the structures that an animal builds exceeds its cost. However, some contexts may enhance the costs of structures that often represent a benefit, reversing their adaptive nature. In leaf-cutting ant nests, thatched mounds are extended phenotypes that offer a stable microclimate for the growth of the fungus culture. We hypothesized that fires will affect the species that build external, easily flammable thatch mounds (*Acromyrmex lobicornis*) more than colonies that build subterranean nests in the less-flammable bare ground (*Amoimyrmex striatus*). We use a stochastic matrix demographic model parameterized with 4 years of data in pre- and post-fire scenarios. Before fires, *Ac. lobicornis* showed higher stochastic population rate (λs) than *Am. striatus*. However, fire frequency every 2 years completely reversed this trend, showing population decline only in *Ac. lobicornis*. Small nests were the stage that most contributed to λs and the most sensitive in all the species and fire scenarios. This illustrates a novel effect of disturbances; the reversion of the adaptive nature of extended phenotypes, which may have strong consequences on population dynamics and assemblage structure through the invert of dominance relationships.

1. Introduction

Animal constructions are considered functionally versatile extensions of their phenotype and a straightforward way to study how organisms adjust to their environment [1]. Given that natural selection operates on animals that build structures through the success of their constructions, structures badly designed imply a negative impact on the builders. Inefficient buildings can directly reduce the probability of animal fitness and survival, and/or represent a waste of energy that could have been allocated to other relevant functions [2,3]. Moreover, animal constructions are often easier to examine, manipulate and measure than the animal actions themselves [4]. For all these reasons, analysing the costs and benefits of these structures allows us to better understand the adaptive nature of animal ecology and behaviour.

A key principle of the extended phenotype concept is that the benefit of the structures that an animal builds exceeds its cost [1,2]. However, some contexts may reverse their adaptive nature, enhancing the costs of certain characteristics of the structures that often represent a benefit. Extended phenotypes are also more prone to fluctuations in costs and benefits than other traits, because—unlike some behaviours—they cannot quickly and easily adapt to disturbances. For example, in South Africa, vultures and raptors prefer large trees to locate their nests because it represents a long-term suitable habitat, but occasionally these large trees are also preferred as a food source by elephants, whose activity, directly and indirectly, increases nest mortality [5]. Larger nests built by

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harvestmen arthropods are often more attractive for females but also can be more negatively affected by the occurrence of heavy rains [6]. Hanging bird nests separated from the tree trunk represent a safer shelter and are easier to build, but are also more affected by the occasional occurrence of heavy winds that can produce their fall [7]. In summary, some construction features that normally represent a benefit for the builder may turn into a cost in occasional situations.

Leaf-cutting ants are a good system to study how the benefits and costs of animal constructions may change according to the context. These ants cut and collect plant fragments to use them as a substrate to cultivate a mutualistic fungus in chambers inside their nests, which is the source of food for the larvae [8]. Their nests are typical examples of extended phenotypes because they are long-lasting, conspicuous structures that play an adaptive function; they offer protection for the brood and a long-term more stable microclimate that are crucial for the proper growth of the fungus culture [9–12]. Leaf-cutting ants show a wide diversity of nest designs that range from the most sophisticated mound-shaped superficial nests, with the fungus garden located shallow and covered by a thatch mound composed mainly of dry plant fragments, to nests with multiple chambers excavated up to a depth of several meters on bare soil [8,12]. The presence of a thatch mound is considered a more elaborate way to achieve the proper microclimate inside the nests for fungus growth; species with this nest type often produce sexual individuals earliest, show ecological dominance and wider geographical ranges than those species of the same genera inhabiting subterranean nests [12–16]. However, this nest feature that commonly represents an adaptive advantage may turn into a cost in a context of a disturbance such as fire [17].

Here, we investigated whether the presence of a nest feature that often represents an adaptive value (i.e. a thatched mound) may turn into a cost under the occurrence of a fire. To do that we use a stochastic matrix demographic model parameterized with 4 years of census data in a large number of ant nests of two leaf-cutting ant species that share several ecological traits but differ in the presence/absence of thatched mounds. We hypothesized that fires will affect more the species that build thatched mounds because these kinds of nests are more flammable, and the location of their fungus gardens are often more superficial. We thus expect that in environments with recurrent fires, this species shows lower population growth than species that build complete underground nests, and that this effect increases as fires do.

2. Material and methods

(a) Study area and leaf-cutting ant species

Fieldwork was performed in a natural reserve of San Luis (La Florida), Argentina (33° 07′ S, 66° 03′ W). The area is a scrubland of 340 ha, located an average altitude of 850 m.a.s.l. (electronic supplementary material, S1). The average annual temperature in January (summer) is 25°C and 9°C in July (winter); the mean annual rainfall is about 600 mm [18]. 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. Owing to these disturbances, native plant species typical of Chaco Serrano as well as exotic species are common in the area [18].

We worked with *Amoimyrmex striatus* (formerly *Acromyrmex striatus* Emery, see [19]) and *Acromyrmex lobicornis* Roger, two of the most common leaf-cutting ant species in Argentina in general, and in the study area in particular [13,14]. These species differ in nest features that may determine the effect of fire on their demography. *Acromyrmex lobicornis* constructs nests with an external thatch-mound that may or may not be built at the base of plants (hereafter, ‘on plants’), and have their fungus garden shallow below the mound [12,14]. Conversely, *Am. striatus* constructs subterranean nests without a mound in areas of bare ground, with multiple chambers excavated up to a depth of several meters where they cultivate the fungal gardens (L.E. Jofré 2013, personal observation; [12,20–22]; figure 1). Second, in the study area nests of both ant species can be found relatively near each other. This fact allows us to easily compare the effect of fire on their survivorship in a similar environment context. Finally, both ant species have a number of traits that facilitate the ability to conduct demographic studies: nests are easily identified at the field, and ecologically relevant proxies for colony size are straightforward to define and measure, which simplifies the construction of demographic models [23–25].

(b) General field methodology

In the spring of 2012, we randomly walked within the natural reserve looking for nests of both ant species. We marked 70 nests in total, 35 of *Ac. lobicornis* and 35 for *Am. striatus*. The sampling includes a broad range of nest sizes to properly perform demographic analyses. Each nest was annually sampled during the peak of ant activity (spring and summer) during 4 years (2012, 2013, 2014 and 2015). At each visit we recorded the following measures: (i) whether the colony was active or inactive (i.e. dead). We considered nests 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 [24,25]; (ii) whether the nest of *Ac. lobicornis* was built or not at the base of plants (figure 1*a*,*b*). Nests of *Am. striatus* are always built on bare ground (figure 1*c*); and (iii) nest size. Nest size is considered a good estimator of the colony size in leaf-cutting ants [8,14,21,24–28]. In the case of *Ac. lobicornis*, we measured the diameter of the mound (figure 2*a*,*b*). For *Am. striatus* we counted the number of nest entrances, a proper estimator for colony size in leaf-cutting ants nest without mounds [20]. After the measurements in 2014, a severe fire occurred in the study area (see the electronic supplementary material, S1). The frequency and intensity of fire was the same throughout the reserve. Therefore, to determine the effect of fire on the demography of these leaf-cutting ant species we obtained measurements from two transition states pre-fire (2012–2013; 2013–2014) and one post-fire (2014–2015).

(c) Population structure and projection matrices

Matrix models are probably the most commonly used in structured population dynamics studies [29]. They are based on two kinds of discretization; life cycle of individuals (*sensu lato*) is subdivided into discrete categories, and its dynamics are described in terms of discrete-time, projecting the population condition from time t to a time $t + 1$ (for matrix models and methodological details see the electronic supplementary material, S2). Here we evaluate by means of stochastic matrix models the demographic dynamics of *Ac. lobicornis* and *Am. striatus*. Our analysis integrates the influence of fire on demographic dynamics according to the species (i.e. nest with/without mounds) and, in the case of *Ac. lobicornis*, whether their mounds were built on plants or not. To do so, we calculated the stochastic population growth rate λs [29] for no fire scenarios and for ones with different fire frequencies.

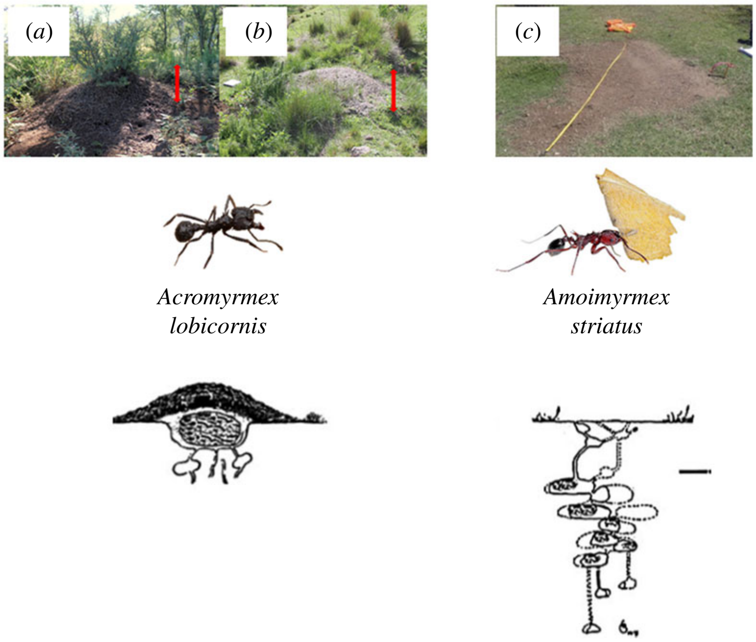

Figure 1. Leaf-cutting ant species studied and their nesting type. *Acromyrmex lobicornis* builds thatched nest-mounds that can be built on plants (*a*), or not (*b*). Their fungus culture is located relatively superficially, in a chamber inside the mound. Conversely, *Amoimyrmex striatus* builds subterranean nests without mounds on bare ground areas (*c*), and with their fungus culture in chamber several metres below ground. Drawings are modifications from Goncalvez (1961) and Carbonel (1943). Original drawn credits: Gonçalves, C. R. (1961). O gênero Acromyrmex no Brasil (Hym. Formicidae). Studia Entomologica, 4(1–4), 113–180 and Carbonell CS (1943) Las hormigas cortadoras del Uruguay. Rev Asoc Ing Agron Montev 15:30–39. (Online version in colour.)

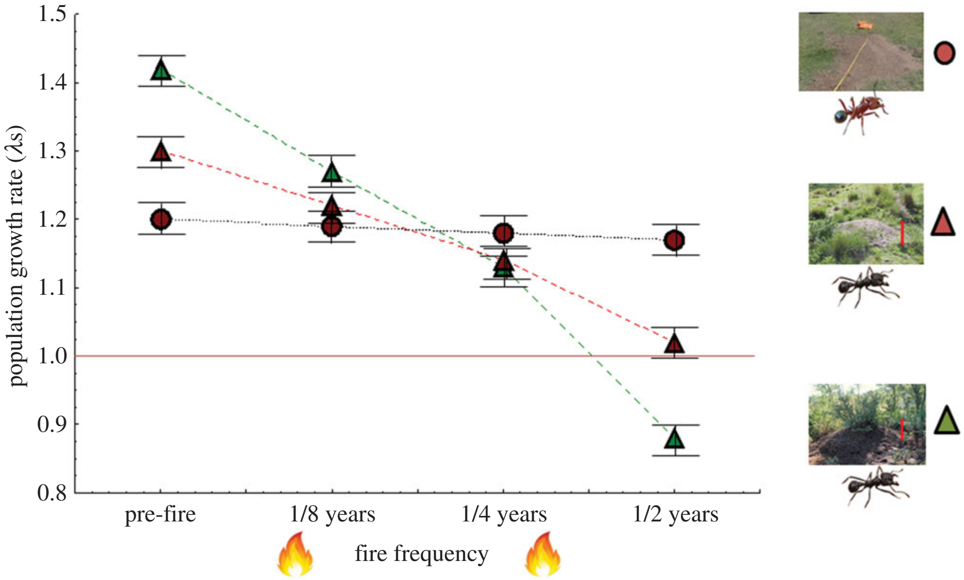

Figure 2. Stochastic growth rate for *Amiomyrmex striatus* (red circles) and *Acromyrmex lobicornis* that built mounds on plants or not (green triangles and red triangles, respectively), previous to fire and in scenarios with fire, with one fire every 8, 4 and 2 years. Fires every two years completely reverse the trend of the population growth rate that the studied species had shown in absence of fire. These stochastic growth rates were obtained from numerical simulations. This simulation was carried out for four environmental scenarios: no fire, one fire every 8 years (last fire record) and for two hypothetical scenarios: one fire every 2 and 4 years. (Online version in colour.)

To build the matrix model and to estimate the demographic parameters, nests were separated in three discrete classes of size: small (1) medium (2) and large (3). In *Ac. lobicornis* we followed the criteria used in [24]. Small nests were those with a mound diameter less than 70 cm, medium those between 71–99 cm, and large those greater than 100 cm diameter. For *Am. striatus*, we followed the criteria suggested by [20]; small nests were those with one or two entrances, medium nests those with three to five entrances, and large nests those with six entrances or more. Matrix entries are constituted by two demographic processes: (i) *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. v_1, v_2, v_3); and (ii) *transition between size classes*. The latter includes *stasis* (the probability of remaining in a class from one census to the next, i.e. α_1, α_2, α_3), *growth* (reaching another class from one census to the next, i.e. $\beta_{1\to2}$, $\beta_{1\to3}$, $\beta_{2\to3}$) and *regression* (i.e. moving to a smaller class from one census to the next, i.e. $\beta_{2\to1}$, $\beta_{3\to1}$, $\beta_{3\to2}$). These transitions involve survival and class changing (electronic supplementary material, S3).

Recruitment was estimated based on the existing information from leaf-cutting ants in general [8,20–27] because there are no data available for the studied species. This kind of estimation has been used in other demographic ant studies [24,25]. The production of reproductive individuals increases as the colony grows, but is affected by predation in the nuptial flights and low survival rate of incipient nests [24–28,30,31]. In both species, we determined a reproductive rate per colony 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 [24]. Because the reproduction was estimated from references, it is important to assess the sensitivity of our results to unavoidable 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 [32]. The results showed that the ranking of most important vital rates did not depend on our estimates of reproductive values (see the electronic supplementary material, S4). 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.

For all species and nesting types, we constructed three projection matrices based on field data: two corresponding to the pre-fire periods (2012–2013 and 2013–2014), and one after fire (2014–2015). After defining the projection matrices, an arbitrary initial population vector was projected and the stochastic population growth rate (λs) was calculated. The stochastic growth rate (λs) and its confidence interval were obtained for each environmental scenario, species and mound condition (i.e. built or not on plants) using the PopBio R-package [33,34]. Two further analyses were carried out to assess the impact that small changes on demographic processes (i.e. projection matrix entries) have on the stochastic population growth rate: sensitivity and elasticity. Sensitivity analysis measures the impact of small changes in vital rates on population growth rate (i.e. the absolute contribution), while elasticity analysis estimates the effect of a proportional change in the vital rates on population growth rate (i.e. a relative measure of that contribution) [35]. 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 [36].

3. Results

(a) Pre-fire scenarios

Before fires, the stochastic growth showed values greater than one in all cases, but with differences among species and nesting type. Mound-nests of *Ac. lobicornis* built on plants showed the highest λs (1.42 ± 0.01), followed by the nests of the same species but with mounds not built on plants (1.30 ± 0.01). Finally, *Am. striatus* showed the lower λs (1.20 ± 0.01). Consequently, the population of *Ac. lobicornis* showed a 42% or 30% annual growth depending on whether their nests were built on plants or not, respectively, whereas the population of *Am. striatus* showed a 20% of annual growth (figure 2). The higher λs of *Ac. lobicornis* with mound built on plants appear to be related to a lower probability of reduction of large to small nest sizes (i.e. $\beta_{3\to1}$). Whereas nests with mounds not built on plants can reduce their size from 1 year to another with a probability of 0.40, none of the nests that built their mounds on plants showed size reductions (figure 3). The comparatively lower λs of *Am. striatus* appear to be related with their low probability that small nests increased to medium size (i.e. $\beta_{1\to2}$). For example, for the sample period 2012–2013, while the mound-nests of *Ac. lobicornis* showed a probability up to 0.33 of change, *Am. striatus* showed only 0.05 (figure 3). Elasticity analyses revealed that the small nest size is the stage that most contributed to the population growth rate in all the cases, with slight differences among species and nesting type (figure 4). In *Am. striatus*, the smallest nests contributed 88% to the population growth rate ($E_{1\to1} = 84\%$ and $E_{1\to2} = 4\%$) and medium nests only 7%. Similarly, in *Ac. lobicornis* that do not built their mounds on plants, the smallest nests contributed 80% to the population growth rate ($E_{1\to1} = 69\%$, $E_{1\to2} = 11\%$) but medium nests increased slightly their contribution to the overall rate of population growth of 16% ($E_{2\to1} = 9\%$, $E_{2\to2} = 5\%$ and $E_{2\to3} = 2\%$). On the other hand, in *Ac. lobicornis* that built their mounds on plants, the smallest nests contributed to 58% to the population growth rate ($E_{1\to1} = 39\%$, $E_{1\to2} = 19\%$), and medium nests increased their contribution to 35% ($E_{2\to1} = 15\%$, $E_{2\to2} = 14\%$ and $E_{2\to3} = 6\%$; figure 5). Finally, in all species and nesting types the population growth rate appears to be more sensitive to perturbations on the transition of nests of small to medium sizes (i.e. $\beta_{1\to2}$), followed by the permanence in small nest sizes (i.e. $\beta_{1\to1}$), and, to a lesser extent, the growth of medium to large size nests (i.e. $\beta_{2\to3}$) (figure 5).

(b) Fire scenarios

The effect of fires on the demography of leaf-cutting ants depended on the species identity and nesting type. Whereas the stochastic growth rate of *Am. striatus* did not show significant changes, the stochastic growth rate of *Ac. lobicornis* decreased as fire frequency increased, especially in the population of nests that built their mounds on plants (figure 2). These differences appear to be related to the probability of permanence of small and medium nests in their size category. *Amoimyrmex striatus* showed almost the same levels of permanence in these categories after and before fires; but the population of *Ac. lobicornis* that did not build nest on plants showed a drop of 50% and 100% in their permanence levels in small and medium nests, respectively. Lastly, the population of *Ac. lobicornis* that built nests on plants were strongly affected in all their sizes, showing almost null probabilities of permanence within and among size-stages (figure 3). Accordingly, in a scenario of fires every 2 years, the population growth rate of *Ac. lobicornis* that did not build their mounds on plants dropped to almost one (i.e. did not show population growth nor decrease), while the population of this species that built their mounds on plants showed a growth rate of less than one, with a population decrease of 15% annually. In consequence, fires every 2 years completely reverse the trend of the population growth rate that the studied species would show in absence of fire (figure 2). On the other hand, the presence of fires did not change the pattern that the small nest size was the stage that most contributed to the population growth rate in all the cases. In scenarios with recurrent fires, elasticity analyses showed similar values to pre-fire conditions, and also highlighted the great importance of small nests on the rate of population growth (figure 4). Finally, in all fire scenarios and for all the ant species and nesting types, the population growth rate appears to be more sensitive to perturbations on growth of small to large size nests (i.e. $\beta_{1\to3}$),

$$\begin{array}{cccc} \text{2012–13} & \begin{pmatrix} 0.6+0.5 & 0.2+1 & 0.11+2.5 \\ 0.05 & 0.2 & 0 \\ 0 & 0.2 & 0.77 \end{pmatrix} & \begin{pmatrix} 0.6+0.5 & 0.33+1 & 0.34+2.5 \\ 0.2 & 0.33 & 0.34 \\ 0 & 0.01 & 0.23 \end{pmatrix} & \begin{pmatrix} 0.5+0.5 & 0.29+1 & 0+2.5 \\ 0.33 & 0.29 & 0.33 \\ 0 & 0.29 & 0.33 \end{pmatrix} \\ \text{2013–14} & \begin{pmatrix} 0.7+0.5 & 0+1 & 0+2.5 \\ 0.01 & 0.5 & 0.11 \\ 0 & 0.01 & 0.78 \end{pmatrix} & \begin{pmatrix} 0.6+0.5 & 0.17+1 & 0.45+2.5 \\ 0.01 & 0.5 & 0.0 \\ 0 & 0.17 & 0.45 \end{pmatrix} & \begin{pmatrix} 0.4+0.5 & 0.17+1 & 0+2.5 \\ 0.2 & 0.8 & 0.6 \\ 0 & 0.01 & 0.29 \end{pmatrix} \\ \text{🔥 2014–15} & \begin{pmatrix} 0.6+0.5 & 0.99+1 & 0.27+2.5 \\ 0.01 & 0 & 0.29 \\ 0 & 0.01 & 0.01 \end{pmatrix} & \begin{pmatrix} 0.29+0.5 & 0.33+1 & 0+2.5 \\ 0.01 & 0 & 0 \\ 0 & 0.01 & 0.01 \end{pmatrix} & \begin{pmatrix} 0+0.5 & 0.14+1 & 0+2.5 \\ 0.01 & 0 & 0 \\ 0 & 0.01 & 0.01 \end{pmatrix} \end{array}$$

Figure 3. Projection matrices for each ant species (AS: *Amoimyrmex striatus*, AL: *Acromyrmex lobicornis*) and nesting type: AL that build mounds on plants (middle), or not (right). In the matrix v_1, v_2, v_3 represent recruitment for each size category, α_1, α_2, α_3 represent stasis (i.e. permanence in each size category), $\beta_{1\to2}$, $\beta_{1\to3}$, $\beta_{2\to3}$ represent growth from one class to a larger one, and $\beta_{2\to1}$, $\beta_{3\to1}$, $\beta_{3\to2}$ represent regressions from one class to a smaller one (see text for a more detailed explanation). Matrices in the two first rows correspond to pre-fire periods (2012–2013 and 2013–2014 transitions) and the matrices on the last row, the post-fire scenario (2014–2015 transition). (Online version in colour.)

followed by the growth of small to medium size nests (i.e. $\beta_{1\to2}$) and the permanence of small nest sizes in their category (i.e. $\beta_{1\to1}$) (figure 5).

4. Discussion

Because natural selection operates on builders through the success of the structures that they build, a common assumption is that the benefits of those constructions exceed their costs [1,2]. Moreover, given that these structures allow the builders to improve the access to food or the colonization of harsh environments, it is common that this kind of species dominate the habitat where they live. Our results suggest that some contexts can increase the costs of certain structures that often represent a benefit, reversing their adaptive value. This effect not only can impact negatively on the populations of builders but also may affect community structure as a whole, suppressing dominant species and incrementing the relevance of subordinate ones. Here we showed that building a thatched mound, a nest feature that often represents an adaptive advantage becomes a cost in a fire context. In the absence of fires, the mound-building species *Ac. lobicornis* has a higher population growth than *Am. striatus*, a species that builds complete subterranean nests without thatched mounds. However, after fires, while *Am. striatus* maintains its population growth rate without significant changes, *Ac. lobicornis* greatly decreases it, probably because of the high flammable nature of its thatched mounds, increasing nest mortality. These results show that some features of animal constructions considered as extended phenotypes can reverse their adaptive value under particular contexts such as fires, with impacts in population and community levels.

In the absence of fire, the population growth rate was higher for *Ac. lobicornis* than *Am. striatus*, especially in colonies that built their thatched mound on plants. Mounds of *Ac. lobicornis* on plants increased their diameter faster and recovered better from perturbations. Moreover, while the approximately 40% of larger *Ac. lobicornis* nests that did not build their mounds on plants reduced their sizes towards the smaller category, none of the nests built on plants did. Mounds built on plants may have better structural support, and can increase in size and recover faster after occasional breaks because plant stems facilitate mound enlargement and repair [14,24]. Compared to *Am. striatus*, *Ac. lobicornis* nests showed higher probability to increase their size, especially in the transition of small towards medium size nests. Given that for both species, smaller nests are the more sensible stage and those that most impact the overall rate of population growth, this higher growth probability of small nests may explain why *Ac. lobicornis* has a higher population growth rate than *Am. striatus*.

Several features of *Ac. lobicornis* can explain its ecological dominance in absence of fire. First, colonies of *Ac. lobicornis* are comparatively large (approx. 10 000 workers) and forage in well-defined foraging trails that can access distant vegetation patches. By contrast, colonies of *Am. striatus* are relatively smaller and forage at close distances from the nest without a defined trail system [16,20,28]. Second, workers of *Ac. lobicornis* can forage at lower temperatures, showing longer periods of activity [16,21,37]. However, its ecological dominance can be mainly attributed to the presence of thatched nest mounds. In the absence of fire, leaf-cutting ant species that build thatched mounds buffer the external temperatures better than species without mounds, allowing faster growth of their fungal culture in temperate environments such as our study site [12,14,15,38]. Indirect evidence also supports the importance of mounds; they are built in an early stage of colony growth, and when a mound is partially destroyed by animal trampling, ants

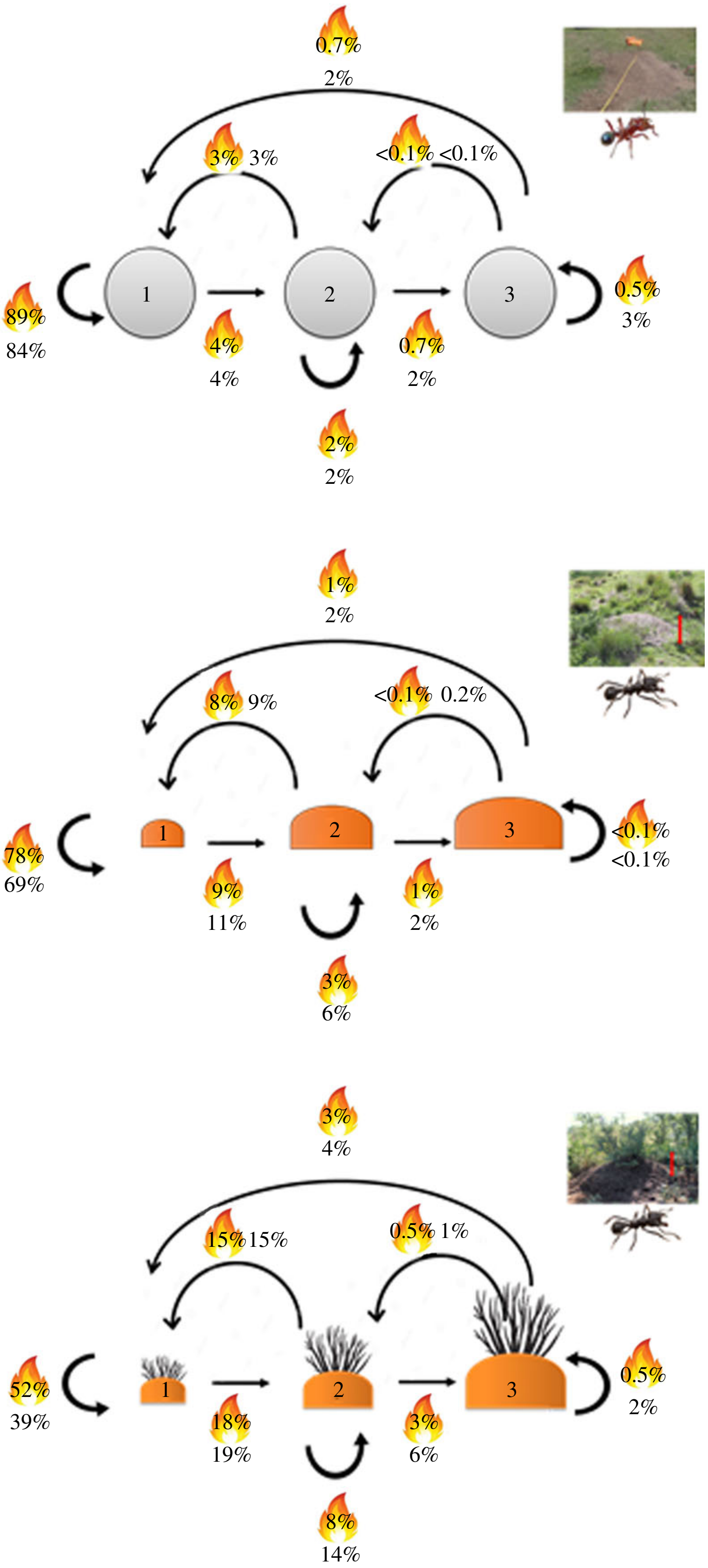

Figure 4. Diagrams of the elasticity analysis for *Amoimyrmex striatus* (above), and *Acromyrmex lobicornis* that build their mounds on plants (below), or not (middle). The values estimate, in per cent, the contribution of the vital rates on population growth rate. The numbers inside the flames correspond to the values in scenarios with fire, and outside the flames, those without fire. (Online version in colour.)

quickly repair it. Also, colonies living in nests with multiple mound damages reduce their survival [14,38]. In summary, the presence of thatched mounds allows a larger fungal culture, which represents more food for larvae and pupae, favouring colony growth.

This adaptive advantage becomes a disadvantage in environments with recurrent fires because the mound features that improve its thermal buffer capacity and facilitate its building are the same that determine a stronger effect of fire. First, using dry wooden material for mound-building

$$\begin{pmatrix} \alpha_1 + \nu_1 & \beta_{2\to1} + \nu_2 & \beta_{3\to1} + \nu_3 \\ \beta_{1\to2} & \alpha_2 & \beta_{3\to2} \\ \beta_{1\to3} & \beta_{2\to3} & \alpha_3 \end{pmatrix}$$

$$\begin{pmatrix} 0.88 & 0.03 & 0.008 \\ 1.83 & 0.06 & 0.02 \\ 0 & 0.19 & 0.05 \end{pmatrix} \begin{pmatrix} 0.80 & 0.09 & 0.01 \\ 1.46 & 0.17 & 0.02 \\ 0 & 0.32 & 0.03 \end{pmatrix} \begin{pmatrix} 0.58 & 0.19 & 0.02 \\ 1.06 & 0.35 & 0.04 \\ 0 & 0.58 & 0.07 \end{pmatrix}$$

$$\begin{pmatrix} 0.78 & 0.02 & 0.003 \\ 1.74\text{–}1.77 & 0.05 & 0.006 \\ 3.36\text{–}3.55 & 0.10 & 0.013 \end{pmatrix} \begin{pmatrix} 0.80\text{–}0.81 & 0.06 & 0.005 \\ 1.40\text{–}1.43 & 0.10\text{–}0.11 & 0.008 \\ 2.62\text{–}2.68 & 0.19\text{–}0.20 & 0.014 \end{pmatrix} \begin{pmatrix} 0.73\text{–}0.77 & 0.13 & 0.01 \\ 1.49\text{–}1.54 & 0.27 & 0.02 \\ 2.68\text{–}2.86 & 0.50 & 0.04 \end{pmatrix}$$

Figure 5. Sensitivity matrices for *Amiomyrmex striatus* (AS), and *Acromyrmex lobicornis* (AL) that build their mounds on plants (middle), or not (right). Matrices on the first row represent the scenario without fires, and those on the second row, the scenario with fires. Ranges were included in matrices that represent scenarios with fires when values among the different fire frequency (each 8, 4 and 2 years) differed. (Online version in colour.)

is the best option to enhance the thermoregulation capacity of the nest [15], but clearly the worst option in case of fire because dry wooden material is highly flammable. Second, building mounds on plants represents an advantage in absence of fires; but plants on mounds represent an extra fuel that strengthens the effect of fire during fires. Additionally, fire can easily propagate inside the fungus chamber in mounds built on plants because often these chambers are located interwoven within the plant roots [14,21]. Accordingly, the population with the higher population growth rate in absence of fires (*Ac. lobicornis* with mounds on plants), becomes the most affected by fire. Conversely, *Am. striatus* is almost not affected by fire, becoming the species with the highest relative population growth in environments with recurrent fires. This is possible because *Am. striatus* build their nests on bare ground and the absence of flammable material around nests often inhibits fire spread [16,17,28,39]. Additionally, fire may not affect the fungus culture because the location of their fungus chambers is deeper than in nests of *Ac. lobicornis*. However, the location of the fungus garden in *Ac. lobicornis* may depend on the region that the species inhabit and the season of the year [21]. While several works showed that these species locate their fungus gardens superficially (5–30 cm depth, see [14,15,22]), others observed a deeper location (30–100 cm depth, see [21,22] and references therein). Independently whether the fungus garden is directly affected by fire, the destruction of the mound in *Ac. lobicornis* determines a thermic unbalance inside the nest and increases the probability that the colony be attacked by phorids and predated by armadillos, increasing the chance of nest mortality [40]. In fact, our data showed that in *Am. striatus* the probability of permanence of small and medium nests into their category almost does not change in the presence of fires, whereas in *Ac. lobicornis* it drops to zero in almost all size categories. However, the role of colony size transitions must be considered carefully because of our relatively small sample size (but see [41]).

We interpreted that the presence of thatched mounds is the main factor that determines the reduction of the population growth rate in *Ac. lobicornis* after a fire. However, other reasons besides the nesting type could explain why populations of *Ac. lobicornis* are more affected by fire than those of *Am. striatus*. First, the suppression of vegetation cover by fire may increase ground temperature restricting the activity of non-thermophilic ants and increasing the presence of heat-tolerant species [42–44]. However, both ant species show similar critical thermal limits and temperature range activity. [16,21]. Second, fires may also modify the availability of food for the ants, increasing herbs and thus favouring grass-cutting species [45]. Nevertheless, both species can use herbs as substrate for culturing their fungus [13,16]. However, *Am. striatus* often forage on dry (dead) plant material while *Ac. lobicornis* forage mainly on green (live) plant material [46], which may represent to *Am. striatus* a relative advantage after fire. Third, fire can reduce habitat complexity and, as the size-grain hypothesis predicts, enhance the performance of larger ant foragers [47,48]. However, workers of *Ac. lobicornis* and *Am. striatus* are similar in size [16,21,28] and thus habitat simplification should affect both species performance equally. Finally, since we did not open abandoned nests, the colony may have emigrated and not be dead. However, we visited each nest during 4 years, and never detected signal of emigration of colonies. Considering all these alternative explanations, the presence of thatched mounds still appears to be the most plausible cause of why fires affect the population growth rate more in *Ac. lobicornis* than in *Am. striatus*.

It has been shown that the effect of fires on ants depends on habitat type and species traits [42,44]. In one hand, fire affects ant diversity more in forests than in open environments because differences in vegetation structure between burnt and unburnt areas are more pronounced in woody habitats [42,49,50]. However, this effect also depends on species traits. For example, ant species pre-adapted to more xeric climatic conditions and that required bare ground to nest becoming more frequent in burned scrub sites [42]. Here we show that nesting type is a trait that also determines the effect of fire on ant species [44,49–51]. It has been proposed that the most important effects of habitat disturbance on ants are typically indirect, through its effects on habitat structure, microclimate, resource availability and competitive interactions [44]. Our results introduce one direct way that disturbances can affect ant species: through the destruction on the structures that they build.

Fire is a natural process in many biomes and has played an important role shaping the ecology and evolution of species [52]. However, human activities have altered natural fire regimes relative to their historical range of variability with profound impacts on land conditions and community structure [53]. Our results showed that an increasing rate of fires can strongly affect those organisms that build easily flammable structures. Consequently, fires should be added to the list of variables that restrict the geographical ranges of mound-building ant species [13]. This also illustrates a novel effect of disturbances, the reversion of the adaptive nature of extended phenotypes, which may have strong consequences on population dynamics and assemblage structure through the invert of dominance relationships.

Data accessibility. The datasets from this study are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.6t1g1jx03 [54].

Authors' contributions. A.G.F.: conceptualization, supervision, writing—original draft, writing—review and editing; M.T.C.: formal analysis, writing—review and editing; L.E.J.: formal analysis, investigation, methodology, writing—review and editing.

Competing interests. We declare we have no competing interests.

Funding. This work had no specific funding.

Acknowledgements. We thank CONICET, Universidad Nacional del Comahue and la Universidad Nacional de San Luis for logistic and partially financial support. The comments of Kety Huberman, four reviewers, and the subject editor improved the quality of this manuscript.

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