SPATIAL AND TEMPORAL PATTERNS OF COLONY DENSITY AND HABITAT ASSOCIATIONS OF A SMALL DESERT ANT

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ABSTRACT

The abundance and distribution of ant colonies can be explained by several processes occurring before and after colony establishment, which potentially associate with natural and anthropogenic factors varying in time and space. We analyzed how the abundance and spatial arrangement of *Pheidole bergi* colonies varied according to habitat heterogeneity at two spatial scales and long-term environmental changes in the central Monte desert. Densities of active *P. bergi* colonies were similar in permanent grids within a protected algarrobal (open woodland) and on disturbed dirt roads crossing that habitat but showed a >50% reduction in the 2001–2025 period. There were also significant variations in colony density along some dirt roads, and they were 40–50% lower on those crossing other habitats (sand dunes and livestock-grazed algarrobal). Colonies within the algarrobal were not arranged randomly. The best-fitted of several spatial point process models proposed maximum probability of active colonies at the inter-patch borders of vegetation, decreasing 56% faster into the vegetated patches than towards the open patches. Further distance-related pairwise interactions between colonies were slightly positive in 2001, resulting in clumped distributions, and became strongly negative by 2019, when densities were less than a half, favoring more random and overdispersed spatial patterns. *Pheidole bergi,* a highly abundant and potentially ecologically significant ant species in the central Monte desert, seems flexible enough to establish colonies in different habitats and microhabitats although with distribution and population dynamics

still shaped by environmental conditions such as soil texture, vegetation cover or resource availability. The strong decline in colony density along the years and associated changes in spatial distribution suggest that both direct and indirect effects of environmental variability, including prolonged drought, play a key role in the establishment and survival of its colonies. Furthermore, the shifting relevance of inter-colony interactions or density-dependent competition highlights the complex interplay between environmental constraints and intraspecific dynamics in the population ecology of *P. bergi*.

Keywords

Spatial distribution, temporal changes, habitat, Monte desert, *Pheidole bergi*, long-term study

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INTRODUCTION

The abundance and spatial distribution of ant colonies are influenced by a range of biotic and abiotic ecological factors and can serve as indicators of underlying environmental processes (Hölldobler and Wilson 1990). In deserts, key regulators of ant colony abundance include food availability, often mediated through competitive interactions, and abiotic factors such as soil type, water availability or microclimatic conditions (e.g., Brown et al. 1979; MacKay 1991; Johnson 1998; Kaspari and Valone 2002; Nicolai 2005). The spatial distribution of colonies is often interpreted as a response to these factors. In general, intraspecific competition is associated with regular colony distributions, as it minimizes overlap in foraging areas of neighboring colonies (Bernstein and Gobbel 1979; De Vita et al. 1979; Levings and Traniello 1981; MacKay 1991). Conversely, clumped distributions may result from habitat selection by founding queens (Wiernasz and Cole 1995) and differential colony survival influenced by spatial heterogeneity in environmental factors such as temperature, vegetation cover, altitude or soil type (e.g., Bernstein and Gobbel 1979; Nicolai 2005; Pol 2008; Milesi et al. MS).

Spatial patterns of ant colonies can change over time, reflecting shifts in ecological processes and the relative importance of environmental drivers. For example, clumped or random patterns may become more regular due to density-dependent mortality (Wiernasz and Cole 1995; Blanco-Moreno et al. 2014), and changing environmental conditions such as unusual multi-year periods of severe droughts in deserts can affect both ant densities (Sanders and Gordon 2004; Gibb et al. 2019) and their spatial distributions (Sundaram et al. 2022). Patterns also change with scale: large-scale aggregation may arise as a result of abiotic environmental limitations but then negative interactions between neighboring colonies may reinforce regular distributions at smaller spatial scales within suitable areas (Crist and Wiens 1996; Sundaram et al. 2022). Finally, spatial patterns can also reflect responses to environmental modifications by anthropogenic factors. In arid and semi-arid areas, livestock grazing is the main economic activity, with important negative impacts on ants (Nash et al. 2001; Goosey et al. 2019), although grazing can sometimes have a neutral or positive effect (Bestelmeyer and Wiens 2001; Nash et al. 2004; Radnan and Eldridge 2018; Eldridge et al. 2020; Neilly et al. 2020) due to species-specific responses to changing conditions.

Pheidole is the most diverse ant genus, comprising approximately 1500 species distributed all over the world except for Antarctica and some islands (Wilson 2003). These

ants are particularly abundant in deserts (MacKay 1991; Johnson 2001), including the Monte desert of Argentina, where species of this genus dominate the seed-carrying ant assemblages (Miretti 2022; Miretti et al. MS). *Pheidole bergi*, one of the most abundant and ubiquitous species (Miretti 2022; Beaumont Fantozzi et al., unpublished data; Miretti et al. MS), is an omnivorous and dimorphic species (major workers: 5.5–6.5 mm; minor: 3.2–4.5 mm; Bruch 1916; Wilson 2003) found in Argentina, Brasil, Paraguay and Uruguay, especially in arid and semi-arid areas (Kusnezov 1951; Wilson 2003; Wild 2007; Janicki et al. 2016; Guénard et al. 2017). It has a broad diet composed mainly of insects and other arthropods, supplemented with seeds and other plant materials (Pirk et al. 2009). Despite its abundance and wide distribution, little is known about its natural history and ecology (but see Pirk et al. 2009; Hierro et al. 2023), particularly the abundance and spatial distribution of its colonies and their relationship with habitat features at different scales.

In the Monte desert, *P. bergi* confronts significant environmental heterogeneity at multiple spatial scales, from regional to intra-patch (Bertiller et al. 2009; Bisigato et al. 2009; Milesi et al. 2019). At landscape and habitat scales, geomorphological and edaphic factors influence vegetation structure, shaping habitats such as the "algarrobal", an open woodland occurring on deep soils of rolling planes, or dune vegetation associated with elevated sandy ridges (Lopez de Casenave 2001; Bisigato et al. 2009). At smaller scales, vegetation exhibits the typical two-phase mosaic structure, with shrub- or tree-dominated patches interspersed with herbaceous vegetation or bare soil. This structure strongly influences water and nutrients distribution, soil seed banks, micro-climatic conditions, and plant-animal interactions (Marone et al. 2004; Milesi et al. 2008, 2019; Bertiller et al. 2009; Bisigato et al. 2009; Andrade 2016). Anthropogenic disturbances further alter spatial heterogeneity: dirt roads modify micro environmental conditions, soil compaction and resources available for ants (Pirk et al. 2004), while livestock grazing reduces plant richness and herbaceous cover, particularly grasses, expanding areas of bare soil (Milesi et al. 2002; Villagra et al. 2009; Pol et al. 2014; Andrade 2016).

In this study, we examine how the abundance and spatial arrangement of *P. bergi* colonies vary according to spatial heterogeneity at two spatial scales (habitats and patches) and whether they show long-term changes in the central Monte desert. We asked: (1) how does *P. bergi* colony density vary across different habitats?, (2) how do long-term environmental changes affect the population dynamics of *P. bergi*?, and (3) what environmental factors explain the spatial distribution and aggregation of *P. bergi* colonies?

METHODS

Study area

The study was conducted in the Biosphere Reserve of Ñacuñán (34°03'S, 67°55'W), located in the central Monte desert, Mendoza Province, Argentina. The region has a dry, highly seasonal climate, with warm and rainy summers and cold and dry winters. The mean (±SD) annual temperature is 16.8 ± 2.1ºC, and the mean annual rainfall is 348.4 ± 123.4 mm (1972–2020). More than three quarters of the rainfall occurs in spring and summer (October–March), with annual accumulation strongly influenced by large summer rainfall events (>10 mm; Pol et al. 2010).

The main habitat of the reserve is the algarrobal, an open woodland of *Neltuma flexuosa* and *Geoffroea decorticans* trees scattered within a matrix of tall shrubs (mostly *Larrea divaricata*, but also *Condalia microphylla, Atamisquea emarginata* and *Atriplex lampa*), low shrubs (*Lycium* spp*., Mulguraea aspera*, *Troncosoa seriphioides*), and perennial grasses (*Leptochloa crinita, Pappophorum* spp., *Sporobolus cryptandrus, Aristida* spp., *Digitaria californica, Setaria* spp., *Jarava ichu*). Forb cover (*Chenopodium papulosum*, *Glandularia mendocina*, *Parthenium hysterophorus*, *Phacelia artemisioides*, *Sphaeralcea miniata*) is highly variable among seasons and years. About one third of the algarrobal consist of open patches of variable size (up to several meters) without perennial vegetation (Marone and Horno 1997; Andrade 2016; Milesi et al. 2019). Other edaphic habitats within the reserve include northwest-southeast oriented sand dunes, stabilized by a similar woody shrub matrix (*L. divaricata*, *Ximenia americana*) with scattered *N. flexuosa* trees and some exclusive herbaceous species (*Panicum urvilleanum*, *Solanum euacanthum*, *Hyalis argentea*, *Gomphrena martiana*).

Livestock grazing, the main economic activity in this region, has been excluded from the reserve since 1972 (Pol et al. 2014). Surrounding cattle ranches share a similar floristic composition but exhibit lower herbaceous cover and smaller shrub and grass patches, resulting in larger areas of bare soil (Milesi et al. 2002; Andrade 2016). Perennial grasses are particularly affected by grazing, showing significant reductions in cover and seed abundance (Pol et al. 2014; Marone and Pol 2021). Both the reserve and nearby cattle ranches are crossed by dirt roads 6–9 m wide, with minimal rural traffic. Woody vegetation along these roads is periodically removed with heavy machinery. The altered soil surface is more compacted and exposed to sun, wind and rain than the adjacent woodland (Pirk et al. 2004).

Sampling design

We assessed the abundance and spatial arrangement of *Pheidole bergi* colonies at different spatial scales: micro (meters) and macro (tens to hundreds of meters) and across multiple years (2001, 2019, 2021, 2025). Sampling was conducted along dirt roads and within permanent grids in the Ñacuñán Reserve and a nearby cattle ranch. We searched and mapped active colonies (i.e., with presence of workers and/or soldiers) during February, coinciding with the peak of external activity (Pirk et al. 2009). Many *P. bergi* nests are rather inconspicuous (with a single, usually semicircular, small entrance 2.8–4.2 cm; Wilson 2003; personal observation), so we always searched for colonies in at least pairs of trained people, twice during hours of their maximum foraging activity (6 to 3 h before solar midday).

For the macro scale, in 2019 and 2025 we searched and mapped (on one dimension; precision: 10 cm) all active colonies of *P. bergi* along two 1500 m segments (~7 m wide) of different dirt roads (D and F) within the Reserve. Following the same protocol, in 2021 we searched and mapped all colonies along three 500 m segments (6 m wide) of dirt roads located in each of three different habitats, two within the reserve (sand dunes and algarrobal) and one in the adjacent cattle ranch (grazed algarrobal).

For the micro scale, in 2001 and 2019 we followed a similar search procedure to map (in two dimensions; precision: 1 m^2) all active colonies of *P. bergi* within two permanent 50×50 m grids (J and V) established in the algarrobal within the reserve, ~80 m apart and >50 m from the nearest dirt road. To facilitate and ensure a thorough census of colonies, each grid was divided in 5×5 m squares with temporal marks. The limits between patches of woody vegetation taller than 1 m and open patches (inter-patch borders hereafter) were drawn on a gridded map of each area (except for V in 2001) and then forced to the same spatial grain (pixel: 1 m^2). The distance to the nearest inter-patch border was calculated for each pixel center, with positive distances for pixels located in open patches and negative values for pixels within woody vegetation patches. Distances for V in 2001 were assumed equal to those measured in 2019, though those results should be taken with some caution (linear correlation between distances estimated in J in 2001 and 2019: $r = 0.67$).

Spatial data analyses

The spatial distribution of *P. bergi* colonies was analyzed using spatial statistics for point patterns in one (roads) and two (grids) dimensions, implemented in several functions within the *spatstat* family of packages (version 3.3-2, Baddeley et al. 2016) in the R platform

(R Core Team 2025; version 4.5.0). Full R code for data processing, exploration and analyses (with partial and additional results) is available at DOI:10.5281/zenodo.15521695 (in Spanish).

Colony distribution along dirt roads (macro scale)

To explore spatial patterns, we first tested the null hypothesis of a Completely Spatial Random (CSR) process, assuming no significant distance-related interactions between neighboring colonies nor associations with environmental variables. Under that hypothesis the location of colonies along roads are outcomes of Poisson spatial processes with constant (spatially-invariant) intensity or expected number of colonies per unit area. Homogeneity of the intensity along each road segment was tested with a Kolmogorov-Smirnov goodness-of-fit test, evaluating the maximum deviation of the observed cumulative distribution function of coordinates of colonies against the expected function under the null hypothesis (Baddeley et al. 2016).

We explored spatial autocorrelation among colonies using two second-order global functions: Ripley's K and pair correlation. These functions may indicate a spatially heterogeneous causal variable that modifies the intensity of the process along the censused road segments (e.g., a fluctuating soil characteristic) or a "true" autocorrelation (i.e, positive/negative distance-dependent interactions among colonies in a non-Poisson spatial process; see Dale and Fortin 2005; Baddeley et al. 2016). Ripley's K function, that estimates the average number of points within an *r* distance of a typical point, performs better as a basis for statistical inference while the pair correlation function, being non-cumulative, is less ambiguous and easier to interpret (Baddeley et al. 2016). The empirical one-dimensional version of the K function (K^L) estimates the average number of points by counting colonies in 2*r* length segments centered at each focal point and standardizing by the intensity so it can be compared among different point patterns (Baddeley et al. 2016). Edge effects (from unobservable points beyond the limits of the segments) were geometrically corrected with a one-dimensional analog of the standard isotropic correction in the bidimensional case (Ang et al. 2011; Baddeley et al. 2016). To avoid artifacts for excessive edge correction, *r* values were up to one quarter of the segment length (Fortin 2020): $r \leq 350$ m for 1500 m segments and $r \leq 120$ m for 500 m segments. We used a centered version of the K function with zero as the expected value at all *r* distances for a CSR process, positive values indicating clustering and negative values, repulsion or overdispersion. The linear pair correlation function (g^L) estimates the ratio between the average number of pairs of points separated by any *r* distance

and the expected number under a CSR process with the same intensity; it is the "instant" version or first derivative (slope) of the K function (Baddeley et al. 2016). For a CSR the expected value is 1, with higher values indicating aggregation at that *r* distance (i.e., more pairs of points observed than expected by chance), and lower values indicating segregation. Confidence envelopes for both functions were obtained by Monte Carlo simulations with 199 iterations of CSR processes with the same intensity as the observed point pattern. The empirically estimated 95% critical envelopes at each *r* were used as local hypothesis tests after a global test of Maximum Absolute Deviation suggested the rejection of the CSR null hypotheses (Baddeley et al. 2014).

When the null hypothesis of homogeneous intensity was rejected, we explored for (further) autocorrelation among colonies with the inhomogeneous versions of the K and pair correlation functions. These modified functions control for the autocorrelation derived from variations in the expected number of colonies along the roads by estimating the intensity function with a non-parametric Gaussian kernel smoothing of the point pattern data. Pointwise envelopes and global Maximum Absolute Deviation tests were estimated as above, though it has been shown that they may result in conservative tests when the intensity is not homogeneous (Baddeley et al. 2017). As a fail-safe we also considered a Balanced Independent Two-Stage Monte Carlo test of goodness-of-fit for composite null hypotheses (Baddeley et al. 2017) with 1560 iterations (39 iterations of the first stage, each with 39+1 iterations for the second nested stage) for a non-conservative global test of the null hypothesis that the spatial process is Poisson (i.e., there are no interactions among colonies) assuming the estimated intensity function.

Colony distribution in the algarrobal (micro scale)

For two-dimensional point pattern, we analyzed spatial autocorrelation with Ripley's L (a transformation of Ripley's *K*: $L = \mathrm{sqrt}(K/\pi)$) and pair correlation functions assuming a stationary process (spatially homogeneous). The L function estimates spatial correlation at different scales by averaging the number of points lying within circles of radius *r* centered on each point in the pattern. Values above expected CSR process suggest aggregation, and values below suggest overdispersion or repulsion. The pair correlation function *g(r)* is similar but considering points separated exactly by each distance *r* (in its empirical version, averaging the number of points lying on thin rings of *r* radius centered at each point in the pattern); values above 1 suggest aggregation, and below 1, repulsion. A Ripley's isotropic edge correction was applied to both functions: the point counts were weighted by the reciprocal of the proportion

of the sampling circle's circumference lying within the observation area (Fortin and Dale 2005; Baddeley et al. 2016). Explored distances of *r* were restricted up to 12 m (~1/4 grid sides) to control for excessive edge effects. Confidence envelopes for *L(r)* and *g(r)* were obtained by Monte Carlo simulations with 399 iterations of CSR processes with the same intensity as the observed point pattern, with the empirically estimated 95% intervals at each *r* used as point-wise hypotheses tests after a global test of Maximum Absolute Deviation suggested rejecting the null hypotheses (Baddeley et al. 2014).

We explored the relationship between *P. bergi* colonies and woody vegetation with Kolmogorov-Smirnov goodness-of-fit tests, comparing the distributions of distances to inter-patch borders of pixels with colonies and those available in each of the grids. We evaluated habitat selection at this scale with Monte Carlo tests comparing the position (mean) and dispersion (standard deviation) of the distributions of distances between pixels with colonies and their nearest inter-patch borders against the distributions of those statistics obtained from 1999 random samples of the same size from the available distances in each grid (a CSR null model).

After several steps of data exploration (see available document with partial and additional results at DOI:10.5281/zenodo.15521695), we fitted several Gibbs point process models of different complexity to the observed bidimensional spatial patterns of colonies considering the two grids as replicates of the same spatial process and Year as a fixed design factor (with two levels: 2001 and 2019) affecting one or more model parameters. Gibbs models explicitly postulate that interactions as attraction (resulting in clustering) and inhibition (repulsion or overdispersion) can occur between the points of the spatial process, reducing to the special case of Poisson models when points are independent (i.e., those interactions are nil). Gibbs models are fitted to data by pseudolikelihood (composite likelihood) methods (Baddeley et al. 2016). We modeled the log of the conditional intensity, or the probability of a random colony occurring in a pixel given the configuration of the other points in the pattern, with two components: a first-order term ("trend", the conditional intensity for an empty point pattern) posing different forms of association (categorical, linear, quadratic) with the covariates describing vegetation heterogeneity (patch type and distance to their borders), and a second term defining the potential distance-dependent pairwise interactions among colonies. The latter was assumed to follow a hybrid Strauss-Hard core point process (Baddeley et al. 2013, with the "hard" component imposing restrictions of our sampling grain (colonies can never occur <1 m apart) and the "Strauss" component

(intimately related to the K-function) allowing for positive (Strauss interaction parameter $\gamma > 1$) or negative ($\gamma < 1$) interactions up to a critical interaction radius of 6 m (determined by likelihood profiling; see DOI:10.5281/zenodo.15521695). Model fits were compared with the Akaike Information Criterion (AIC, which penalizes model complexity), with $\Delta AIC > 2$ suggesting a significant change favoring the model with the lowest AIC value.

RESULTS

Spatial and temporal trends in colony density

Densities of *Pheidole bergi* colonies were similar in the algarrobal and on dirt roads crossing this habitat when sampled in the same season (2019). However, strong temporal changes were observed, with a >50% reduction in both permanent grids over the 18-year period (2001–2019) and a >40% reduction along both dirt roads between 2019 and 2025 (Fig. 1). In 2021, colony densities were higher in every dirt road segment crossing the algarrobal than in those crossing the sand dunes or the grazed algarrobal (Fig. 1).

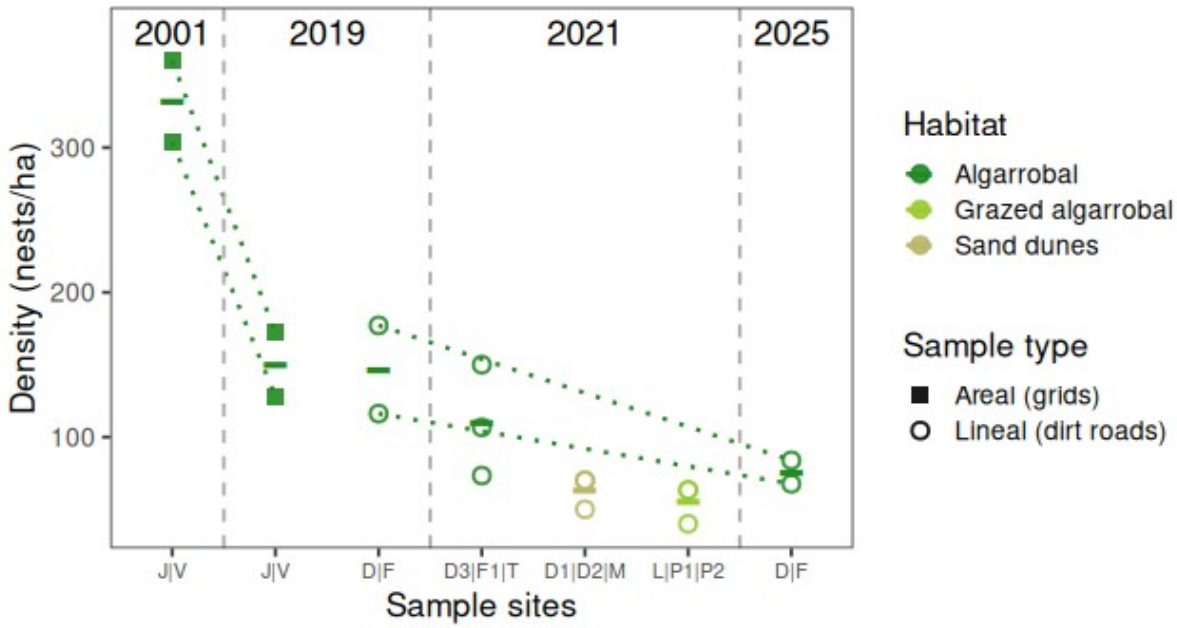

Fig. 1. Density of colonies of *Pheidole bergi* in permanent grids on the algarrobal (squares) and on dirt roads crossing different habitats (circles) of the Ñacuñán Reserve and an adjacent cattle ranch in 2001, 2019, 2021 and 2025. Horizontal bars indicate the mean value for each group of samples; dotted lines join censuses of the same permanent grid and the same dirt road. Note that in the two last groups for 2021 there are overlapping circles for pairs of samples with the same estimated densities.

Colony distribution along dirt roads (macro scale)

We found strong evidence that the intensity of the linear spatial process was significantly heterogeneous in both 2019 and 2025 along the dirt road crossing the algarrobal that had more colonies of *P. bergi* (D; 186 and 88 colonies / 1500 m in 2019 and 2025 respectively), where colonies appeared clumped on scales at least up to 150 m (Fig. 2). In contrast, no significant heterogeneity was detected along road F in 2019 (122 colonies / 1500 m) though by 2025, with reduced colony density (77 colonies / 1500 m) it was slightly more heterogeneous; Fig. 2). Among the three shorter segments of roads crossing the algarrobal sampled in 2021, two showed strong evidence of colony aggregation at scales of at least 60–100 m (Fig. 3). Dirt roads crossing the sand dunes and grazed algarrobal had fewer colonies (Fig. 1) but more homogeneously distributed, with only one of the six segments (M, crossing the sand dunes) showing clear evidence of heterogeneous intensity (most colonies concentrated in one half; Fig. 3).

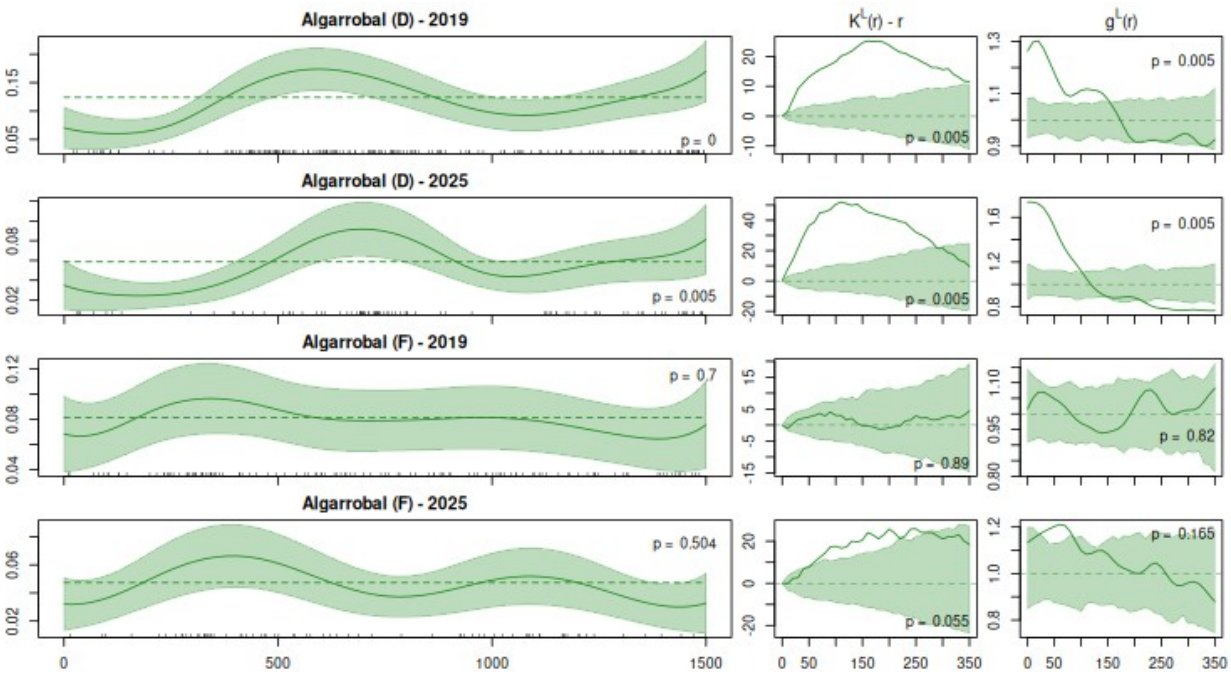

Fig 2. Spatial distributions of *Pheidole bergi* colonies along 1500-m segments of two dirt roads (D, F) crossing the algarrobal of the Ñacuñán Reserve in 2019 and 2025. Left: colony positions (black ticks over x axis) and estimated intensity of the corresponding Poisson linear point pattern process when assumed homogeneous (dashed line) or variable along each segment (estimated by non-parametric gaussian kernel smoothing, continuous line, with shading for its 95% confidence interval); p-value corresponds to a cumulative distribution function test for homogeneous intensity. Right: spatial correlation of the colonies according to Ripley's K (centered) and pair correlation (*g*) functions (line: observed; shade: 95% critical pointwise envelope assuming homogeneous Poisson processes) of the distance among colonies (*r*, in m); p-value corresponds to a global Maximum Absolute Deviation test that the process is Poisson (= no spatial correlation).

All road segments with significant colony aggregation (D in 2019 and 2025, D3, F1 and M in 2021) were well described by Poisson models with variable intensity along the roads, assuming no further autocorrelation (i.e., distance-dependent pairwise interactions) among colonies (Fig. 4).

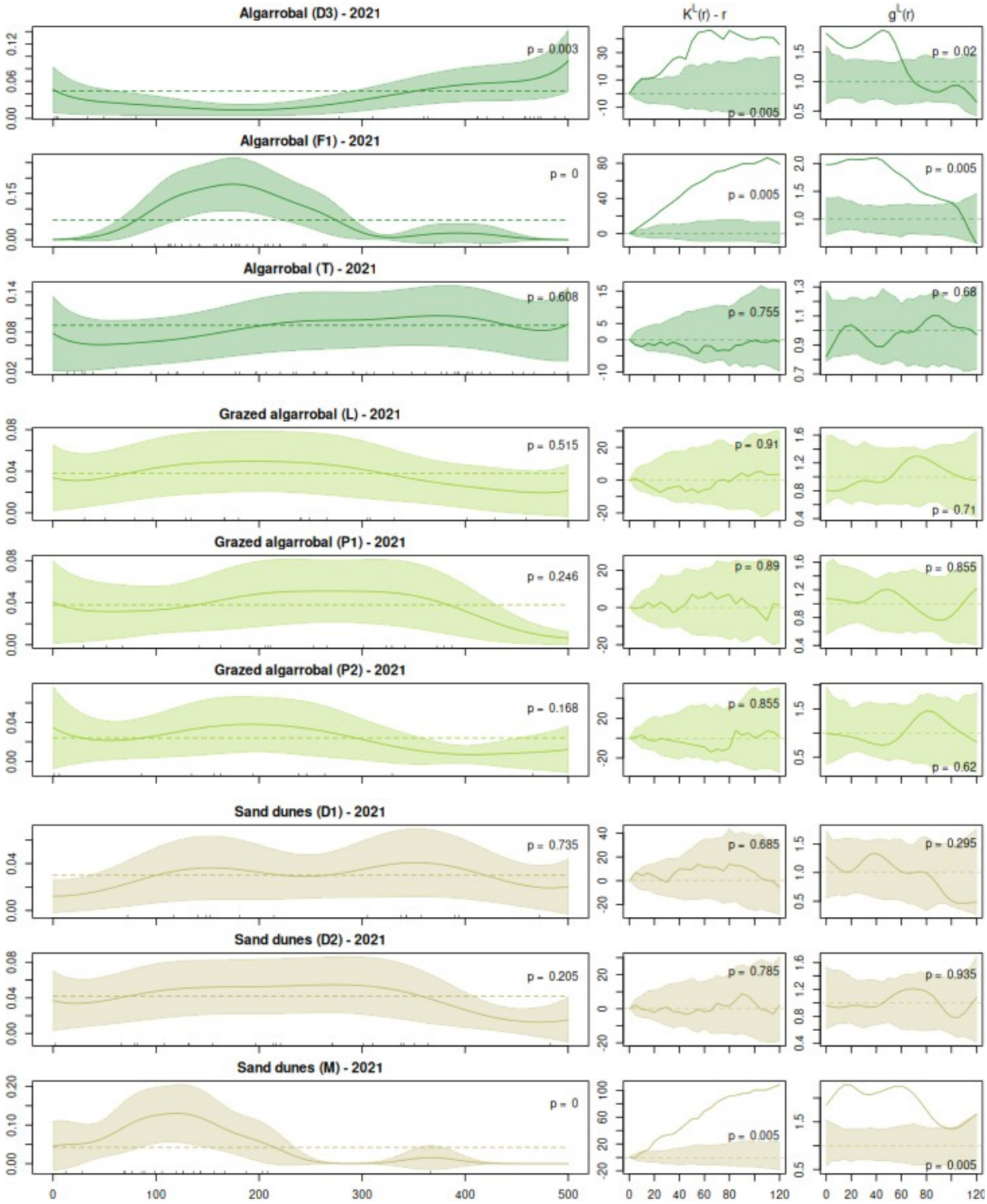

Fig 3. Spatial distributions of *Pheidole bergi* colonies along 500-m segments of dirt roads crossing the algarrobal of the Ñacuñán Reserve (D3, F1, T), a grazed algarrobal in an adjacent cattle ranch (L, P1, P2), and sand dunes within the reserve (D1, D2, M) in 2021. See Fig. 2 for references on subfigures, symbols and statistical values.

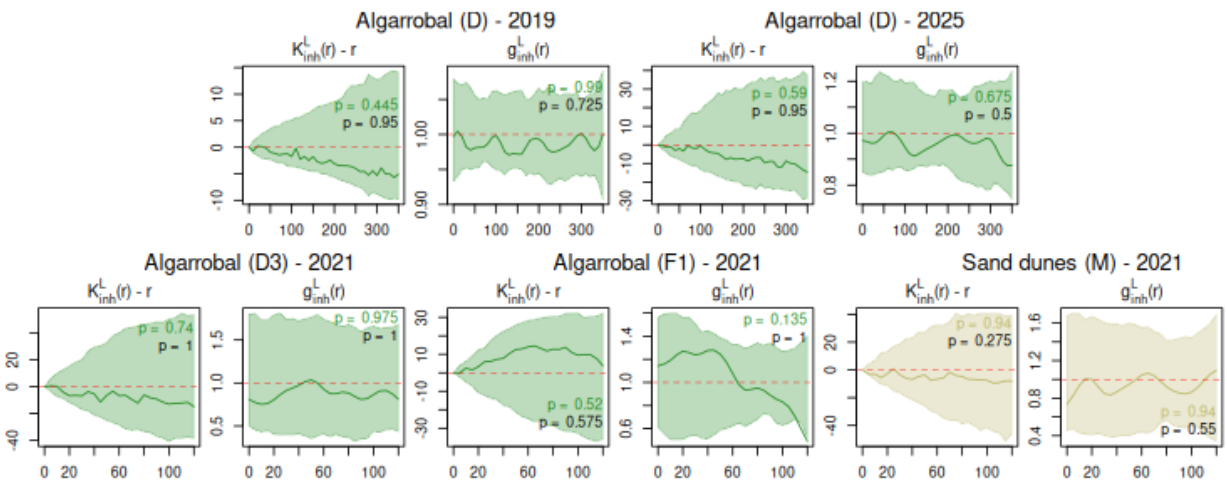

Fig 4. Spatial correlation of the *Pheidole bergi* colonies according to the inhomogeneous versions of the Ripley's K (centered) and pair correlation (*g*) functions of the distance among colonies (*r*, in m) for those segments of dirt roads where the intensity changes along the road (line: observed; shade: 95% critical pointwise envelope assuming the intensity functions estimated in Figs. 2 and 3); p-values correspond to a (probably conservative) one-stage global Maximum Absolute Deviation test (coloured) and to a Balanced Independent Two-Stage Monte Carlo test (black), both testing the null hypothesis that the process is Poisson with heterogeneous intensity (= no further spatial interdependence among colonies).

Colony distribution in the algarrobal (micro scale)

Although colony densities consistently differed between the permanent grids J and V (Fig. 1), both showed clumped distributions of nests in 2001: there were more colonies than expected for a CSR process ($g \geq 1$) at all explored distances resulting in significative aggregation at all scales bigger than 4–5 m (pointwise L above the CSR envelope; Fig. 5). In 2019, with less than half of the colonies (Fig. 1), the spatial pattern in V shifted to a repulsive or uniform pattern up to 6–7 m, while spatial autocorrelation in J became more homogeneous (i.e., not different than expected under CSR; Fig. 5).

Vegetation in the two permanent grids was generally similar. Tall woody cover (>1 m high) was slightly higher in J (2001: 61%; 2019: 69%) than in V (2019: 58%). However, grid V contained a larger vegetation patch, allowing for greater “negative” distances to inter-patch borders (Fig. 6). In grid J, pixels with *P. bergi* colonies showed a non-random distribution of distances to the inter-patch borders, being more associated with open patches, whereas in grid V similar tendencies were observed but without deviation from a random process (Fig. 6).

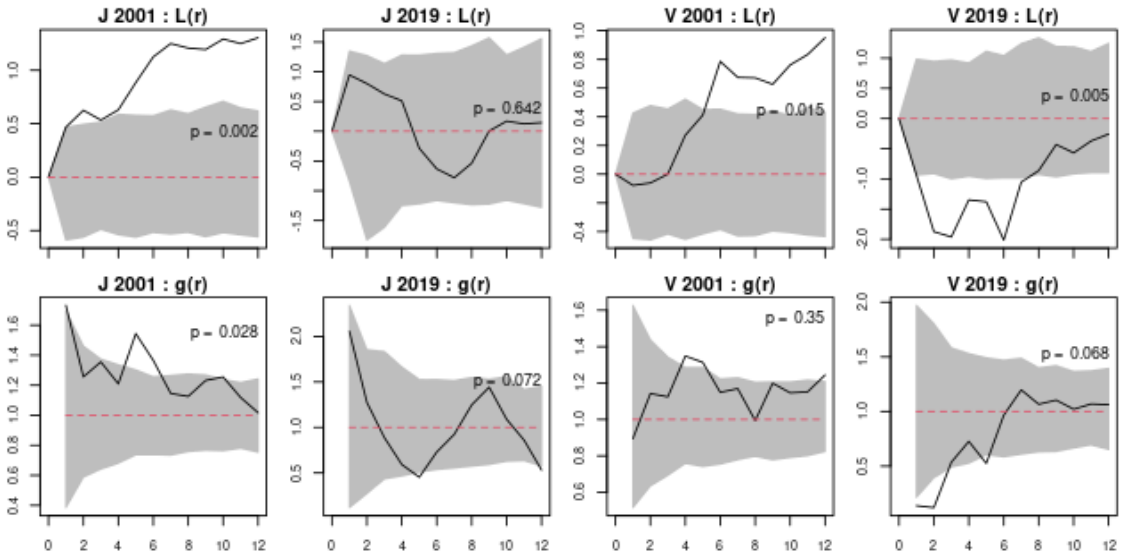

Fig 5.: Spatial correlation of the *Pheidole bergi* colonies in two permanent 50×50 m grids (J, V) in the algarrobal of the Ñacuñán Reserve in 2001 and 2019, according to the two dimensional Ripley's L function (above) and the pair correlation function (*g*, below) of the distance among colonies (*r*, in m). Red dashed lines are the expected values for a CSR process, black lines the observed values and shaded areas the 95% critical envelopes for pointwise tests of a CSR process with the same intensity; p-value corresponds to a global Maximum Absolute Deviation test that the spatial process is CSR (i.e., with homogeneous intensity and no spatial interactions among colonies).

All Poisson point process models incorporating heterogeneous intensity based on the location and type of vegetation fitted data better than models assuming homogeneous intensities for each grid (CSR; Table 1). Among the tested associations with vegetation, models with intensity potentially varying both with the distance to the nearest inter-patch border and the type of patch (quadratic relationship with distance to inter-patch border: $DIST^2$; different linear slopes for each type of patch: BRDHET) provided better fits than those models considering only one of those relationships with vegetation (only patch type: HET; single slope with distance: BRD). All models accounting for intercolony interactions (Strauss-Hard models), either positive or negative, fitted better than their corresponding Poisson models with the same structure but assuming no interactions (e.g., $AIC_{HOM} < AIC_{CSR}$, $AIC_{HET+} < AIC_{HET}$, $AIC_{BRD+} < AIC_{BRD}$; Table 1). Importantly, the spatial effect of vegetation patches on *P. bergi* colonies was still relevant with inter-colony interactions allowed (e.g., $AIC_{HET+} < AIC_{HOM}$; $AIC_{BRD+} < AIC_{HOM}$), preserving their relative likelihoods within the set ($AIC_{BRDHET+} < AIC_{DIST^2+} < AIC_{HET+} < AIC_{BRD+}$; Table 1).

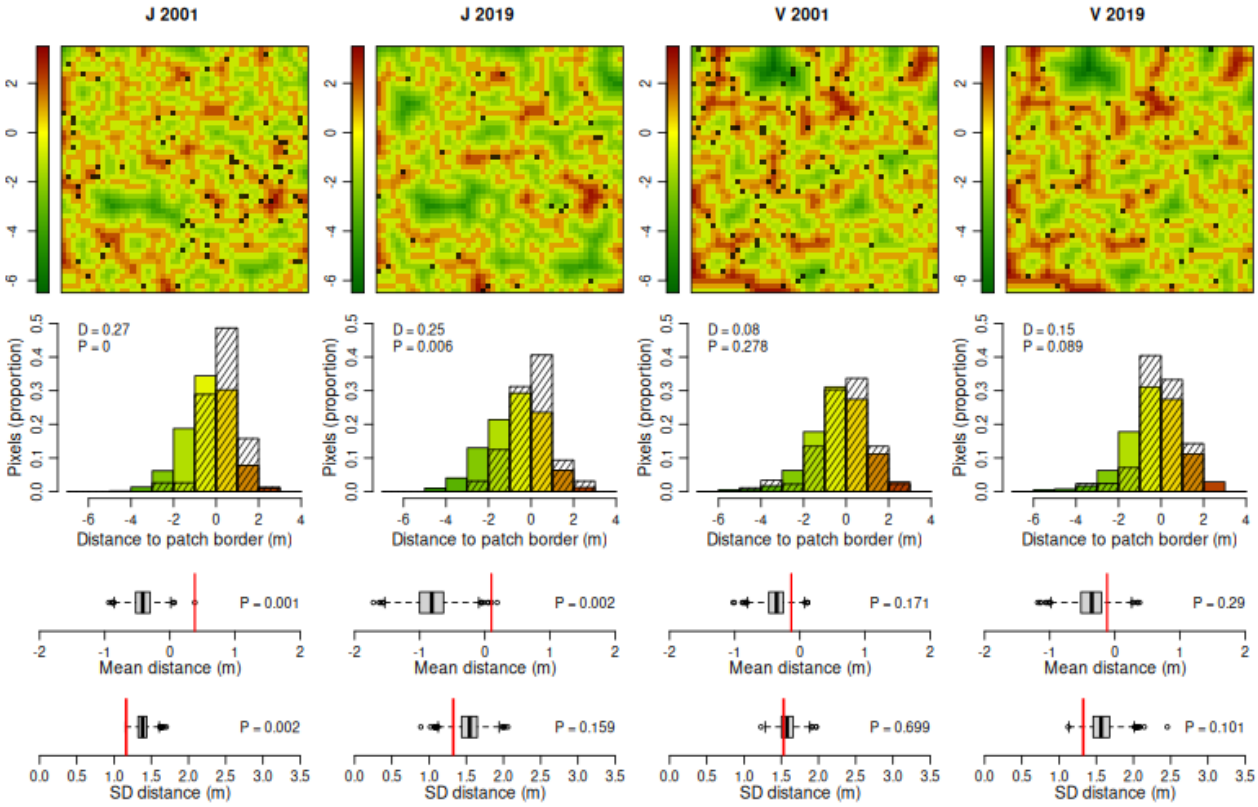

Fig 6. Top: distance to the nearest inter-patch border (negative values for pixels within woody vegetation patches, positive values for pixels located in open patches) of each 1 m^2 pixel in two permanent 50×50 m grids (J, V) in the algarrobal of the Ñacuñán Reserve in 2001 and 2019; black pixels are those with *Pheidole bergi* colonies. Second row: frequency distribution of all pixels (n = 2500, coloured bars) in each distance category and of those pixels with colonies (hatched bars), with statistics corresponding to the Kolmogorov-Smirnov goodness-of-fit tests. Below: statistics of position (mean, third row) and dispersion (SD, fourth row) of the observed distribution of distances for pixels with colonies (red vertical line) and those obtained from 1999 random samples (of the same size) from the available distances (box and whiskers); the empirical p-value tests CSR as null model.

According to the best-fitting model (BRDHET+; Table 1), the probability of an active colony was highest at inter-patch borders. The base probability declined 56% (linearly in the scale of the model) faster into the vegetated patch than towards the open patch, strongly favoring the presence of colonies in the latter (Fig. 7). The interaction between pairs of colonies (1–6 m apart) was slightly positive in 2001, favoring nest aggregation, but became strongly negative in 2019, favoring more regular patterns (particularly in V; Fig. 5). It should be noted, however, that the two components of these Gibbs models resulting in the point process intensity (first-order: trend; second-order: inter-colony interactions) are partially confounded, as both operate at a very similar spatial scale (maximum distance to an inter-

patch border in grid V: 6.4 m; maximum distance for interactions: 6 m). In fact, including time-variable interaction parameters inverted the estimated intercepts for the first-order term (i.e., base probability at the inter-patch borders) compared to those in the Poisson model (BRDHET: $\beta_{2001} > \beta_{2019}$; BRDHET+: $\beta_{2001} < \beta_{2019}$; Table 1 and Fig. 7). Gibbs point process models with alternative structures showed reduced likelihoods (higher AIC values) than BRDHET+, such as a model with a time-invariant inhomogeneous first order trend and differences between years only depending on intercolony interactions (~abs(dist) * veg/open + Strauss-Hard$_{Year}$, AIC = 2137.8), or with inhomogeneous first-order trend but a constant parameter for interactions (~Year + abs(dist) * veg/open + Strauss-Hard, AIC = 2183.7). A more complex model with temporal changes in the vegetation effect on the first order trend was not significantly better than with the single, permanent relationship modeled in BRDHET+ (~Year * abs(dist) * veg/open + Strauss-Hard$_{Year}$, AIC = 2127.78).

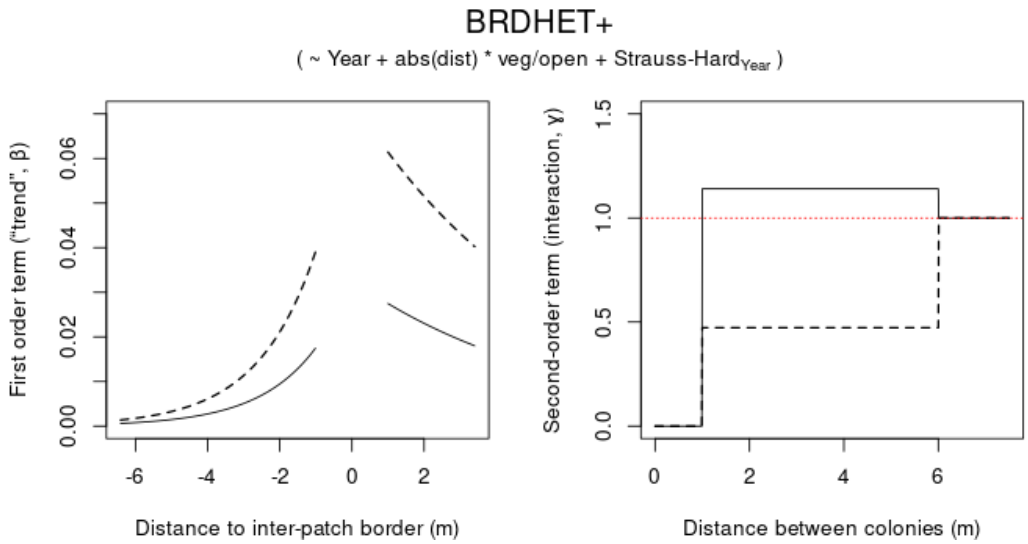

Fig 7. Selected Gibbs point process model (BRDHET+, Table 1) to explain the spatial distribution of *Pheidole bergi* colonies in the algarrobal of the Ñacuñán Reserve. Its first-order term (left) is the conditional intensity of the spatial pattern of the colonies that depends on time (2001: continuous line; 2019: dashed line) and distance to the nearest inter-patch border (negative values for pixels within woody vegetation patches). Its second-order term (right) is a Strauss-Hard model with interactions between active colonies up to 6 m ($\gamma > 1$: positive or attractive; $\gamma < 1$: negative or repulsive) also depending on time.

Table 1. Structure and parameters for Poisson and Gibbs point process models fitted to the distributions of the *Pheidole bergi* colonies in two permanent 50×50 m grids in the algarrobal of the Ñacuñán Reserve in 2001 and 2019, considered replicates of the same spatial process. CSR is a Complete Spatial Random Model (= homogeneous intensity for each year, assuming independence between points) while HOM+ is the corresponding Gibbs model with a homogeneous first order term and interaction intensity varying in time. For the rest of the fitted models, those allowing for inter-point interactions are identified with a "+" following the name of the corresponding Poisson model with the same structure for the first-order term. In the Intensities/Trends column, "m" is the value of distance (in m) to the nearest inter-patch border (with negative values for distances toward the interior of the woody vegetation patches). The model with the lowest Akaike's Information Criterion (AIC) value in the set is shown in bold.

Model	Structure	Interactions	Intensities/Trends	AIC
CSR	year	—	β_{2001}: 0.033 β_{2019}: 0.015	2231.25
HOM+	year	γ_{2001}: 1.147 γ_{2019}: 0.53	β_{2001}: 0.019 β_{2019}: 0.033	2166.97
HET	year + veg/open	—	2001: β_{veg}: 0.024 / β_{open}: 0.046 2019: β_{veg}: 0.011 / β_{open}: 0.021	2209.3
HET+	year + veg/open	γ_{2001}: 1.138 γ_{2019}: 0.503	2001: β_{veg}: 0.014 / β_{open}: 0.027 2019: β_{veg}: 0.027 / β_{open}: 0.053	2142.3
BRD	year + abs(dist)	—	2001: 0.061×0.622^{m} 2019: 0.029×0.622^{m}	2216.34
BRD+	year + abs(dist)	γ_{2001}: 1.149 γ_{2019}: 0.49	2001: 0.038×0.571^{m} 2019: 0.082×0.571^{m}	2144.63
BRDHET	year + abs(dist) * veg/open	—	2001: β_{veg}: 0.052×0.583^{m} / β_{open}: 0.052×0.891^{m} 2019: β_{veg}: 0.025×0.583^{m} / β_{open}: 0.025×0.891^{m}	2200.03
BRDHET+	year + abs(dist) * veg/open	γ_{2001}: 1.14 γ_{2019}: 0.473	2001: β_{veg}: 0.033×0.537^{m} / β_{open}: 0.033×0.839^{m} 2019: β_{veg}: 0.073×0.537^{m} / β_{open}: 0.073×0.839^{m}	2126.89
$DIST^2$	year + $dist^2$	—	2001: $0.039 \times 1.238^{m} \times 0.936^{m2}$ 2019: $0.018 \times 1.238^{m} \times 0.936^{m2}$	2202.6
$DIST^2$+	year + $dist^2$	γ_{2001}: 1.139 γ_{2019}: 0.474	2001: $0.023 \times 1.251^{m} \times 0.918^{m2}$ 2019: $0.052 \times 1.251^{m} \times 0.918^{m2}$	2130.04

DISCUSSION

Pheidole bergi is very abundant in Ñacuñán, with a colony density far exceeding previous records for the species and for several other arid and semiarid ant species in South America. The density recorded in the algarrobal (67–360 colonies/ha) was much higher than those reported for the same species in the Caldenal woodland (8 colonies/ha; Tizón et al. 2010) and for all other ant species with available data in the central Monte (*Pogonomyrmex mendozanus*, *P. inermis, P. rastratus*, *Acromyrmex striatus*, *A. lobicornis*; Nobua Behrmann 2014; Pirk et al. 2004; Pol et al. 2017). Several studies, although not directly estimating colony densities, have also identified *P. bergi* as one of the most abundant ant species (Claver et al. 2014; Barrientos et al. 2024). In particular, it numerically dominates the assemblages of seed-carrying ants in Ñacuñán (Miretti 2022; Beaumont Fantozzi et al., unpublished data; Miretti et al. MS), and the colony densities recorded in 2001 (304–360 colonies/ha) are comparable to the highest values reported for the entire seed-harvesting ant assemblages in some North American deserts: 340–520 colonies/ha in the Chihuahuan desert (Schumacher and Whitford 1976) and 61–463 colonies/ha in the Mojave and Great Basin deserts (Bernstein and Gobbel 1979). With its high densities, *P. bergi* may play a relevant ecological role in South American ecosystems, as other species of the genus have been recognized in tropical regions ("ecosystem engineers": Shukla et al. 2013).

Pheidole bergi did not show lower densities in natural habitats compared to disturbed areas such as dirt roads, unlike many arid and semi-arid ants (e.g., Farji-Brener 1996; Terranella et al. 1999; Pirk et al. 2004; Tizón et al. 2010; Uhey et al. 2021). The striking microhabitat differences between roads and surrounding environments (e.g., temperature, soil compaction, plant cover) do not seem to significantly impact the establishment and survival of *P. bergi* colonies. However, at the landscape scale, *P. bergi* showed a clear spatial preference, with higher colony densities in the algarrobal than in roads crossing sand dunes or grazed algarrobal. The lower density of colonies in the grazed woodland may be associated with its reduced cover of the lowest vegetation strata (Milesi et al. 2002; Andrade 2016) or to the negative effect of cattle grazing on arthropod abundance, the main food source of *P. bergi* (Pirk et al. 2009), as commonly observed in arid ecosystems (e.g., Cheli and Martínez 2017; Pol et al. 2017; Martínez et al. 2021). Claver et al. (2014) also reported higher *P. bergi* abundance in the algarrobal than in the surrounding grazed ranches in Ñacuñán, and Calcaterra et al. (2010) found higher *P. bergi* occurrence in ungrazed than grazed sites in

eastern Argentina savannas. The sandy and permeable dune soils, with low water retention, may limit the establishment and survival of *P. bergi*. Soil texture affects the abundance and distribution of many ant species (e.g., Kirkham and Fisser 1972; Johnson 1992, 2000; Boulton et al. 2005; Ríos-Casanova et al. 2006). Furthermore, we detected strong and persistent variations in colony density along 1500 m of a dirt road crossing the algarrobal, maybe also as response to environmental constraints such as soil or vegetation characteristics. In Ñacuñán, the segregated distribution of colonies of two granivorous ant species has been previously associated with variations in soil texture within the algarrobal: *Pogonomyrmex inermis* associated with soils with higher clay content and *P. mendozanus* with looser, coarser-textured soils (Pol 2008; Milesi et al. MS).

A particularly striking result of our study was the marked decline in the abundance of *P. bergi* over time. Colony density at the same sites decreased by approximately half between 2001 and 2019, and by at least 40% between 2019 and 2025. Although these fluctuations could be part of natural population dynamics, as seen in many animal groups (Strong 1986; Pimm 1991), the magnitude and persistence of the decrease suggest a true population drop, mirroring recent reports of insect populations decline at global scale (Sánchez-Bayo and Wyckhuys 2019; Møller 2020). The strong observed decline could be driven by recent or sustained changes in environmental conditions. A drastic reduction of perennial herbaceous cover has been recorded in Ñacuñán over recent decades (perennial grasses reduced their horizontal cover by more than 75% since 2002; Milesi et al., unpublished data), with a particular sharp decline since 2018, coinciding with a multiyear drought (Miretti et al. 2024; Vullo et al. 2024). Precipitation in the 2018–2023 period was approximately half of that recorded in 2000-2001, which in turn coincided with a period of 5-6 years of above-average precipitation (Miretti 2022). Both reduced soil moisture and lower herbaceous plant cover, with its probable negative effect on the arthropods on which *P. bergi* feeds, may have contributed to the marked temporal decrease in colony density. A poor herbaceous layer caused by domestic herbivores and the scarcer associated entomofauna may also explain the lower density of active colonies we observed in the grazed algarrobal. Negative responses to drought and anthropogenic disturbances have been observed in desert ants driven by factors such as low production of reproductive individuals, insufficient rainfall to trigger mating flights, higher desiccation risk, lower foundress survival, decreasing foraging activity under low food availability, and increased colony mortality (Sanders and Gordon 2004; Gibb et al. 2019; Parr and Bishop 2022; Sundaram et al. 2022).

At smaller spatial scales, *P. bergi* consistently showed more active colonies near the borders between patches of woody perennials (shrubs >1 m tall) and surrounding open or herbaceous patches, avoiding woody vegetated patches. Further inter-colony interactions of aggregation or repulsion depended on environmental conditions or population densities. The selection of open nesting sites aligns with patterns observed in other desert ants (Carlson and Gentry 1973; Bernstein and Gobbel 1979; Bestelmeyer and Schooley 1999; Nicolai 2005). Factors such as lower soil temperature reducing foraging activity and food intake (Nobua Behrmann et al. 2017), slower egg development (Bar et al. 2022), or lower efficiency of food detection and transport in litter accumulating under canopy (Bin Kalban et al. 2024) may explain why *P. bergi* avoids dense vegetation patches. Nevertheless, borders of these woody patches may still offer suitable nesting and foraging conditions, as the sparse external branches and inverted conical shape of *Larrea divaricata* shrubs that dominate most of them result in microclimatic conditions rather similar to open patches.

Once primary environmental selection is accounted for (i.e., a spatial selection for inter-patch borders and open spaces), repulsion between neighbouring colonies is expected for individually foraging ants such as *P. bergi* (as opposed to trunk-trails foraging ants; Warburg and Steinberger 1997) because the intensity of foraging territory defense should increase with nest proximity. However, inter-colony spacing dynamics of *P. bergi* appeared more complex than expected, shifting over time. In 2001, when colony density was at its peak, colonies were mostly aggregated in the algarrobal, but by 2019, as densities declined, colony distribution shifted towards random or uniform patterns. This change is not consistent with the expected positive correlation between density and intercolony repulsion resulting in regular spatial patterns (Schooley and Wiens 2003). Alternatively, inter-colony attraction (exceeding responses to environmental heterogeneity) may result from restricted dispersal of new founding queens from natal nests or mating sites (Rissing and Pollock 1989; Cole and Wiernasz 2002). If 2001, with rainfall well above long-term average, represented an optimal period for reproduction and colony foundation of *P. bergi* (see Fig. 1), new young colonies with few workers and small foraging territories may have coexisted with closer inter-colony distances during a (short) period of relaxed competition and abundant resources. As conditions worsened and resources declined, intraspecific competition likely favoured larger, well-established colonies, leading to density-dependent thinning and increased inter-colony spacing by 2019 (Hölldobler and Wilson 1990; Wiernasz and Cole 1995). Similar patterns have been documented in other desert ants where competition intensifies with drought: Sanders and Gordon (2004) found that the net interaction between *Pogonomyrmex barbatus*

and *Aphaenogaster cockerelli* colonies switched from positive to negative after dry summers in New Mexico, whereas Sundaram et al. (2022) proposed that the impact of foraging area size and crowding by intraspecific neighbors became a critical influence on *P. barbatus* colony survival after a drought. The proposed mechanism, then, is that stricter environmental conditions resulted in both reduced densities and increased intraspecific competition, especially in the most densely occupied areas (density-dependent thinning), resulting in the observed change in the spatial arrangement of colonies.

In summary, *P. bergi* is a highly abundant and potentially ecologically significant ant species in the central Monte desert. This ant species behaves as a diet and habitat generalist, flexible enough to establish colonies in different habitats and microhabitat conditions although with distribution and population dynamics still shaped by environmental conditions such as vegetation cover, soil texture or resource availability. Colony abundance varies across habitats, with lower densities in livestock-grazed ranches and sand dunes and high colony density along dirt roads and well-preserved open woodlands. Within the algarrobal, *P. bergi* selects inter-patch borders and open patches, with very few colonies far into woody patches. The strong decline in colony density along the last decades with associated changes in spatial distribution suggest that both direct and indirect effects of environmental variability, including prolonged drought, play a key role in the establishment and survival of its colonies. Furthermore, the shifting relevance of distance-related inter-colony interactions or density-dependent competition highlights the complex interplay between environmental constraints and intraspecific dynamics in the population ecology of *P. bergi*.

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