



Evolutionary transitions in social organization and the relationship between climate and queen number in ant societies



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In about one fourth of ant species, multiple queens reproduce within the same colony ('polygyny'), reducing relatedness and potentially fuelling evolutionary conflicts among colony members. Polygyny is more common at higher altitudes / latitudes in several species, suggesting that cold climates favour multiple queens. We tested this prediction with phylogenetic analyses comparing 263 ant species and modelled the evolutionary pathways between alternative social structures. Queen number was phylogenetically labile, with bidirectional transitions between single and multi-queen species passing through socially polymorphic species (with both types of colonies). Contrary to our predictions, polygyny was not more common at higher latitudes or altitudes. Socially polymorphic species tended to occur in environments with more uniform precipitation throughout the year, and queen number increased towards the tropics. We discuss how multiple queening may be favoured in warm climates due to competitive advantages of faster colony growth and higher genetic diversity. We also call for more studies in tropical regions, as most studies were performed in the northern hemisphere.

The ancestors of all ants are thought to have lived in colonies with a single, once-mated queen and her worker daughters¹. This social structure maximized relatedness among nest-mates, which facilitated the evolution of the extreme reproductive altruism that exists in ant societies today². While many ants seem to have retained this ancestral form of social organization, multi-queen colonies (secondary polygyny, hereafter 'polygyny' or 'polygyne species'^{3,4}, meaning that multiple mated queens reproduce in each colony) have evolved several times across the ant phylogeny^{2,4,5}. Today, about 25% of known ant species are polygyne¹. In some polygyne populations, all colonies have multiple queens (obligate polygyny). In others, monogyne and polygyne colonies co-exist (i.e. they are socially polymorphic, which can be genetically determined (reviewed in refs. 6,7) or phenotypically plastic). Explaining the evolution of polygyny is challenging since it lowers relatedness within colonies³, thereby decreasing the incentive for reproductive altruism and increasing the potential for evolutionary conflicts (i.e. when the fitness of different individuals is maximized in different ways, causing natural selection to act differently on genes expressed in each of them) among less related lineages⁸. Although insect societies have

several mechanisms to prevent costly conflicts, and synergetic benefits may compensate for the costs of low relatedness^{9,10}, the environmental factors favouring polygyny remain to be identified.

There are several life-history changes linked to polygyny which could compensate for reduced relatedness. Specifically, polygyny reduces the risks associated with dispersal and independent colony founding by new queens, accelerates colony growth, and can increase colony lifespan, size, and genetic diversity (Supplementary Table S1). In monogyne colonies, dispersal typically occurs when mature colonies produce winged queens and males that mate in swarms¹¹. Queens then attempt to found nests independently after these mating flights and most nests fail¹². In contrast, young queens produced by polygyne colonies can mate locally and seek re-adoption in their natal nest or start a new nest with the help of sister workers^{11,13,14}. This reduces queen mortality and increases colony growth rates because there are multiple reproductive queens per colony. Polygyny also increases colony lifespan, as queens can be replaced continually, while monogyne colonies typically die out when their single queen dies¹⁵ (but queens in monogyne colonies typically have a longer lifespan than queens in polygyne colonies¹⁶).

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Traits associated with polygyny, like local dispersal, reduced queen mortality, increased colony size, colony longevity and genetic diversity, and rapid colony growth could be beneficial in either cold or warm climates. In cold climates (i.e. at higher absolute latitude/altitude), local dispersal and natal recruitment of queens reduces the mortality of young queens due to low temperatures, short periods of good weather, and limited food availability. Similarly, rapid colony growth allows for the efficient use of temporal resources even when the yearly period of activity is shorter than at lower absolute latitudes/altitudes. Having multiple queens is also likely to be beneficial because it increases colony genetic diversity, e.g. for better disease resistance^{17–19} and likely improves thermoregulation (as happens in bees²⁰), and because larger nests also have better thermoregulation^{17,21,22}. In warm climates, local dispersal, increased colony lifespan and growth could be beneficial if the environment is saturated and contains few available nesting sites.

Although polygyny can theoretically be beneficial in these contrasting environments, current available evidence from within-species or within genera variation suggests that cold climates with short breeding seasons correlate with the evolution of polygyny²³. Polygyny was associated with high latitudes and altitudes in several ant species or genera, including in the subfamilies Formicinae and Myrmicinae in the Swiss Alps²⁴, in the subgenus *Leptothorax* and *Myrafant* (now *Temnothorax*)²⁵, in the *Camponotus*^{18,29,30} and *Liometopum*^{31–33} genera, and in the species *Temnothorax rugatulus*³⁴ and *T. longispinosus*³⁵ (Supplementary Table S2) (but see ref. 36). Similarly, experimental evidence has shown that cold winters limit independent reproduction of young queens emerging from multi-queen colonies, but not from single-queen colonies²³. Nevertheless, a recent analysis across biomes documented that polygyny was more frequent in deserts and temperate climates³⁷. However, most of these studies have not tested whether climatic conditions influence evolutionary transitions in ant social organization within a phylogenetic framework, and large-scale studies classify species' social organization based in the observation of one or a few colonies.

To test the prediction that harsh or cold climates favour the evolution of polygyny in ants, and to investigate evolutionary transitions between social structures, we conducted phylogenetic comparative analyses across 259 species. First, we modelled the evolutionary transitions between alternative social structures (obligate monogyny, hereafter 'monogyny' or 'monogyny species', socially polymorphic, hereafter 'polymorphic', and obligate polygyny, hereafter 'polygyny' or 'polygyny species'). Second, we examined if polygyny, polymorphic, and monogyny species occur at different altitudes, latitudes, and in climates with different seasonal precipitation. If cold climates favour polygyny, then polygyny species should occur at higher absolute latitudes and altitudes than monogyny species, while polymorphic species, which harbour both monogyny and polygyny colonies, may occur across a broader range of latitudes and altitudes. Similarly, we tested the prediction that, for polygyny species, average queen number per colony would co-vary positively with absolute latitude and altitude. In this phylogenetic analysis, we do not examine the proximate mechanisms underlying variation in social structure, nor whether this variation is genetically determined or phenotypically plastic. Supergenes are known to control social polymorphisms in at least five independent ant clades (reviewed in ref. 6,7), with derived haplotypes inducing multi-queen colonies. Although the genetic basis of colony queen number remains unstudied for most ant species, and may therefore also be plastic, it is possible that social structure is often genetically determined, both within and between species. This possibility further highlights the importance of accounting for phylogenetic inertia when inferring the ecological drivers of polygyny.

Methods

Overview

We investigated evolutionary transitions between social structures and tested if cold or warm climates are associated with polygyny in ants. We first collected data on ant social organization, including number of queens per

nest, across species. We then extracted the latitude and longitude of each study, and retrieved climatic data and the altitude of each study location from the WorldClim database³⁸. Three main statistical analyses were performed across a sample of 50 ant phylogenies: i) evolutionary pathways from monogyny to obligate polygyny, ii) social organization in relation to latitude, altitude, and precipitation, iii) queen number in relation to latitude, altitude, and precipitation.

Data collection

Social organization and queen number. We used three sources to identify studies with data on ant social structure: Boomsma et al.¹, Boulay et al.⁴ and Bell-Roberts et al.³⁹. From these, we went through the primary references and classified 116 species as monogyny (all nests have one queen), 99 species as socially polymorphic (nests have either one or multiple queens), and 48 species as obligately polygyny (all nests have multiple queens). All primary references are available at Figshare. Social polymorphisms can be genetically determined or phenotypically plastic^{6,7,40}, and we considered them together in our analyses. When data from multiple populations of a species were available, we kept the population with the largest number of colonies studied, if social structure did not vary across populations. When social structure varied across populations, we kept the obligately polygyny population first, followed by the socially polymorphic population, to increase our sample sizes for these categories. For a colony to be considered polygyny, multiple queens had to be found in a colony and dissected to infer their mated status, and/or genetic analyses of the colony inferring multiple matriline (as opposed to multiple mating) had to be included. If either of these criteria was not met, the study was not included in our dataset. For a colony to be considered monogyny, genetic analyses inferring a single matriline, or complete excavation of the colony had to be carried out. If the primary reference did not provide these descriptions, we did not include that population/species in our dataset. Furthermore, because many studies explored a single or few colonies, we repeated all analyses in a restricted dataset, which included at least 20 colonies evaluated for populations classified as obligate polygyny and at least 20 colonies classified as monogyny, to exclude potential misclassification based on few colonies. As polymorphic species must have met these criteria for at least one monogyny and at least one polygyny colony within a population, we included all species classified as polymorphic in the restricted dataset (but the majority evaluated >10 nests).

Latitude, altitude, and climate variable selection. Study coordinates were extracted directly from primary studies or inferred using the description of the study location. Data on altitude, temperature (annual mean, annual range, minimum, maximum, diurnal range, seasonality), isothermality, and precipitation (annual and seasonality) for each study location were then extracted from WorldClim using the R statistical programming language⁴¹. These climate variables were strongly correlated with latitude/altitude and with each other (Supplementary Table S3). To avoid performing multiple analyses on highly correlated variables, we focused on just three (chosen before performing any analysis): absolute latitude, altitude (log transformed +1 meter), and seasonal precipitation (bioclim variable number 15, with higher values reflecting rainfall concentrated in distinct wet seasons, whereas lower values indicating more uniform precipitation throughout the year). Absolute latitude is highly correlated with temperature (mean, minimum, maximum, seasonality, and annual range), isothermality, and annual precipitation (Spearman's r ranges from 0.59 to 0.89). Altitude (log + 1) is not correlated with latitude (Spearman's $r = 0.06$) but is strongly correlated with temperature diurnal range (Spearman's $r = 0.59$). Seasonal precipitation is correlated with absolute latitude (Spearman's $r = 0.50$) but weakly correlated with altitude (Spearman's $r = 0.08$). Spearman's rank correlations among climate variables for all study locations are provided in Supplementary Table S3.

When we modelled social organization (treated as an ordered numeric variable) as a function of absolute latitude, altitude ($\log + 1$) and all eight climate variables, the variance inflation factors (VIFs), which measure the degree of multicollinearity among predictor variables, ranged from 2.0 to 125.6. In a model only including absolute latitude, altitude ($\log + 1$), and seasonal precipitation as predictors, the VIFs were all < 1.3 , indicating limited autocorrelation (VIFs > 5 suggest high autocorrelation, which can bias parameter estimates). We repeated all models including a fourth category, ‘supercoloniality’, data which was extracted from the primary references cited in ref. 42. Results are described in the ESM.

Phylogenies. We used the posterior distribution of fossilized birth-death ant phylogenies⁴³. We sampled 50 trees at random (from the 100 provided) and pruned each tree to match those in our data set (263 species) using the Ape R package⁴⁴. All analyses described below were run across these 50 trees to account for phylogenetic uncertainty⁴⁵.

Statistical analyses

Evolutionary pathways to and from polygyny. Social polymorphism could be an intermediate evolutionary step between monogyny and obligate polygyny. To test this hypothesis, we compared four transition-rate models for the evolution of polygyny in ants using Akaike’s information criteria (AIC). AIC ranks models based on the trade-off between their goodness of fit and the number of parameters estimated. The minimum AIC value indicates the preferred model. We calculated the relative support for each model using Akaike weights, which provides a continuous measure of the strength of evidence. The weight of each model is the probability that it is the best model given the data and the set of models being compared.

The first model only allows two transitions: monogyny to social polymorphism and social polymorphism to obligate polygyny. This corresponds to the hypothesis that the evolution of obligate polygyny must pass through a socially polymorphic ancestor. The second model is similar but allows reversals from social polymorphism to monogyny and from obligate polygyny to social polymorphism (four transitions). This model does not allow transitions between monogyny and obligate polygyny, in either direction. The third model corresponds to the opposite hypothesis: it forces obligate polygyny to evolve from monogyny without passing through a socially polymorphic state. We allow transitions from monogyny to obligate polygyny (in either direction) and from obligate polygyny to social polymorphism (in either direction). Transitions from monogyny to social polymorphism are not allowed (in either direction). Finally, the fourth model estimates six transition rates, with all possible transitions between states allowed. We used the Geiger R package to fit these models⁴⁶.

To account for phylogenetic uncertainty, we fit each model to each of the 50 phylogenies and averaged the transition rates, log likelihoods, and AIC values. Full details are provided in the supplementary R code. To visualize ancestral states, we estimated the probability that each node on the phylogeny was in each state using the best fitting model. This was done via maximum likelihood in the Ape R package⁴⁴ using one phylogeny chosen at random.

Social structure and altitude, latitude, and seasonal precipitation. We used Bayesian Phylogenetic Mixed Models (BPMs) with Markov Chain Monte Carlo (MCMC) estimation, implemented in the MCMCglmm R package⁴⁷ to estimate the following parameters for absolute latitude, altitude ($\log + 1$), and seasonal precipitation: the mean value of each variable for each social type and the residual and phylogenetic variance of each variable for each social type. This allowed us to test if there are mean differences in the environments that monogynous, polymorphic, and polygynous species inhabit, and if there are differences in the variances of those environments (three models in total, one for absolute latitude, altitude ($\log + 1$), and seasonal precipitation). Parameters were estimated from a model with the environmental variable as the response variable and social type as the fixed effect (three level factor:

monogyny, polymorphic, polygyny) with the global intercept removed to estimate the mean value for each level of social type. We estimated the residual and phylogenetic variances for each level of social type by fitting two 3×3 unstructured (co)variance matrices as random effects. We used a vague normal prior for fixed effects and a parameter expanded prior for our random effects, which improves chain mixing when variances are expected to be small⁴⁸. We explored the sensitivity of our results to the choice of prior by fitting the models described above using an inverse Gamma prior. Results from the parameter expanded prior are reported below while those from the Gamma prior, which are quantitatively consistent, are shown in Supplementary Table S4.

Absolute queen number and altitude, latitude, and seasonal precipitation. By classifying ant species into discrete categories, our analysis misses continuous variation in queen number, which can be substantial (e.g. *Wasmania auropunctata* colonies host > 1000 queens⁴⁹; *Acromyrmex insinuator* tends to have two queens per colony⁵⁰). We therefore conducted a third set of analyses on a subset of species ($N = 202$) for which the average number of queens per colony was known. To test whether queen number variation is associated with absolute latitude, altitude ($\log + 1$), and seasonal precipitation, we constructed three BPMs. Either absolute latitude, altitude ($\log + 1$), or seasonal precipitation was the response variable and queen number ($\log$) was the fixed effect. We treated queen number as a fixed effect for consistency with our previous models. These models included a random term for phylogeny. We used a parameter expanded prior for our random effect and explored the sensitivity of our results to this choice by re-fitting the above models using an inverse Gamma prior. Results from the parameter expanded prior are reported below while those from the Gamma prior, which are quantitatively consistent, are shown in Supplementary Table S5.

Restricted dataset

The number of colonies used to assign each species to a social type varied widely across studies (from 1 to over 100). In the analyses described above, we made use of the entire dataset. Small sample sizes can result in detection bias, however. Specifically, a classification of obligate monogyny (or obligate polygyny) based on one or two colonies is unreliable, easily missing polygynous (or monogynous) colonies in the population. We therefore repeated the analyses described above on a subset of data that included social classification based on a minimum of 20 colonies per species, for monogynous and polygynous species. We included all species classified as polymorphic species, on the basis that at least one polygynous and one monogynous colony had been described. Each model was run using parameter expanded and inverse Gamma priors.

Each model was run for 510,000 iterations per tree with a burn-in of 10,000 iterations and a thinning interval of 500 iterations. This gave a posterior distribution of 1000 iterations (and an effective sample size of 1000 for each parameter in our preliminary analyses). Twenty iterations were then sampled from each tree (every 50th) and combined to give 1000 iterations in the posterior distribution of each parameter (i.e. 20×50). Model convergence was examined by calculating the degree of autocorrelation between posterior samples and by inspecting traces of posterior distributions. Full details are provided in the supplementary R code. We report posterior modes and 95% credible intervals (CI) from the posterior distributions of each parameter in the results. *P* values testing differences between environmental variables (e.g. latitude in monogynous versus obligate polygynous species) are the number of iterations when one level is greater or less than the other level divided by the total number of iterations. *P* values comparing variances were calculated in a similar way.

Supercoloniality

We carried out a fifth set of analyses, in which we investigated ‘supercoloniality’ as a fourth discrete social form category. Supercoloniality is an extreme form of polygynous social organization with connectivity and resource sharing between neighbouring nests⁴². In our sample of 263 species,

11 polygynous species are classified as forming supercolonies in the specific study site⁴². This reduced the number of species classified as polygyny from 48 to 37. The number of monogyny and socially polymorphic species remained the same (116 and 99, respectively). To investigate the evolutionary origins of supercoloniality, we began by extending our best supported transitions model (model 2) to allow transitions from polygyny to supercoloniality (model 5). This model does not allow losses of supercoloniality once it has arisen. To allow this possibility, we built two further models. First, supercoloniality could revert to polygyny only (model 6), or to any social state (model 7). In models 6 and 7, supercoloniality must still originate from polygynous ancestors. We relaxed this restriction by building a fully parameterised model, which allows transitions between all states (model 8). To account for phylogenetic uncertainty, we again fit each model to each of the 50 phylogenies and averaged the transition rates, log likelihoods, and AIC values.

Results

Evolutionary pathways to and from polygyny

Our final sample comprised 263 species, with 116 species classified as monogyny (all nests have one queen), 99 species as socially polymorphic (nests have either one or multiple queens), and 48 species as polygyny (all nests have multiple queens). Most studies came from the northern hemisphere (Fig. 1).

Our phylogenetic analyses of transitions between alternative social structures showed that polygyny most likely evolved from polymorphic

ancestors, which evolved from monogyny ancestors (Table 1, Fig. 2). Transitions between monogyny and polymorphism occurred in both directions, indicating that switching between states has occurred repeatedly through evolutionary time. Similarly, transitions between polymorphisms and polygyny occurred in both directions. These inferences are based on our finding that model two (which forces obligate polygyny to evolve from obligate monogyny via polymorphic ancestors) was the best supported model, accounting for 73% of the weight. Model one received the lowest support. As this model does not allow switching between states, this reinforces the finding that queen number is a labile trait over evolutionary time.

Social structure and altitude, latitude, and seasonal precipitation

Monogyny, polymorphic, and polygyny species occurred at similar absolute latitudes (smaller values closer to the equator, large values closer to the polar regions), altitudes and across precipitation seasonality (Table 2). Specifically, monogyny, polymorphic, and polygyny species occurred at similar absolute latitudes (Fig. 3a; Tables 2 and 3; $P_{\text{monogyny vs polymorphic}} = 0.37$; $P_{\text{monogyny vs polygyny}} = 0.45$; $P_{\text{polymorphic vs polygyny}} = 0.58$). The total variance in absolute latitudes was similar across social types, with similar proportions of the variance being explained by phylogeny (Table 2), and there were no differences in residual variance between social types ($P_{\text{monogyny vs polymorphic}} = 0.64$; $P_{\text{monogyny vs polygyny}} = 0.11$; $P_{\text{polymorphic vs polygyny}} = 0.21$).

Monogyny, polymorphic, and polygyny species also occurred at similar altitudes (back transformed) (Fig. 3b; Table 2; $P_{\text{monogyny vs polymorphic}} = 0.28$; $P_{\text{monogyny vs polygyny}} = 0.40$; $P_{\text{polymorphic vs polygyny}} = 0.30$). The total variance in

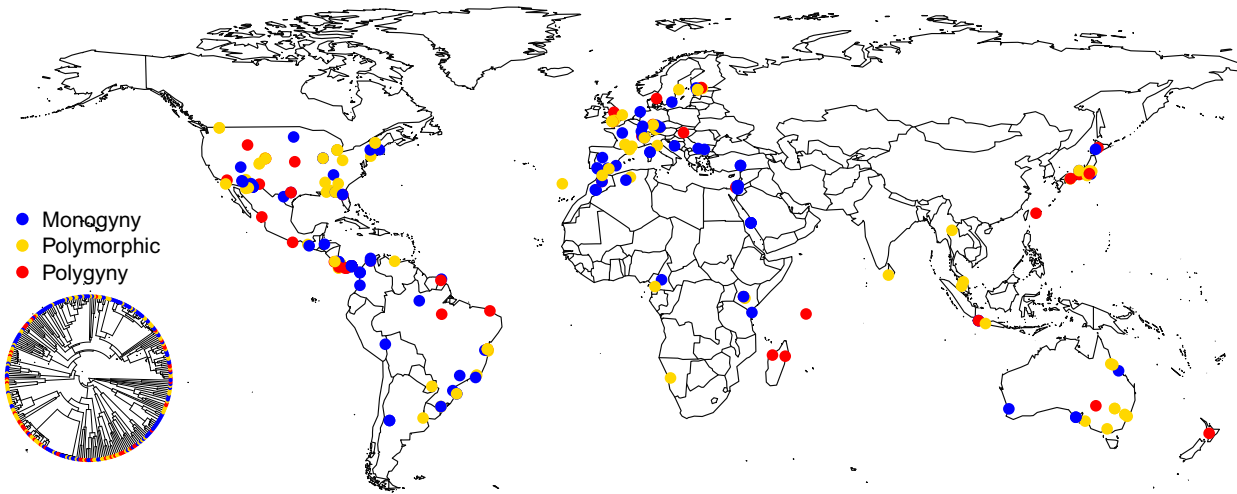


Fig. 1 | Most species were studied in the northern hemisphere. Geographic location of study sites and social form for 263 species. Blue reflects monogyny species, red polygyny species, and yellow polymorphic species.

Table 1 | Queen number is a labile trait over evolutionary time

Model	Full dataset				Restricted dataset			
	K	logL	AIC	Akaike.w	K	logL	AIC	Akaike.w
two (M ↔ SP ↔ P)	4	−253	515	0.79	4	−129	265	0.82
four (M ↔ SP ↔ P ↔ M)	6	−253	518	0.14	6	−129	269	0.11
three (M ↔ P ↔ SP)	4	−256	520	0.07	4	−131	270	0.07
one (M → SP → P)	2	−306	617	0.00	2	−166	334	0.00

Results from model comparisons (Fig. 1). K is the number of parameters estimated, logL is the loglikelihood (smaller numbers reflect better fit), AIC is the Akaike Information Criterion, which balances model fit and complexity, with lower values showing a better fit, and Akaike.w is the weight of the model. The best supported model has the highest Akaike weight. The left side of the table shows the result using the full dataset, and the right side the results from the restricted dataset.
M obligate monogyny, SP socially polymorphic, P obligate polygyny.

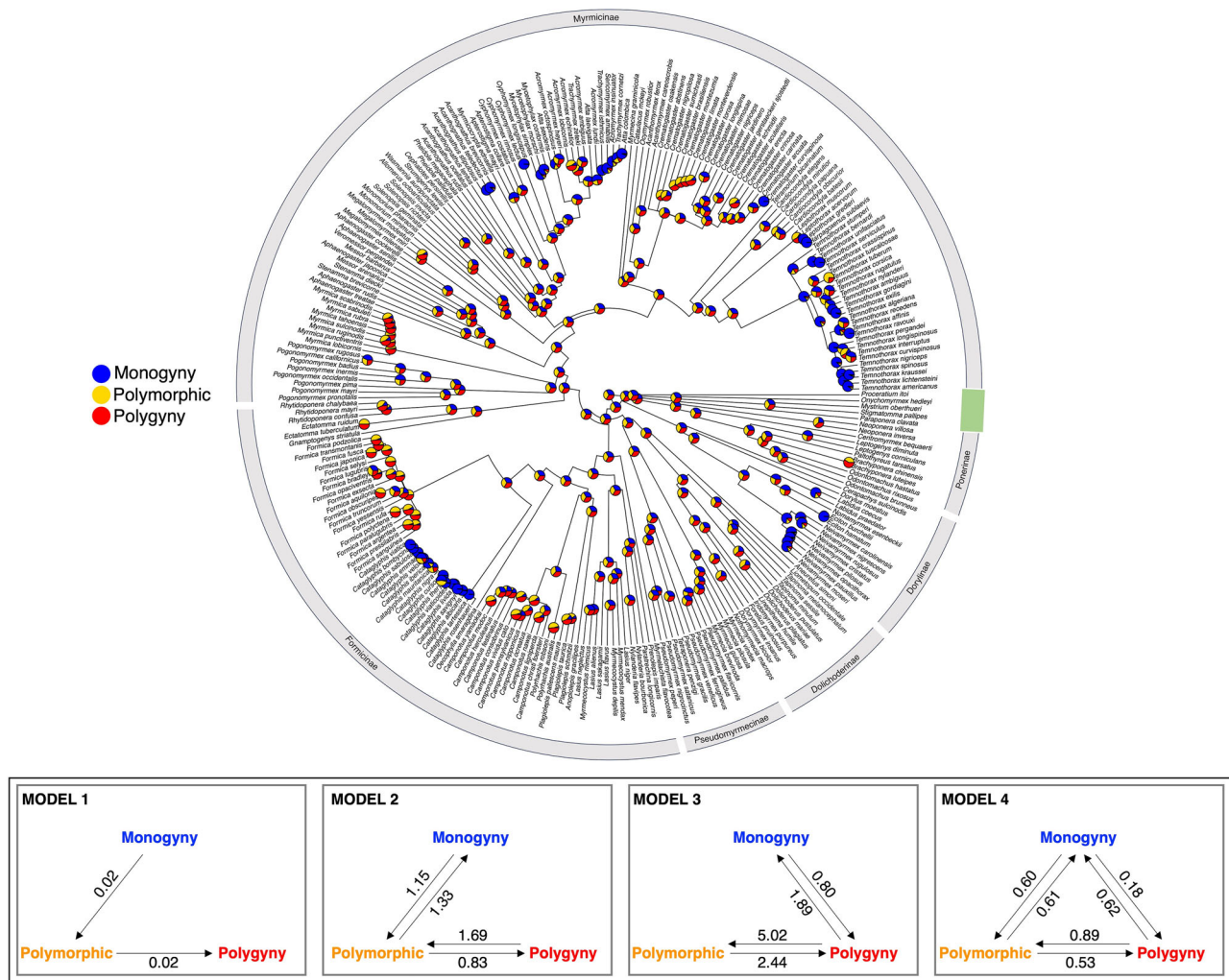


Fig. 2 | Social form is a labile trait over evolutionary time. The evolution of obligate polygyny and polymorphism in our sample of 263 ants. Inset are the transition rate estimates from the four models compared. These rates are average values from our sample of 50 phylogenies. The ancestral states plotted on the phylogeny were

estimated using model two, for one tree sampled at random. Blue represents monogyny, red polygyny, and yellow polymorphic. Subfamilies are shown in grey boxes, the small green box on the right side represents the subfamily Amblyoponinae.

altitude was higher for monogynous species (Table 2), but after accounting for phylogeny, there were no differences in residual variance ($P_{\text{monogyny vs polymorphic}} = 0.14$; $P_{\text{monogyny vs polygyny}} = 0.46$; $P_{\text{polymorphic vs polygyny}} = 0.16$).

Polymorphic species tended to occur in environments with lower seasonal precipitation than obligately monogynous (Fig. 3c; Table 2; $P_{\text{monogyny vs polymorphic}} = 0.04$; $P_{\text{monogyny vs polygyny}} = 0.53$; $P_{\text{polymorphic vs polygyny}} = 0.22$). The total variance in seasonal precipitation was almost twice as high in polygynous species, but after accounting for phylogeny, residual variance in seasonal precipitation was significantly higher in monogynous and polymorphic species than in polygynous species ($P_{\text{monogyny vs polymorphic}} = 0.09$; $P_{\text{monogyny vs polygyny}} < 0.01$; $P_{\text{polymorphic vs polygyny}} < 0.01$). For polygynous species, 90% of the variance in seasonal precipitation was explained by phylogeny. For monogynous, and polymorphic species, most of the variance was residual, indicating that closely related species can occur in areas with different seasonal precipitation.

Queen number and absolute altitude, latitude, and seasonal precipitation

We obtained data on queen number for 202 ant species. We found no significant associations between absolute latitude, altitude (log + 1), or seasonal precipitation and log queen number (Fig. 4a–c; absolute latitude: slope = -0.2 , 95% CI = -1.4 to 1.6 ; altitude (back transformed): slope = 0.0 , 95% CI = -0.2 to 0.2 ; seasonal precipitation: slope = -1.7 , 95% CI = -5.3 to

1.1). Most of the variance in absolute latitude was explained by phylogeny (80%) while most of the variance in altitude (73%) and seasonal precipitation (75%) was residual (Table 3).

Restricted dataset

Our restricted dataset comprised 160 species: 39 species were monogynous, 99 were polymorphic, and 22 were polygynous. Transitions between alternative social structures were consistent with the full dataset, with obligate polygyny having evolved from polymorphic ancestors, which evolved from obligate monogynous ancestors (Table 1). Monogynous, polymorphic, and polygynous species occurred at similar absolute latitudes, altitudes, and in environments with similar seasonal precipitation (Table 2).

When comparing absolute queen number in this restricted dataset, we found that queen number was negatively and significantly associated with absolute latitude (slope = -2.6 , 95% CI = -4.0 to -0.2), suggesting that more queens share reproduction closer to the tropics. We found no significant associations between altitude (log + 1) or seasonal precipitation and log queen number (altitude (back transformed): slope = -0.1 , 95% CI = -0.3 to 0.2 ; seasonal precipitation: slope = -1.5 , 95% CI = -4.7 to 2.1). Most of the variance in latitude and seasonal precipitation was residual (82% and 86%, respectively), whereas 87% of the variance in absolute latitude was explained by phylogeny.

Table 2 | Monogyne, polymorphic, and polygyne ant species live in similar environments

Variable	Social organization	Mean (95% CI)	Total variance	% Phylo	% Residual
Full dataset					
Latitude (absolute)	Monogyne	22.2 (10.0–34.2)	309.8	85	15
	Polymorphic	25.6 (13.3–38.6)	382.9	89	11
	Polygyne	22.4 (10.0–38.7)	429.4	96	4
Altitude (back transformed)	Monogyne	57.8 (12.9–267.4)	4.9	48	52
	Polymorphic	131.2 (69.5–263.5)	3.7	12	88
	Polygyne	101.5 (42.3–231.1)	2.9	13	87
Seasonal precipitation	Monogyne	51.4 (40.7–58.1)	739.6	9	91
	Polymorphic	38.8 (30.3–45.7)	577.6	11	89
	Polygyne	52.1 (20.6–73.0)	1301.6	90	10
Restricted dataset (sensitivity analyses)					
Latitude (absolute)	Monogyne	34.0 (16.8–46.0)	324.1	99	1
	Polymorphic	23.7 (14.6–39.6)	386.7	90	10
	Polygyne	33.0 (10.6–47.7)	447.2	99	1
Altitude (back transformed)	Monogyne	99.9 (11.1–301.7)	4.1	49	51
	Polymorphic	154.5 (67.1–270.4)	3.7	11	89
	Polygyne	84.3 (0.9–354.7)	4.7	37	63
Seasonal precipitation	Monogyne	39.6 (27.5–53.1)	582.3	21	79
	Polymorphic	38.8 (30.8–46.4)	580.2	11	89
	Polygyne	48.8 (20.1–86.5)	1351.4	99	1

Parameter estimates from our BPMMs, for the full dataset, and for the restricted dataset (sensitivity analyses). For absolute latitude, altitude (back transformed), and seasonal precipitation, the posterior mode (its 95% CI is in brackets), phylogenetic variance and residual variance are shown for each type of social organization.

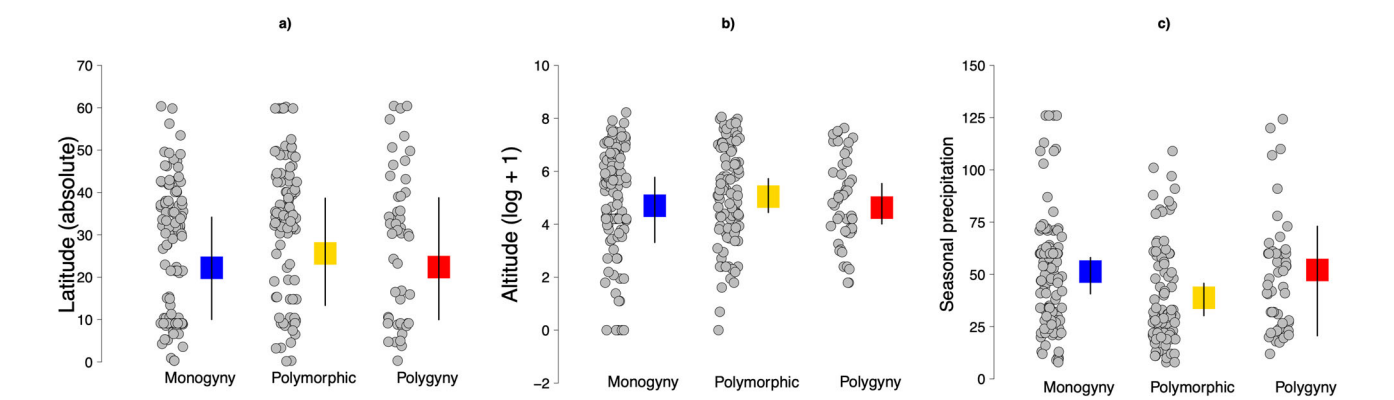


Fig. 3 | Monogyne, polymorphic, and polygyne ant species live in similar environments. Differences in (a) absolute latitude, (b) altitude (log + 1), and (c) seasonal precipitation between monogyne, polymorphic, and polygyne ant species. Each data point is a different species ($N = 263$). The blue, yellow and red squares are the posterior modes per social form, bracketed by their 95% credible intervals (error bars) estimated from the Bayesian Phylogenetic Mixed Models. These values correspond to those shown in Table 2. Blue represents monogyne, red polygyne, and yellow polymorphic species.

Supercoloniality

The most likely origin of supercoloniality in our sample was from polygynous species, and supercoloniality could reverse to this state (Table 4, Fig. 5). This inference is based on our finding that model 6 received the most support, accounting for 85% of the weight (Table 4). This is supported by a visual inspection of the phylogeny, which shows that supercolonial species tend to be nested within polygynous clades (Supplementary Fig. S1). Supercolonial species did not differ from any other social state in latitude (absolute), altitude, or seasonal precipitation (Supplementary Fig. S2).

Discussion

The evolution of multi-queen colonies in ants is puzzling, because it lowers relatedness among colony members, potentially fuelling evolutionary

conflicts. Within several ant species and genera, the proportion of polygyne colonies increases with altitude and latitude (Supplementary Table S2), suggesting that cold climates drive or correlate with the evolution of polygyne across species. Moreover, polygyny was more common in deserts and temperate or boreal climates across over 3000 species³⁷, suggesting this social form is common in harsh environments. However, most of these studies had been carried out without controlling for phylogeny, and those that have, typically classify social form based on few colonies per study site. Our study addressed this shortcoming, and our results highlight three main conclusions. The first is that social organization in ants is a labile trait over evolutionary time, with many transitions back and forward between monogyne and polygyny. Similarly, when we split supercoloniality from polygyny, we found that supercoloniality originated multiple times independently from

Table 3 | Colonies with more queens live closer to the tropics, but only in the restricted dataset

Variable		Estimate	% Phylo	% Residual
Full dataset				
Latitude (absolute)	Intercept	23.5 (13.7–34.5)	80	20
	Slope	−0.2 (−1.4 to 1.6)		
Altitude (back transformed)	Intercept	115.3 (38.2–222.6)	27	73
	Slope	0.0 (−0.2 to 0.2)		
Seasonal precipitation	Intercept	44.5 (34.2–57.4)	25	75
	Slope	−1.7 (−5.3 to 1.1)		
Restricted dataset (sensitivity analyses)				
Latitude (absolute)	Intercept	28.6 (17.9–41.5)	87	13
	Slope	−2.6 (−4.0 to −0.2)		
Altitude (back transformed)	Intercept	109.8 (41.4–241.1)	19	81
	Slope	−0.1 (−0.3 to 0.2)		
Seasonal precipitation	Intercept	40.0 (28.8–49.8)	25	75
	Slope	−1.5 (−4.7 to 2.1)		

Parameter estimates from our BPMMs, for the full dataset, and for the restricted dataset (sensitivity analyses). Queen number (log transformed) is shown as a function of latitude, altitude, and seasonal precipitation.

polygynous ancestors, and that reversals of supercoloniality to polygyny are possible. The second main conclusion is that we found no association between either polygyny or supercoloniality and latitude or altitude. Contrary to our prediction, absolute queen number was negatively associated with absolute latitude in the restricted dataset, suggesting more queens cohabit closer to the tropics. Lastly, our conclusions changed depending on whether we included studies that used multiple colonies to define social type, highlighting that social structure classification based on a few colonies may not be reliable. Overall, our conclusions must be taken cautiously for two reasons. Firstly, our sample was biased towards temperate species (Fig. 1). Secondly, we were unable to examine the ancestral environments in which the different forms of social organization evolved, because there are many transitions between states, and consequently ancestral states were poorly resolved (Fig. 2).

Our results suggest that queen number is a labile trait over evolutionary time, with transitions to and from multi-queen colonies passing through socially polymorphic species. This result was consistent in our transition models in both the full and restricted dataset. Specifically, although obligate polygyny evolves from polymorphic species, which evolve from obligate monogyne species, transitions between polymorphic and monogyne species are common, as are transitions between polymorphic and polygyne species. Similarly, when we included supercolonial species, we found transitions back and forth from polygyny to supercoloniality. This is an interesting finding, because in at least five independent ant lineages, social polymorphisms are genetically determined by very ancient and large supergenes⁶. Hence, long-term balancing selection within lineages seems not to preclude transitions over evolutionary time, as revealed by contrasting social forms (obligate monogyne, polymorphic, or obligate polygyne) across the ant phylogeny (Fig. 2).

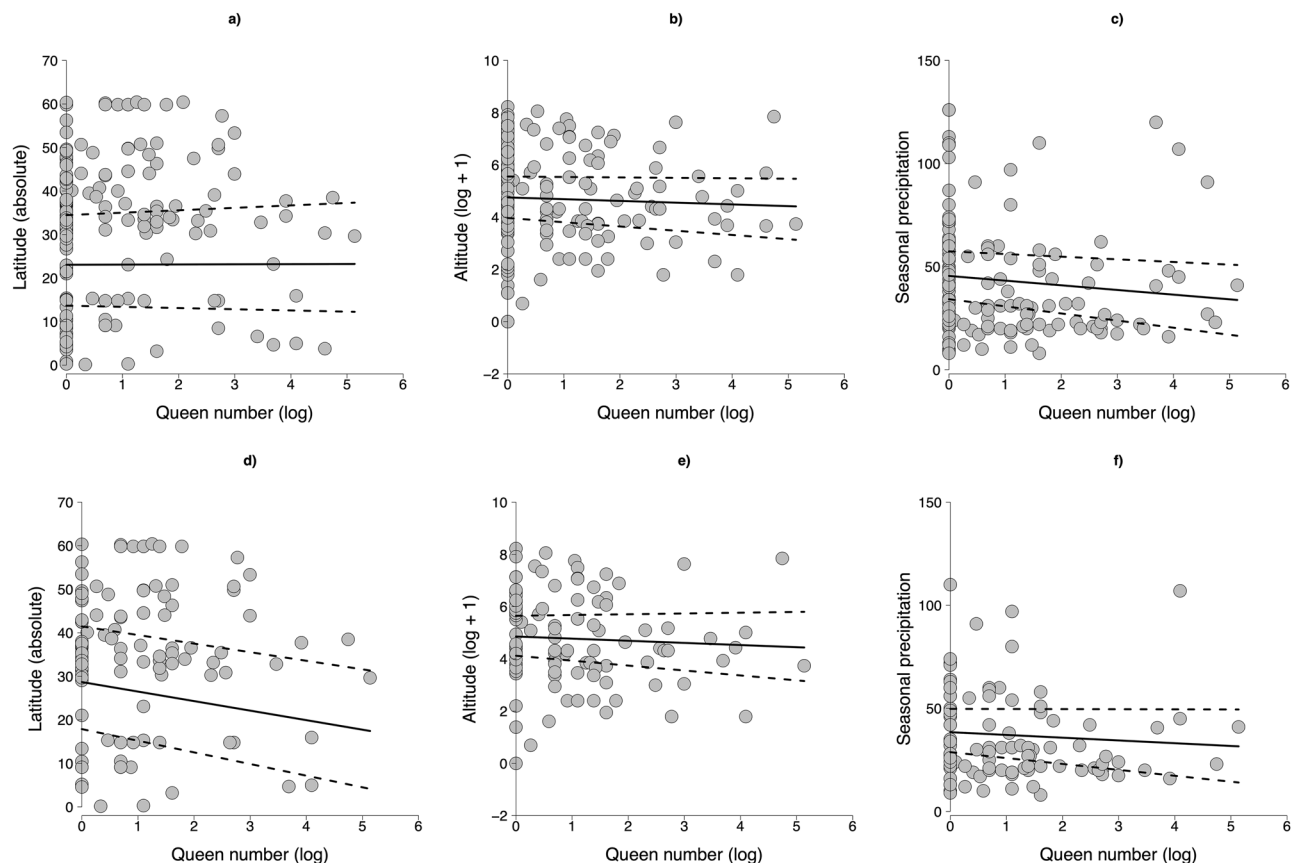


Fig. 4 | Average queen number per colony was not related to climatic traits in the full dataset, but was negatively related to absolute latitude in the restricted dataset. Queen number (log) as a predictor of absolute latitude (a, d), altitude (log + 1) (b, e), and seasonal precipitation (c, f), for the full (top) and restricted

(bottom) panels. Each data point is a different ant species ($N = 218$). Solid lines are the slope estimates from the BPMMs and are bracketed by their 95% credible intervals estimated.

Contrary to our predictions, we found no association between polygyny and altitude or latitude, and absolute queen number was negatively associated with latitude in the restricted dataset. We cautiously take this as evidence that polygyny can be selected in both cold and warm climates. This result is interesting, because many studies found that polygyny in ants is more common at higher altitudes/latitudes (Supplementary Table S2). Intuitively, colder habitats limit independent colony founding by young queens, forcing them to stay in their maternal nest, which is in line with experimental work showing that cold temperature constrains independent colony founding²³. However, the warm habitats that allow for independent colony founding (i.e. in the tropics) likely impose other ecological constraints, such as increased inter-colony competition and saturated habitats. In these habitats, polygyny may be highly beneficial, providing increased division of labour, rapid colony growth, longer colony lifespan, and larger nests may have better capacity to maintain humidity and thermal stability. These benefits may partly explain why we did not detect a link between climate and polygyny, and why more queens may co-habit closer to the tropics.

Polygyny also increases genetic diversity within a colony. Higher genetic diversity may improve nest thermoregulation in ants, as happens in bees²⁰, and may also improve resistance to parasites. However, predicting global spatial patterns of parasite pressure remains challenging. Although species' richness of free-living organisms generally increases towards the tropics (reviewed in refs. 51,52), including in ants⁴³, parasitism rates often (but not always) show the opposite trend, i.e., there is lower parasitism at higher latitude (a so-called reverse latitudinal diversity gradient). For example, ant social parasites⁵³, ectoparasites in *Odonata*⁵⁴ and in amphibians⁵⁵, as well as blood parasites in birds⁵⁶ and in herbivorous insects⁵⁷ tend to decrease with increasing latitude. A similar pattern of

decreasing parasitism with increasing altitude has also been reported⁵⁸. In contrast, other studies report opposite patterns: birds at higher latitudes and altitudes have more *Leucocytozoon* and other haemosporidians parasite infections^{56,59}. Together, these diverse patterns suggest that parasite pressure does not follow a simple latitudinal or altitudinal gradient rule. Parasitism may thus be an important selective force favouring polygyny, but its geographic influence is difficult to predict given the variability observed across taxa and environments.

Polyandry, when a queen mates with more than one male, may partly mask the effect of altitude or latitude on ant social organization. Polyandry and polygyny both increase colony genetic diversity and tend to be negatively correlated across species^{39,60–62}. An early study did not detect this association⁶³, perhaps because of the lack of a well-resolved ant phylogeny at this time. Polyandry has been experimentally shown to increase disease resistance in leaf-cutting ants⁶⁴, and different patriline produce variation in the size of antibiotic-producing metapleural gland in *Acromyrmex* leaf-cutting ants⁶⁵. It is possible that monogyne species living in harsh environments (warm or cold) have multiply mated queens, with polyandry improving colony homeostasis, genetic diversity, and division of labour (something polygyny also allows, even if polyandry does not reduce queen mortality during colony founding)^{20,66–70}. Moreover, within the same latitude and altitude, lee and windward sections of a mountain can have drastic differences in species' diversity (e.g. ref. 71), which in turn can change habitat saturation, parasitism rates, and competition for ants. In general, disentangling the relationships between polyandry, polygyny, parasites and microenvironments, and understanding when do polygyny or polyandry evolve, are key avenues for future work.

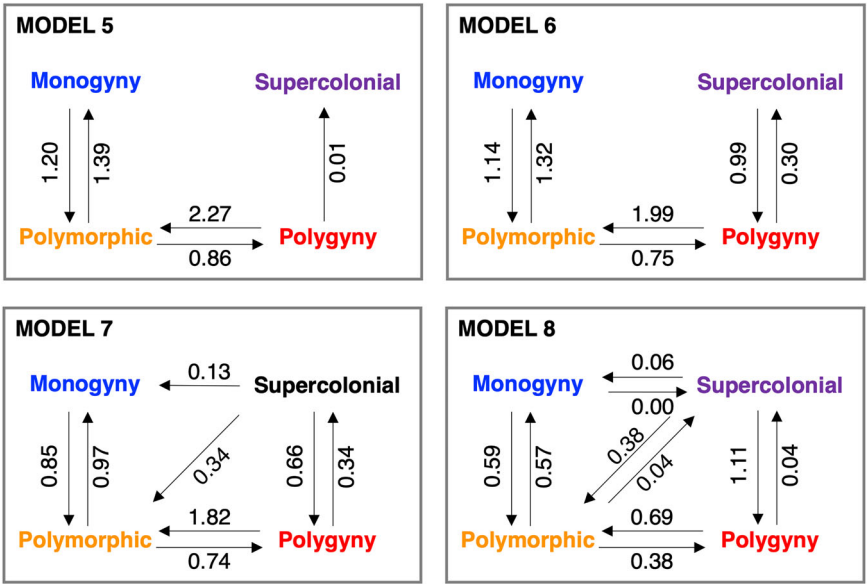
Our finding that polygyne ants occur in a wide range of environments, and are not more frequent in cold climates, contrasts with some findings from cooperatively breeding vertebrates. Across cooperative vertebrate species, group-living is associated with harsh and unpredictable environments^{18,29,34,72–77}. Similarly, alloparental care in humans is more common in harsher environments⁷⁸. This association is assumed to arise because it takes the combined efforts of multiple individuals to successfully raise young in such habitats. In vertebrates, alloparental care occurs both in cooperatively breeding systems, in which non-breeding helpers assist a breeding pair, and in communal breeding systems, in which multiple females reproduce and care for offspring jointly. In ants, both monogyne and polygyne societies exhibit alloparental care. However, colonies with multiple queens may benefit from an advantage analogous to group living in cooperative breeding vertebrates in harsh environments, as queens can

Table 4 | Transitions including supercolonial species

Model	K	logL	AIC	Akaike.w
Six	6	−293	598	0.85
Seven	8	−292	601	0.13
Eight	12	−291	607	0.01
Five	5	−298	607	0.01

Results from model comparisons examining transitions between social forms, including supercoloniality (Fig. 5). Models are ordered according to the best support.

Fig. 5 | Supercoloniality in ants evolved from polygynous ancestors and can revert to this state. Inset are the transition rate estimates from the four models compared. These rates are average values from our sample of 50 phylogenies.



become reproductively established without the risky independent founding stage. The lack of association between polygyny and harsh climate suggests that polygyny in ants and at least some cooperative breeding systems in vertebrates are not parallel solutions to the same ecological problem.

Variation in colony queen number can be phenotypically plastic or genetically determined. In at least five independent ant lineages, supergenes underlie intraspecific polymorphism in social organization (reviewed in refs. 6,7), with derived supergene haplotypes inducing polygyny. Throughout this study, we treated socially polymorphic species independently of the proximate mechanisms underlying variation in social structure. This choice was motivated by two considerations. First, the basis of social structure has not been investigated in most species, so it remains unclear whether variation is plastic or genetic. Second, there are still relatively few independent evolutionary origins of supergenes, limiting robust comparison between genetically determined and plastic lineages. An important unresolved question is whether specific climatic or ecological variables predict the evolution of social supergenes versus phenotypic plasticity. Some theoretical models suggest that plasticity evolves when environmental cues are reliable enough to predict future conditions, whereas genetic polymorphism evolve when such cues are less reliable^{79–81}. Future research may reveal if environmental stability predicts whether social polymorphisms are determined by genetic or environmental mechanisms across the ant phylogeny.

In conclusion, despite several case studies showing that polygynous ant species or genera are more common at higher altitude and latitude (Supplementary Table S2), our phylogenetic study found no association between polygyny and altitude, and the relationship between queen number and latitude suggested that more queens co-habit in the tropics. Overall, our study indicates that multiple transitions of social forms occurred across the ant phylogeny, and that both monogyny and polygyny can be favoured in a broad range of environmental conditions, harsh or mild. More broadly, we call for more studies to be carried out in the tropics, as most of the evidence were carried out in the northern hemisphere.

Data availability

All primary references used and datasheets are available from Figshare: <https://figshare.com/s/1120fc71eee8af996e85>.

Code availability

All analyses codes and model outputs available from Figshare: <https://figshare.com/s/1120fc71eee8af996e85>.

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Author contributions

O.D.G. and M.C. conceived the study; O.D.G. collected data; O.D.G., D.S., and P.D. did analyses; O.D.G., M.C., and P.D. wrote the first version of the M.S.; O.D.G., M.C., P.D., D.S., H.H., and A.L.B. contributed to the final version of the paper. O.D.G., M.C., P.D., D.S., H.H., and A.L.B. agree to be held accountable for all aspects of the work and for the content therein and approve the final version of the manuscript.

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Competing interests

The authors declare no competing interests.

Additional information

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