

RESEARCH ARTICLE

Ecological traits of social insects: Colony, queen and worker size relationships reveal a nexus trait with broad ecological relevance

Leo Ohyama^{1,2}  | Douglas B. Booher³ | Joshua R. King⁴ 

¹University of Florida Biodiversity Institute, Gainesville, Florida, USA

²Department of Entomology and Nematology, University of Florida, Gainesville, Florida, USA

³US Forest Service, Southern Research Station, Athens, Georgia, USA

⁴Department of Biology, University of Central Florida, Orlando, Florida, USA

Correspondence

Leo Ohyama

Email: leoohyama12@gmail.com

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Abstract

1. Trait-based ecology has surged in recent decades but a framework to assess eusocial taxa, such as ants and termites, has been left underdeveloped because ecological trait-based approaches have yet to examine the ecological relationships and potential mechanisms between different trait components (i.e. queen, colony and worker).
2. We collected worker-, queen- and colony-scale traits of the ants of Florida, an ant fauna comprised of ~25% nonnative species, based on morphology, natural and life histories and combined these traits with geospatial data.
3. We used these data to assess and develop the beginnings of a hypothesis-testing framework to aid in better understanding trait ecology for eusocial organisms and to understand the spatial structure and drivers of eusocial insect traits by examining individual- and colony-scale trait relationships.
4. Results show that queen-worker dimorphism, the morphological difference between workers and queens, shows exceptional potential as a nexus trait for which other colony-scale traits, especially colony size, have significant relationships with. Colony size is therefore the key trait that should be measured, whenever possible, to better understand these other, emergent relationships.
5. We also find differences between native and nonnative regional patterns of colony size and queen-worker dimorphism across environmental gradients.
6. We show the potential for a more holistic trait approach to ants and potentially other eusocial taxa given the state of current trait knowledge, providing an advanced path forward in functional and trait ecology of eusocial organisms.

KEYWORDS

ants, fire ant, invasion biology, social traits, trait ecology

1 | INTRODUCTION

Ecological traits are typically observed and catalogued for individuals, but this approach is problematic if applied to eusocial organisms where both individual and collective traits need to be considered

(Dawson et al., 2021; Mittelbach & McGill, 2019; Wong et al., 2019b). While ecological traits of eusocial organisms, such as ants, have received increased attention (Elizalde et al., 2020; Gibb et al., 2022; Sosiak & Barden, 2020; Weiser & Kaspari, 2006; Wong et al., 2019b), most trait-based approaches have focused on workers without also

considering their organismal unit (the unit of selection and ecological impact)—the colony. Therefore, an important question is: what ecologically relevant traits do we measure for organisms that have both individual and collective traits? Eusocial insects are ecologically important, contributing to many ecosystem services (Elizalde et al., 2020; Lach et al., 2009; Sugimoto et al., 2000) and are dominant animal groups in terms of biomass (King et al., 2013; Schultheiss et al., 2022). While likely to be taxa specific to an extent (Dawson et al., 2021; Waite & Sack, 2010), it is important to first understand how colony-level ecological traits for a eusocial organism differ from individual traits and second, how individual traits relate to colony traits (Tschinkel, 2010). How these traits are distributed across space and what traits tell us about their ecological function are important to help understand the roles and ecosystem contributions of eusocial organisms. Here we investigate both individual- and colony-level traits and their relationships to one another, their ecological role, and to their environment in a well-studied ant assemblage.

Most ants live in colonies where the reproductive unit is the queen(s) and the workers perform nest maintenance, care for brood (larvae and pupae) and gather resources (Hölldobler et al., 2009). Worker traits have been the focus of trait ecology in ants because they are expected to tie more directly to ecological function as workers interact with the external environment and are more common than reproductives, making them easier to collect traits from (Gibb et al., 2015, 2022; Johnson & Rutowski, 2022; Ohyama, 2022; Sosiak & Barden, 2020; Wong et al., 2019b). However, colony-level traits are more ecologically important than worker traits as colonies are the functional organismal unit for eusocial species within ecosystems. Therefore, the colony has important ecological impacts determined by morphological, natural and life history traits that are necessary to consider. However, the primary reason these data are rarely included in ecological trait studies is because collecting whole colonies can sometimes be very challenging or even impossible (e.g. rock-crevice nesting species).

The majority of an ant queen's life is spent producing brood within her nest limiting her exposure to the conditions that workers are exposed to (Gibb et al., 2022; Hölldobler & Wilson, 1990; Johnson, 2006). Because of this, worker traits are shaped by environmental pressures outside of nests that select for characteristics that improve whole colony survival, whereas queen traits are shaped by reproductive and within-nest selective pressures. This selection differential has produced a cline of worker-reproductive morphologies among different ant species depending on their level of specialization to colony function. As such, colonies with greater differences in morphologies between reproductives and workers, and between workers should exhibit a wider variety of behavioural repertoires and task allocations facilitating increased behavioural/social complexity across whole colonies (Bourke, 1999; Ferguson-Gow et al., 2014).

We emphasize colony size as an important and measurable ecological trait in this study as colony size has direct ecological relevance (Tschinkel, 1991). Specifically, colony size is perhaps the trait with direct relevance to colony traits impacting ecology

of different species as it is the primary information necessary to measure the 'body' size of whole colonies. Once known, biomass and the subunits of colony size can then be used to determine and predict other ecologically relevant, emergent colony-level traits (Tschinkel, 1991). Furthermore, colony size is shown to track climatic variables (Kaspari, 2005) and thus can reveal relationships with both local- and regional-scale variables of ecological interest which is important for understanding questions within and across regional assemblages. This study benefits from the fact that colony size and queen size for many species is relatively well-sampled across the southeastern US ant faunas, especially in Florida (Deyrup, 2016; King, 2010; King et al., 2013). Therefore, we suggest that colony size and its relationship with other worker and queen characteristics is perhaps the most important colony-level trait to add to field measurements for social insects, and here we take the opportunity to explore the best available dataset for colony size for the ant fauna of an entire region.

Other well-studied traits with important relationships to colony size in ants include worker polymorphism, queen-worker dimorphism (QWD) and polygyny. Worker polymorphism, the presence of more than one worker caste, is associated with the division of labour in ants and has been linked to a broader repertoire of effective responses to environmental changes (Peeters, 1997) and competitive interactions among species (Wills et al., 2018). Polymorphism and colony size, are important indicators of foraging range, increased task allocation and food size range (Beckers et al., 1989; Bourke, 1999; Ferguson-Gow et al., 2014; Wills et al., 2018). QWD, the morphological difference (typically summarized and measured as the difference in size) between worker and queens, is positively related to colony size and other traits of social complexity (Bourke, 1999) but colony size and other social complexity traits are not necessarily associated with one another. Polygyny refers to the presence or absence of multiple queens and is often used as a proxy for reproductive output (Gibb et al., 2022; Shik et al., 2012). Ecological studies of colony-level traits are rare but have shown potential where predictions of colony metabolic activity and biomass production (Hou et al., 2010) have been sometimes correlated with ecological importance as estimated by abundance, density or standing biomass (King, 2010; Shik et al., 2012).

For this study, we sought to test a general hypothesis (Wong et al., 2019a and references therein) formulated for understanding patterns of ecological traits of terrestrial arthropods, modified here to be more specific to eusocial insects. Specifically, we hypothesized that traits of colonies and constituent workers and queens share common physiological, morphological, behavioural and life history characteristics in response to environmental conditions affecting colonies (Wong et al., 2019a). However, there is an important caveat about available data that we further consider as specific to social insects, that is, many traits are likely emergent properties apparent only when colony size and queen size (and number) data are available to understand relationships with worker and other ecologically relevant traits. Thus, again, we emphasize colony size as a key measure for better understanding the ecological traits of social insects.

To test this general hypothesis and more specific morphological, behavioural and life history hypotheses (below), we curated trait data from the ant species of Florida, USA and assessed the relationships between traits across colony components (Table 1). We also assessed the assemblage-scale geographic patterns of two colony-level traits, QWD and colony size. Not all species analysed necessarily co-occur with one another in any given local area, as such our term 'assemblage' refers to all ants known to occur within a given spatial area of 2000 km. The Florida ant fauna is taxonomically diverse and is one of the most well-studied ant assemblages (Deyrup, 2016; King & Porter, 2007; Ohyama, 2022; Ohyama et al., 2018, 2020; Wiescher et al., 2012). As a result, traits across colony components are relatively well documented compared to other regions of the world. Furthermore, ~25% of the ant fauna is considered nonnative (Deyrup, 2016) providing an additional opportunity as it allows comparisons between nonnative and native species' traits. Our specific hypotheses are as follows:

1. Here we test the 'size-complexity' hypothesis (Ferguson-Gow et al., 2014). This hypothesis proposes that colony size should increase the variety of behavioural specializations, especially task allocation of workers thereby increasing QWD (Bourke, 1999; Ferguson-Gow et al., 2014). Increased specialization between

colony components likely influences the efficiency of resource appropriation thereby increasing colony size. Additionally given evidence of polymorphism being strongly associated with larger colony sizes and QWD (Anderson & McShea, 2001; Ferguson-Gow et al., 2014; Kwapich et al., 2017; Molet et al., 2012; Oster & Wilson, 1978), polymorphic species are predicted to have larger colony sizes relative to monomorphic species.

2. A common observation is that more polygynous species (two to many same-colony queens) have larger colony sizes (Boulay et al., 2014; Fletcher et al., 1980). This has been attributed to the assumption that additional queens increase a colony's fecundity (Shik, 2008). We evaluate the generality of this prediction by comparing colony sizes of monogyne to polygyne species.
3. We hypothesize that QWD, which we use as an ecological trait due to the potential impact on worker number and size range (Peeters, 1997; Peeters & Ito, 2015), is associated with species natural history traits. For example, species with larger differences between workers and queens are likely to exhibit a larger repertoire of behavioural and morphological diversities which may increase efficiency in resource capture, nest creation and task allocation. Therefore, we predict colonies with high QWD to exhibit natural history traits of a generalist species (i.e. omnivory) versus

TABLE 1 A table detailing the traits used in this study along with their ecological importance.

Trait	Definition and importance
Natural history or life history traits	
Colony size	The number of individuals in a colony. Colony size informs the relative ecological function of an ant species such as total organismal size, colony metabolism, foraging area and efficiency
Dietary role—omnivorous, specialist, predator	Dietary roles reflect the trophic position of a species
Nesting strata—ground nesting, arboreal nesting, leaf litter nesting, mixed	Nesting strata reflects the microhabitat an ant species occupies
Polygyne versus monogyne	The number of queens in a colony can impact a colony's fecundity
Polymorphic versus monomorphic	Polymorphism is considered a metric of strong division of labour within a species
Morphological traits for both worker and queen	
Head width	Determines how wide of a space an ant can navigate through and correlates with load carry of soil movement or food size an individual can carry or process, that is, granivores
Head length	Head length covaries with head width and reflects mandible musculature that would be necessary for granivorous species or predators
Eye length	Eye size can determine the visual acuity of the individual and correlates with nesting and foraging strata, for example, subterranean ants often have reduced or absent eyes
Mandible length	Mandible length helps assess an ant's trophic position, for example, longer mandibles relative to body size often correlate with predatory diets
Weber's length	The diagonal length of the ant's thorax. This is often used a proxy for body size in ants. However, this may also be misleading as some ants such as <i>Pheidole</i> often retain the same Weber's length but differ in head size
Queen-worker dimorphism (QWD) across all morphological traits	In our study QWD was calculated as the ratio of queen to worker measurements across the previously mentioned five morphological traits. QWD is interpreted as a per cent. With values over 100% indicating that the queen is larger in a morphological measurement than the worker
Other designations used	
Native versus nonnative	Designates whether the species is native or nonnative

those of a specialist such as predatory ants which exhibit smaller QWD (Peeters, 1997).

4. Given evidence showcasing strong associations of worker and colony-level traits to invasive ant species (Fournier et al., 2019) especially in our study system (King & Porter, 2007) we hypothesize that the majority of traits are likely to differ between native and non-native fauna. Traits that facilitate nonnative species success have been suggested to correlate with perceived 'generalist invader' traits that include, for example, larger colony sizes or polygyny (Holway et al., 2002). We test this by comparing individual- and colony-level traits between native and nonnative assemblages.
5. Environmental drivers of colony-level traits remains understudied (Purcell, 2011). Nonetheless, Purcell (2011) outlines four major environmental drivers of sociality: seasonality, temperature, precipitation and drought. Because QWD and colony size have previously been shown to be correlated with certain life history strategies and reproductive traits, we hypothesize that abiotic drivers influence the geographic distribution of both. Dryness was excluded because Florida rarely experiences large-scale droughts. We predicted increased colony size and QWD in cooler and seasonal areas as such environments exhibit large fluctuations in resource availability, prioritizing generalist tendencies which can be linked have been linked to larger colony sizes (Kaspari, 2005; Kaspari & Vargo, 1995; Purcell, 2011).

2 | MATERIALS AND METHODS

2.1 | Trait data

Trait data were collected through a variety of sources including unpublished data from the authors, literature and specimen images from AntWeb (<http://www.antweb.org>). We have included all trait data and sources as a Data S1 to this study. We categorized species based on native versus nonnative status using Deyrup (2016) as well as expert observations from the authors. Colony size data were primarily collected from the literature (Burchill & Moreau, 2016; Deyrup, 2016; King, 2010; King & Porter, 2007) while morphological traits for workers and queens were collected from specimen images following the same approaches as Ohyama (2022) and the trait definitions from Parr et al. (2017). Colony sizes were recorded for mature colonies when possible. Colony sizes only reported once or twice were included in the dataset and considered representative if they were reasonably close to the genus average. While seasonal variation exists in colony size, we were not able to capture this as few species have their seasonal variation documented. We did not collect traits for males as male specimens have not been collected enough to attain comprehensive assemblage coverage. For worker and queen morphological traits, we measured head width, head length, mandible length, eye length and Weber's length. Unfortunately, information regarding specific specimen images and whether they were sourced from mature or immature colonies was not available. An explanation of each trait and its posited ecological

role is listed in Table 1. For workers we measured multiple specimens per species when available. This was done especially for polymorphic species with multiple specimens spanning different sizes. Twenty-two species only had one suitable worker image to measure. On average we measured four worker specimen images per species and in total measured 845 worker specimens. Priority for measurements were highest for Florida specimens but to account for intraspecific variation, specimens from outside the state were also measured. For queens, only one imaged specimen was measured due to the rarity of imaged queens for many species.

We categorized species into three dietary groups: predators, specialists and omnivores. For nesting strata, we categorized species as: ground nesting, leaf litter nesting, arboreal nesting or mixed. The mixed category represented a catch all for species that nested in multiple strata. For both diet and nest categorizations, categorizations were based on reports from published studies (see Data S1). Queen-worker dimorphism was quantified as the per cent ratio of queen to worker measurements across all five morphological traits using the same calculation as (Ferguson-Gow et al., 2014). This resulted in five different QWD measurements and allowed us to identify specific QWD traits that may vary across species. Finally, a phylogenetic tree of the Florida ant assemblage was sourced from Booher et al. (2023) for phylogenetic-based analyses of traits.

2.2 | Spatial data

Geospatial data on Florida ant occurrences were obtained from Booher et al. (2023). In addition, we included arboreal and ground nesting species from the original dataset. This dataset was curated from digitized collection data as well as AntWeb specimen data. Climatic data in the form of mean annual temperature, mean annual precipitation and annual temperature range (representing seasonality) were extracted from Worldclim data (Fick & Hijmans, 2017). We assessed the environmental drivers of geographical trait patterns at a biogeographic scale using hexagonal bins at the same resolution (2000 km²) as Booher et al. (2023).

2.3 | Analysis

2.3.1 | Species-level traits

Prior to formal analyses, trait data were summarized at the species level. For colony size data we used the median value for species with multiple colony size estimates. Numerous sources did not distinguish counts including or excluding brood and sexuals, and as such we used the total number of all identified individuals within a colony. The average trait values of worker traits per species were used, including majors if the species was polymorphic. We did not differentiate different castes into size classes as not all polymorphic species had enough available images. All worker and queen traits were standardized for body size by dividing measurements by

Weber's length. When assessing colony size as a function of QWD, we averaged all five morphological QWD values per species resulting in an average QWD.

Our analyses utilized phylogenetic least squares (PGLS) regressions to correct for phylogenetic nonindependence as morphological traits and colony size have been shown to exhibit phylogenetic signals (Burchill & Moreau, 2016; Ferguson-Gow et al., 2014). If species were missing from the phylogenetic tree, then the most closely related sister taxa's phylogenetic position was used (the same substitutions from Booher et al. (2023) were used). Given the lack of full coverage in trait data as well as phylogenetic data, these PGLS regressions varied in sample size from 87 to 163 species (average $n=141$ species). Based on the questions of this study, 29 PGLS regressions were run (model outputs available in Data S1).

We transformed response variables to meet assumptions of residuals with log or square root operations. In some cases, response values were negative values and so transformations were done with an added constant (absolute value of the minimum value). We ran PGLS regressions with a Brownian motion and a Pagel's lambda correlation structure and chose the most plausible model based on Akaike's information criterion (AIC). Across all models the Pagel's lambda correlation structure model ranked better the Brownian motion model based on AIC. To interpret results on original scales and conduct post-hoc analyses we used the R package 'EMMEANS' (Lenth et al., 2018). Residuals were assessed using diagnostic plots and goodness-of-fit metrics (R^2) were calculated using the RR2 package in 'R' (Ives & Li, 2018). We specifically used the $rr2::R2.pred$, or the R^2 for prediction as it most directly quantifies the variation that is explained in the data from the model (Ives, 2019), but all versions of the coefficient are available in Data S1. All models included a single predictor except for the model assessing colony size as a function of QWD, where we included a covariate to account for the native and nonnative status of the species. All analyses were executed in the 'R' programming environment (Version 4.2.1). All graphics were made using the R package 'GGPLOT2' (Wickham, 2009).

2.4 | Spatial and climate modelling

Prior to analyses, we treated our geospatial data for common pitfalls when running biogeographical analyses. We first removed singleton species in the dataset. Because our spatial analyses relied on occurrence data, we filtered the dataset to only include unique species within a hexagonal bin. To prevent widespread species from over-contributing to trait patterns we first removed any bins containing less than five species. We then split the original data into native and nonnative datasets and subsampled both by randomly subsetting a percentage of hexbins that the species occurred in. The native dataset contained 113 species with QWD or colony size values and the nonnative dataset contained 49 species. The subset percentage was determined by the species' prevalence and was calculated as half the prevalence percentage of that species. For example, a species occurring in 90% of all hexbins would only retain a random sample of

45% of the hexbins it occurred in. This was done 1000 times for all species and the average trait values from these subsampled hexbins were used in statistical models where traits were assessed as a function of a climatic driver for both native and nonnative datasets.

Prior to analyses, a Moran's I test on the geospatial data showed evidence that spatial autocorrelation was present in the QWD and colony size data. To account for this, we used spatial generalized linear models from the R package 'SDMTMB' (Anderson et al., 2022). These models allow for the implementation of a spatial random field to approximate the spatial surface of the data through the creation of a triangular mesh object. To approximate this spatial field a predetermined number of knots, specific vertices in the random field, are determined. The approximation uses a Matérn covariance function to estimate unknown values of the surface from the predetermined number of knots. To select the appropriate number of knots we set the knots value to 75 and used the 'cut off search' option in the package to find the optimal number of knots. We used the coordinates from the centroid of the hexagonal bins for generating the random field. After fitting, models were checked for spatial autocorrelation again using the residuals with a Moran's I test.

The modelling framework involved developing four different models for QWD and eight different models for colony size for both native and nonnative data (24 models total). The four models for QWD included three models that used environmental predictors (MAT, ATR and MAP). The fourth model was an intercept-only model which served as a null model. The same model structures were implemented for colony size. For QWD, a gamma error distribution with a log link was utilized. For colony size, both Poisson and negative binomial error distributions were used hence the doubling of models. Models for each respective trait were ranked using AIC from the 'BBMLE' package (Bolker & R Development Core Team, 2020). This framework sets up the models up as competing hypotheses and ranks them based on model plausibility (Burnham & Anderson, 2002). We chose this approach because the multiple climatic drivers would encounter collinearity issues if introduced into the model together. While the best ranked model is considered the most plausible, the framework does not discount information derived from other competing models. We used a cutoff of a ΔAIC of 2 to determine whether models are commensurate in plausibility with one another. Because this cutoff is arbitrary but widespread throughout the literature, we also based our rankings using AIC weights, which is considered a measure of likelihood relative to other models being compared. To assess model quality, residual diagnostics were carried out using the 'DHARMA' package (Hartig & Hartig, 2017).

3 | RESULTS

3.1 | Data coverage

In total we collected trait data for 211 species (~80% of Florida's known species roster, species list from AntWeb.org). For natural history traits we collected species-level data on the presence/

absence of polymorphism (nearly 100% coverage, except *Solenopsis phoretica*), colony size (69% of species, 65 species without data), the presence/absence of polygyny (57.2% of species, 92 species without data), diet (93% coverage, 15 species without data) and nesting strata (97% coverage, 7 species without data). Coverage for the five QWD traits is as follows: 174 species for QWD of Weber's length (80% coverage), 172 for QWD of head length (79%), 173 for QWD of head width (79%), 170 for QWD of eye length (79%) and 167 for QWD of mandible lengths (77%).

3.2 | Colony size

PGLS analyses show no significant differences in average colony size between polygyne and monogyne species ($n=88$, $ns=62$, and $nns=26$; n represents number of species assessed, ns represents number of native species and nns represents number of nonnative species) but did yield significant differences between polymorphic and monomorphic species ($n=130$, $ns=95$ and $nns=35$). Monomorphic species had fewer individuals per colony (estimated mean: 140 ± 74.2 individuals) than polymorphic species (759 ± 558 individuals). Colony size as a response variable positively correlated

with average QWD ($n=114$, $ns=79$ and $nns=35$) where an increase for every unit of QWD yielded a slope value of 264 ± 148 individuals ($R^2=0.49$, Figure 1). For full model output see Data S1.

3.3 | Queen-worker dimorphism

Queen-worker dimorphisms metrics assessed as a function of natural history traits showed significant differences in QWD of Weber's length (QWD_{WL}) among dietary groups. Omnivores had larger QWD_{WL} compared to predators ($n=143$, $ns=95$ and $nns=49$) and specialists (marginal significance: p -value=0.05). Averages from the model indicate that omnivores had a QWD_{WL} of 1.21 and 1.49 times larger relative to predators and specialists respectively. No differences were observed for QWD of head width ($n=143$, $ns=95$, $nns=48$), head length ($n=142$, $ns=94$, $nns=48$), mandible length ($n=126$, $ns=82$, $nns=44$) and eye size ($n=139$, $ns=90$, $nns=49$).

No significant differences were observed for QWD across nesting sites except for marginal support (p -value=0.05) in QWD_{EL} where ground-, mixed- and leaf litter nesting species had larger QWD_{EL} compared to arboreal nesters. The strongest QWD_{EL} difference was between arboreal nesters and leaf litter nesting species.

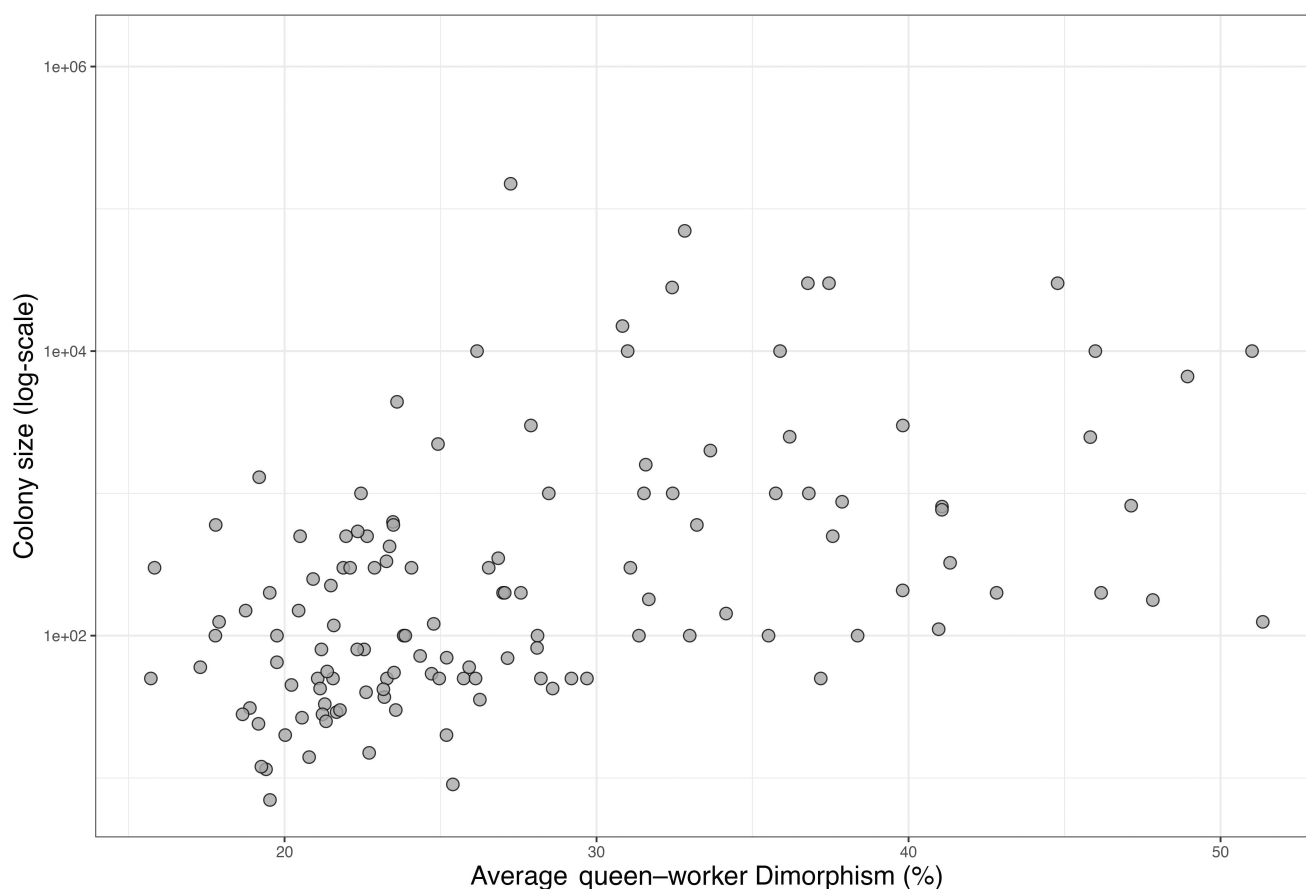


FIGURE 1 Plot showing colony size (log-transformed) on y-axis and average queen-worker dimorphism at the species level (percentage) along the x-axis.

Average QWD_{EL} values for leaf litter, mixed-nest species and ground nesting species were: 68.5%, 58.5% and 51.1% respectively relative to arboreal nesting species (26.8%).

3.4 | Native versus nonnative species

We observed significant differences between native and nonnative worker traits and marginal differences in queen size and QWD. In workers, eye lengths were smaller in native species (model estimates: 0.130 mm vs. 0.144 mm), while mandible lengths were larger (model estimates: 0.338 mm vs. 0.295 mm) in nonnative versus native species ($n=164$, $ns=110$ and $nns=54$ for all worker trait models). For queens, native species were larger than nonnative species (1.87 mm vs. 1.65 mm), but this effect was marginally significant. Finally, QWD of head width was larger in native species versus nonnative (model estimates: 24.7% vs. 17.5%) but this effect was also marginally significant (Figure 2, p -value=0.05).

3.5 | Climate effects on traits

AIC ranked the most plausible climatic driver from our native species spatial models as mean annual temperature (MAT) for both QWD and colony size (Table 2). QWD correlated significantly with increasing temperature and the same was observed for colony size. While MAT, annual temperature range (ATR) and mean annual precipitation (MAP)

TABLE 2 AIC rankings for spatial generalized linear models assessing queen-worker dimorphism (QWD) and colony size for both native and nonnative ant data.

Model	AIC	Δ AIC	Weight
Spatial models of native QWD: knots=77			
MAT	778.3	0	0.39
ATR	778.5	0.1	0.36
MAP	779.2	0.9	0.25
Null model	796.9	9.9	<0.1
Spatial models of native colony size: knots=69			
MAT NB	1287.1	0	0.73
ATR NB	1289.4	2.4	0.21
MAP NB	1291.1	5.0	<0.1
MAP Poisson	5965.2	4678.1	<0.1
ATR Poisson	6283.2	4996.1	<0.1
MAT Poisson	6323.7	5036.5	<0.1
Null model	30,131	28,843.9	<0.1
Spatial models of nonnative colony size: knots=65			
MAT NB	1099.3	0	0.54
ATR NB	1100.7	1.4	0.27
MAP NB	1101.4	2.0	0.19
MAT Poisson	3717	2444.2	<0.01
ATR Poisson	2617.7	2617.7	<0.01
MAP Poisson	4205.7	3106.4	<0.01
Null model	16,554.8	15,455.1	<0.01

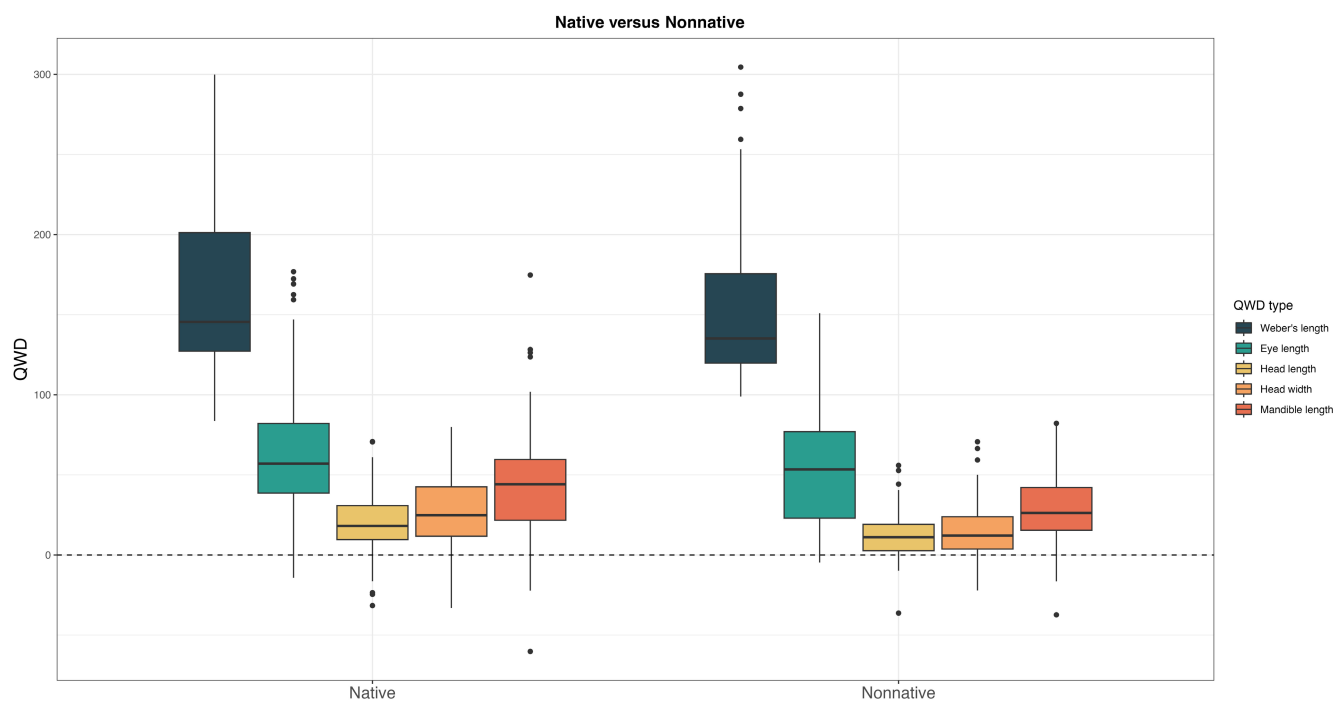


FIGURE 2 Boxplots showing queen-worker dimorphism (QWD) between native and nonnative ant species. Colours represent specific morphological QWDs. Dotted line represents no morphological difference (0% QWD).

models all ranked within a ΔAIC of 2, we chose the MAT model as the most plausible model as the ATR and MAP models had estimates with 95% confidence intervals overlapping with zero adding uncertainty to the directionality of the effect size (Data S1). For nonnatives, AIC ranked the intercept-only model as the most plausible model assessing QWD. Because of this, models assessing nonnative QWD are not discussed further. The most plausible environmental driver of nonnative colony size was MAT where colony size decreased with higher MAT. The model was ranked within a ΔAIC of 2 of both ATR and MAP model (Table 2). Both models' 95% confidence intervals overlapped with zero. This combined with the relatively low AIC weight (Table 2) provided justification to prefer the MAT model.

4 | DISCUSSION

Our analyses show evidence of significant trait associations across a regional assemblage of ants spanning multiple subfamilies that are in-line with patterns observed by studies from other regions (Ferguson-Gow et al., 2014; Fjerdingstad & Crozier, 2006). Furthermore, our results yield evidence of environmental correlates of colony-level traits, specifically QWD and colony size that support the general hypothesis that traits of colonies and constituent workers and queens (thus not just individual ants) share common physiological, morphological, behavioural, and life history characteristics in response to specific environmental conditions affecting colonies. Given strong signals after accounting for evolutionary relatedness these results suggest that our data yield probabilistic support to many of the specific hypotheses examined. Furthermore, the analytical approach we present provides a starting point towards a more holistic hypothesis-testing framework that incorporates queen and worker traits, colony-level traits and species natural history information (Figure 5). Ultimately, results strongly suggest that field collecting and analyses should, whenever possible, incorporate colony size and queen size data to advance our understanding of the ecological traits of social insects.

4.1 | Colony size

Results support hypothesis 1 where QWD and colony size are positively correlated (Ferguson-Gow et al., 2014) and agrees with previous studies observing larger colonies exhibiting a more pronounced division of labour through worker polymorphism (Anderson & McShea, 2001; Molet, 2021; Wills et al., 2018). In our study, colony size was significantly associated with both worker polymorphism and increasing QWD. Polymorphic species have colony sizes on average of ~5.5 times larger relative to monomorphic species. Furthermore, for every unit increase in the ratio of morphological difference of queen to worker in our data, there is an increase of approximately ~264 individuals. These predictions provide a promising starting place for making further general inferences suggesting a 'common' rule. However, more species across the ant clades and geographies need to be examined.

The trend between QWD and colony size across an entire regional assemblage after accounting for phylogenetic relatedness is remarkable. Ecologically, larger colony sizes can facilitate effective resource collection, buffer against difficult conditions (e.g. local drought) and provide competitive advantages (Hölldobler & Wilson, 1990; Kwapich & Tschinkel, 2013; Palmer, 2004). This competitive advantage is likely amplified with polymorphism as it facilitates better size matching between ant species and resources (Anderson & McShea, 2001). Queen-worker dimorphism could be an effective metric in inferring or possibly predicting colony size across species. However, QWD should also be considered in the context of the colony founding stage, an ecological trait that we did not assess. Low QWD is often associated with nonclaustral founding, a process where a queen founds a colony but must also forage to feed its workers versus claustral founding where the queen does not go out to forage and instead rears the first generation of workers from energetic reserves (Helms IV, 2018; Hölldobler & Wilson, 1990; Peeters & Ito, 2015). We note that nonclaustral founding is, as far as we are aware, a much less common founding strategy. Therefore, QWD is a trait that could potentially be a proxy for both colony size and life history strategies.

It is worth mentioning that QWD is not purely a product of ecology and evolutionary selection. Worker and queen traits such as their size is also a product of the developmental process of both caste development and differentiation (Trible & Kronauer, 2017). While the generality of existing theoretical models of the underpinning of how ant castes develop remains in discussion, we know for example that both queen and worker size are regulated by different hormones, caste ratios and nutrition throughout their development (Abouheif, 2021). In addition, size of both queens and workers themselves can constrain colony size as species with larger workers tend to not have larger colonies. As such, it is important to consider these developmental processes and limitations, if possible, when evaluating the ecological context of QWD in future work on this subject.

We found partial support for hypothesis 2 where we expected polygyne species to have larger colonies than monogyne species in the form of a marginally significant effect size. The lack of signal may be due to an underlying environmental effect that is not accounted for as polygyny has been predicted to provide ants with an advantage in harsher conditions where dispersal and nest founding is likely more unsuccessful (Keller, 1995). However, testing of this hypothesis is limited given our data are confined to a single region. Alternatively, the lower sample size of this analysis also highlights the paucity in data for this important trait for ants in general. Despite these limitations, to our knowledge, the data analysed here represent the most complete accounting of colony-level traits for a region.

4.2 | Queen-worker dimorphism

Generally, we found partial support for hypothesis 3 where we predict QWD to be associated with the natural history traits of ant species. While our results show QWD exhibited significant differences

across diet for body size, we find lack of support across other traits like nesting niches. Omnivorous species had larger queen to worker Weber's length (QWD_{WL}) compared to predators and specialists. Differences in Weber's length, often used as proxies of body size (Kaspari & Weiser, 1999; Tschinkel et al., 2003), offer support for observations that ecologically specialized ants, such as predators from the Poneroid clade, exhibit low QWD (Peeters, 1997). Note, that some subfamilies may contain overrepresentation in different dimorphisms and allometries as worker dimorphism and polymorphism is likely overrepresented in the Myrmicines while monophasic allometry is likely overrepresented in the Formicines. Additionally, predatory species often employ a solitary foraging strategy that does not support sufficient energetic intake to support large colonies (Beckers et al., 1989) and thus agrees with the colony size by average QWD trend. Differences in QWD_{WL} can be linked to queen founding strategies of species with different dietary preferences where queens of predatory species with low QWD are often nonclaustral founders that need to forage (Peeters, 1997). Unfortunately while founding strategies have yet to be comprehensively documented and applied in trait-based approaches, recent work has pointed towards the importance of them (Gibb et al., 2022).

Lack of differences in nesting niches may be because QWD accounts for both worker and queen traits and while worker traits correlate well with nesting niches (Sosiak & Barden, 2020), the same may not be true for queen traits. Because the nest buffers the queen from abiotic and biotic threats (Tschinkel, 2015, 2021), queen traits are likely under ecological selective pressures primarily during the founding stages of a colony when they lack the protection. As such, QWD may not be an ideal indicator for nesting niches, typically assessed for mature, in ants.

4.3 | Nonnative species

With only differences observed in worker traits (mandible and eye lengths), our results yield evidence for lack of support of hypothesis 4 in the context of colony traits. Workers of nonnative species on average had longer mandibles and larger eyes relative to natives. Larger eyes are associated with visual acuity and an arboreal ecology (Sosiak & Barden, 2020) while longer mandibles in workers are tied with a predatory diet (Weiser & Kaspari, 2006). These differences are opposite of what would be expected for nonnative ants if the hypothesis were supported. Nonnatives and successful invasive ants are usually generalist omnivores (Fournier et al., 2019; Holway et al., 2002). While no significant differences were found between native and nonnative worker body sizes, McGlynn (1999) showed that nonnative species were smaller than native ones when considered at a larger geographic scale and proposed several hypotheses relating to colony size, release from intraspecific competition, and climate or life history strategies associated with nonnative ants. The size relationship between nonnative and native species may in part depend on the geographic location, spatial scale of consideration, and associated abiotic and biotic conditions.

Most surprising was the parity in QWD traits between native and nonnative species while worker traits showed differences. Because QWD in this assemblage tracks colony size and diet, one would expect distinct differences between native and nonnative species in an assemblage where nonnative species have proven to be persistent and widespread (King & Porter, 2007; Ohyama et al., 2020; Wetterer, 2019; Wetterer et al., 2018). Based on literature and results from this study, a successful nonnative species would have high QWD that is positively correlated with larger colony size and possibly polymorphic division of labour, all of which are traits tied to ecological success in invasive ants like *Solenopsis invicta*, the red imported fire ant (Tschinkel, 2013). Yet with no differences in QWD metrics, QWD may have very little impact or may only be different between highly invasive and native species. Given the steady accumulation of nonnative ants in Florida (Booher et al., 2023; Deyrup et al., 2000; Ohyama et al., 2020), research focused on nonnatives and their entire trait profile is warranted.

4.4 | Geospatial attributes of colony traits

We observed partial support for hypothesis 5, which delves into the environmental drivers of colony-level traits for native or nonnatives. For natives, our hypothesis was unsupported as QWD and colony size increased in warmer areas in the lower latitudes of peninsular Florida (Figure 3). This could be because advantages associated with larger body sizes (in this case colony size) may not apply to eusocial organisms like ants as their sociality allows them to evolve and develop different behavioural traits that sidestep the need for larger sizes. For example, smaller colonies can exhibit stronger foraging site fidelity and navigation that ultimately facilitates efficient foraging (Beckers et al., 1989). Furthermore colony size may not necessarily translate to foraging efficiency (such as foraging distance) (Bengston & Dornhaus, 2013).

However, for nonnatives, larger colony sizes were associated with colder areas (Figure 4). This could be because they are better able to adapt to harsher conditions. Based on results, species with larger colonies tend to be omnivorous which would help facilitate ecological success. However, this pattern is also likely a product of ant invasion histories where high levels of urban sprawl may influence the distribution of nonnative ants to a greater degree than temperature. Speculating on the biological mechanisms that could result in this pattern is difficult and beyond the scope of this paper. However, nonnative and invasive species may operate outside general ecological 'rules' with alternative mechanisms (e.g. anthropogenic activity centres) playing a significant role in their distributions (Deyrup et al., 2000).

4.5 | Colony traits are ecological traits for eusocial insects

Understanding ecological traits across colony components is fundamental for moving our understanding of trait ecology of

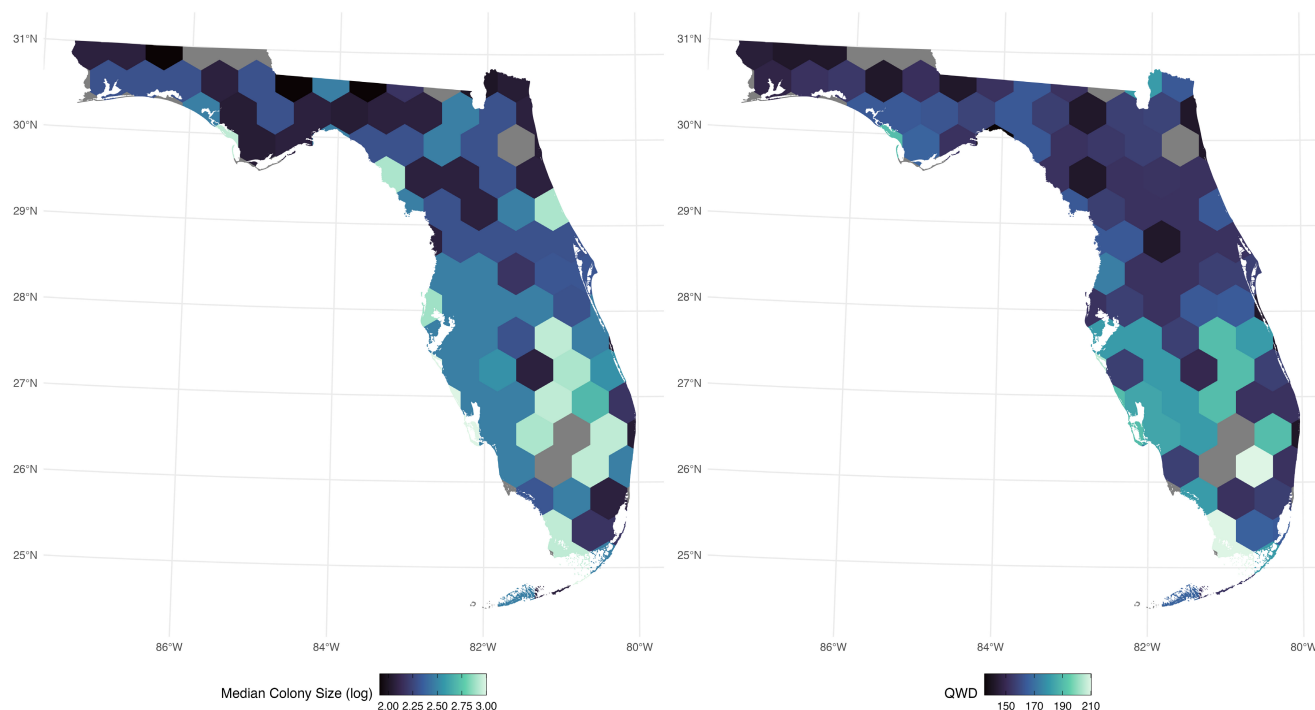


FIGURE 3 Geographic distribution of native ant QWD and colony size (log-transformed). Data shown are subsampled data and represent averaged trait values across all 1000 iterations of subsampling. Hexagonal bins represent areas of approximately 2000 km².

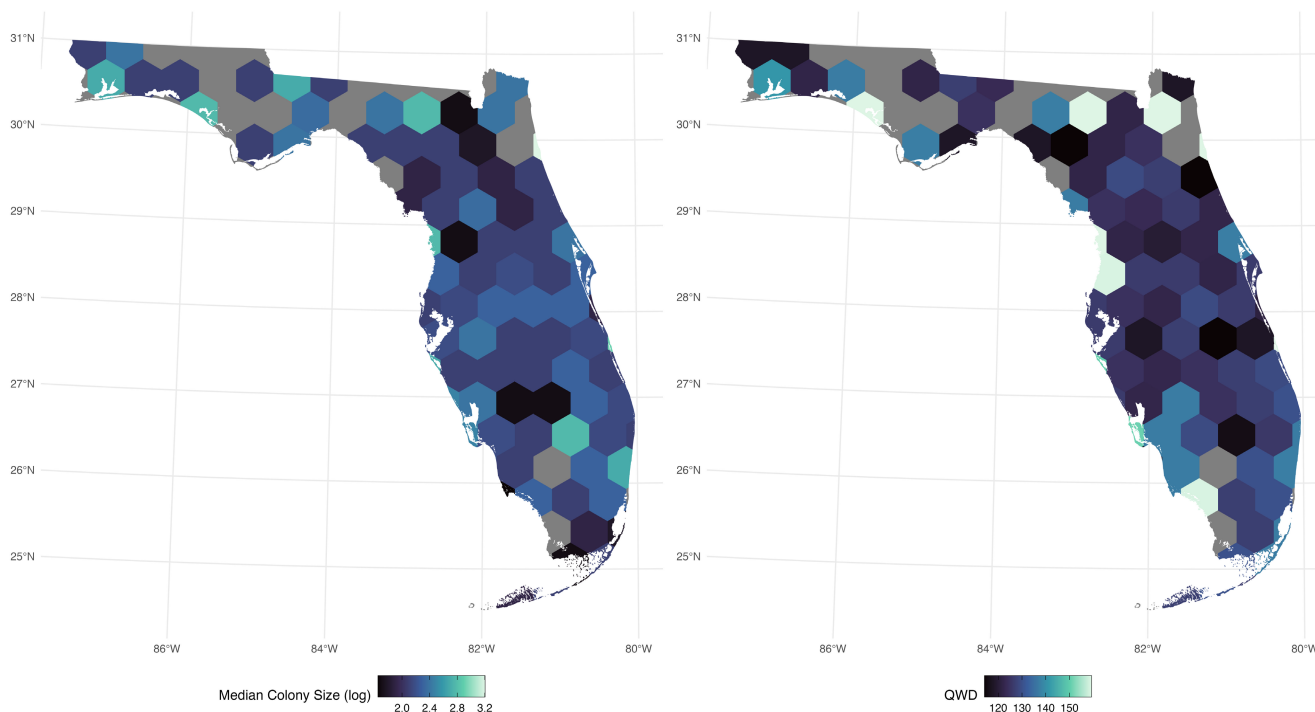


FIGURE 4 Geographic distribution of nonnative ant QWD and colony size (log-transformed). Data shown are subsampled data and represent averaged trait values across all 1000 iterations of subsampling. Hexagonal bins represent areas of approximately 2000 km².

eusocial insects forward. With our results, we again emphasize the importance of adding measurements of colony and queen size to better understand ecological traits of social insects. While not considered here, we note that important insights may also be gained from inclusion of larvae and pupae size as these,

in combination with queen traits, may add further insights into the interplay of developmental limitations affecting ecological traits (Tribble & Kronauer, 2017). While worker trait ecology is well studied there remains a research gap concerning the link between worker and colony-scale traits. These gaps are slowly

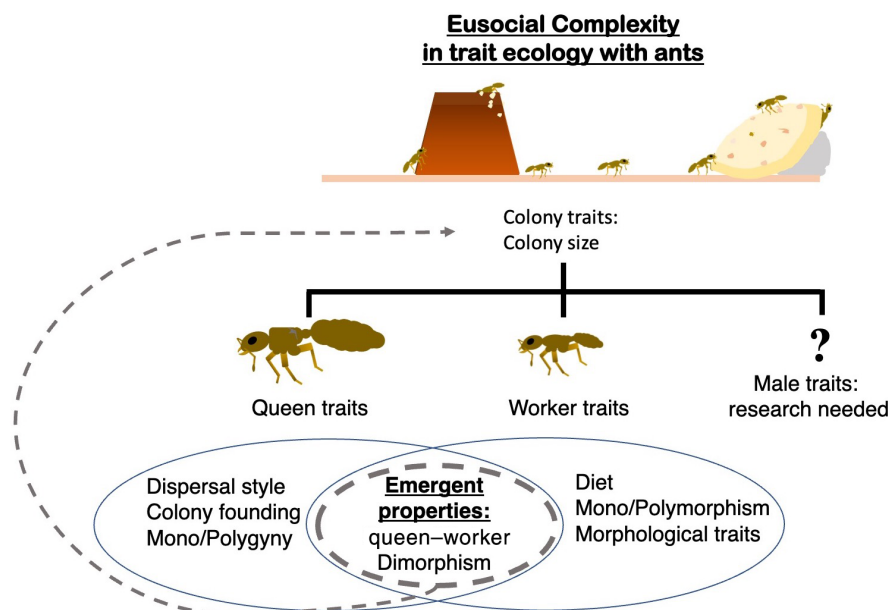


FIGURE 5 The beginnings of a proposed conceptual model that aims to develop a framework whereby eusocial complexity is explained in the context of trait ecology.

being filled as these harder-to-collect traits have become more available. The field of sociometry (Tschinkel, 1991, 2010), provides important guideposts for our analyses here, as the relationships among the traits of workers, queens and the colony as a whole are necessary to quantify the actual traits of social insects. With, sociometry Tschinkel (2010) describes how quantifying relationships among whole colony attributes can facilitate a more complete understanding of ant species. This approach has been applied across a variety of subtropical ant species in Florida, USA (Tschinkel, 1987, 1993, 1998, 2011). Although sociometry was developed to deepen our understanding of ant species as colonial organisms, here we have applied sociometric data across ant assemblages to examine queen and colony ecological traits and their geographic distribution. In doing so we hope to develop the beginnings of a framework for studying trait patterns, across a taxonomically diverse assemblage of eusocial insects, that can be broadly applied to other animal societies. This framework extends our understanding of the ecological trade-offs that impact different components of a colony between species and across space by leveraging established relationships between and among traits (Figure 5).

By curating data from queens, natural history, workers and life history traits we constructed a comprehensive trait dataset for one of the best studied ant assemblages in the world. With this dataset, our analyses have provided remarkable evidence of geographic and taxonomic patterns that can be used to link ecological components of eusocial animal systems together under one conceptual framework. While trait ecology continues to struggle with the inclusion of social or group-living organisms, here we show that with well-studied assemblages it is possible to begin the development of a conceptual framework to assess such traits in eusocial fauna. Given how widespread and important social and eusocial organisms are, moving forward, we would suggest that

a requirement is the need to continue the collection and exploration of eusocial organismal traits using a sociometric approach (recent example see Brassard et al., 2021). This requires a bottom-up data-gathering approach of cataloguing colony-level traits that are difficult to measure or observe but vital to further our understanding.

AUTHOR CONTRIBUTIONS

Leo Ohyama conceived the idea, designed the methodology, collected the data, analysed the data and led the writing of the manuscript. Leo Ohyama, Doug Booher and Josh King developed the ideas. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors state no conflict of interest.

DATA AVAILABILITY STATEMENT

All code and data as separate files available on Github (https://github.com/leoohyama/Sociometry_trait_ecology) and Zenodo (<https://zenodo.org/record/7886982#.ZF4axXMKww>) while supplementary materials will be made available online.

ORCID

Leo Ohyama  <https://orcid.org/0000-0002-1874-2972>

Joshua R. King  <https://orcid.org/0000-0003-4293-914X>

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Data S1: Datasets used in analyses including references.

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