Tropical arboreal ants form dominance hierarchies over nesting resources

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Interspecific dominance hierarchies have been widely reported across animal systems. High-ranking species are expected to monopolize more resources than low-ranking species via resource monopolization. In some ant species, dominance hierarchies have been used to explain species coexistence and community structure. However, it remains unclear whether or in what contexts dominance hierarchies occur in tropical ant communities. This study seeks to examine whether arboreal twig-nesting ants competing for nesting resources in a Mexican coffee agricultural ecosystem are arranged in a linear dominance hierarchy. We described the dominance relationships among 10 species of ants and measured the uncertainty and steepness of the inferred dominance hierarchy. We also assessed the orderliness of the hierarchy by considering species interactions at the network level. Based on the randomized Elo-rating method, we found that the twig-nesting ant species *Myrmelachista mexicana* ranked highest in the ranking, while *Pseudomyrmex ejectus* was ranked as the lowest in the hierarchy. Our results show that the hierarchy was intermediate in its steepness, suggesting that the probability of higher ranked species winning contests against lower ranked species was fairly high. Motif analysis and significant excess of triads further revealed that the species networks were largely transitive. This study highlights that some tropical arboreal ant communities organize into dominance hierarchies.

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Abstract

Interspecific dominance hierarchies have been widely reported across animal systems. High-ranking species are expected to monopolize more resources than low-ranking species via resource monopolization. In some ant species, dominance hierarchies have been used to explain species coexistence and community structure. However, it remains unclear whether or in what contexts dominance hierarchies occur in tropical ant communities. This study seeks to examine whether arboreal twig-nesting ants competing for nesting resources in a Mexican coffee agricultural ecosystem are arranged in a linear dominance hierarchy. We described the dominance relationships among 10 species of ants and measured the uncertainty and steepness of the inferred dominance hierarchy. We also assessed the orderliness of the hierarchy by considering species interactions at the network level. Based on the randomized Elo-rating method, we found that the twig-nesting ant species *Myrmelachista mexicana* ranked highest in the ranking, while *Pseudomyrmex ejectus* was ranked as the lowest in the hierarchy. Our results show that the hierarchy was intermediate in its steepness, suggesting that the probability of higher ranked species winning contests against lower ranked species was fairly high. Motif analysis and significant excess of triads further revealed that the species networks were largely transitive. This study highlights that some tropical arboreal ant communities organize into dominance hierarchies.

Key Words: dominance hierarchy, arboreal ants, interspecific competition, networks

Introduction

A long-standing goal in ecology has been to determine the underlying mechanisms that give rise to species coexistence in local communities, especially in assemblages with multiple competing species (MacArthur 1958, Hutchinson 1959). Numerous mechanisms have been proposed for maintaining species coexistence (Wright 2002, Silvertown 2004). Interspecific competitive trade-offs, whereby the dominance of a particular species in one environment is offset by the dominance of another species in a different environment, can lead to spatial segregation between species (Tilman 1994, Levine et al. 2004). These interspecific interactions are thought to lead to the long-term stable coexistence of ecologically similar species (Levins 1979, Holt et al. 1994, Chesson 2000, Bever 2003, Rudolf and Antonovics 2005), and may also be characterized by dominance hierarchies. Dominance hierarchies have been observed in a wide range of taxa, from vertebrates to invertebrates (Chase and Seitz 2011). Species can be ranked into a hierarchy based on their behavioral dominance during interspecific competitive encounters for resources. (Davidson 1998). For example, dominance ranking was positively associated with body mass in bird species, with heavier species more likely to monopolize food sources in contrast to lighter species(Francis et al. 2018). However, dominance rankings can be determined by many other factors including age, sex, aggressiveness, and previous encounters(Haley et al. 1994, Zucker and Murray 1996). Furthermore, interspecific dominance hierarchies have been used to understand patterns of local species coexistence in ecological communities (Morse 1974, Schoener 1983).

In ant communities, dominance hierarchies have been used to examine interspecific tradeoffs that may explain species coexistence patterns (Stuble et al. 2013). These trade-offs include the discovery-dominance trade-off, the discovery-thermal tolerance tradeoff, and the discovery-colonization trade-offs (Cerdá et al. 1998a, Stanton et al. 2002a, Lebrun and Feener 2007, Stuble et al. 2013). In addition to testing interspecific trade-offs, dominance hierarchies have been used to understand the role of dominant species in structuring local communities and species composition, such as partitioning dominant and subdominant species within guilds (Baccaro et al. 2010, Arnan et al. 2012). Dominant ant species can play an important role in the structuring of local communities. For example, *Formica* species dominating a boreal ecosystem divert resources away from subdominant competitors (Savolainen and Vepsäläinen 1988). In Mediterranean ecosystems, subdominant species forage at nearly lethal environmental conditions while dominant species reduce their own mortality risk by foraging at more favorable temperatures (Cerdá et al. 1998b). In tropical ecosystems, competing arboreal ants can be structured into a dominance hierarchy with higher ranked ant species having greater access to nesting sites and extrafloral nectaries (Blüthgen et al. 2004). However, levels of uncertainty associated with outcomes of interspecific interactions between ants are often not quantified (Stuble et al. 2017). Furthermore, its remains unclear how arboreal ants or tropical ants are structured at the community level, such as when interspecific interactions are viewed as a network.

In this study, we examine dominance hierarchies for a community of arboreal twig-nesting ants in a coffee agroecosystem. Both arboreal and ground-dwelling twig-nesting ants in coffee agroecosystems are nest-site limited (Philpott and Foster 2005)(Philpott and Foster 2005a) in terms of number (Philpott and Foster 2005), diversity (Armbrecht et al. 2004, Gillette et al. 2015), and size (Jiménez-Soto and Philpott 2015) of nesting resources. For twig-nesting ants, nest takeovers are common, and therefore dominance in this system is defined as competition for nest sites (Brian 1952), and in one case dominance over nest sites has been experimentally demonstrated (Palmer et al. 2000).This present study aims to describe dominance hierarchies for twig-nesting ants due to competition for nest resources in a Mexican coffee agricultural ecosystems. We adopt statistical methods to infer a dominance hierarchy from competitive interactions over nest resources and estimate uncertainty and steepness of that dominance (Shizuka and McDonald 2012, Pinter-Wollman et al. 2014, Sánchez-Tójar et al. 2018). Furthermore, we estimate the orderliness of the hierarchy within the community. Specifically, we tested the hypothesis that tropical, arboreal twig-nesting ants form a clear, dominance hierarchy for nesting sites.

Methods

Study Site and System

We conducted fieldwork at Finca Irlanda (15°20' N, 90°20' W), a 300 ha, privately owned shaded coffee farm in the Soconusco region of Chiapas, Mexico with ~250 shade trees per ha. The farm is located between 900-1100 m a.s.l (Perfecto et al. 2014). Between 2006-2011, the field site received an average rainfall of 5726 mm per year with most rain falling during the rainy season between May and October. The farm hosts ~50 species of shade trees that provide between 30-75% canopy cover to the coffee bushes below. The farm has two distinct management areas -- one that is a traditional polyculture and the other that is a mixture of commercial polyculture coffee and shade monoculture coffee according to the classification system of (Moguel and Toledo 1999).

The arboreal twig-nesting ant community in coffee agroecosystems in Mexico is diverse. There are ~40 species of arboreal twig-nesting ants at the study site including *Brachymyrmex* (3 species), *Camponotus* (8), *Cephalotes* (2), *Crematogaster* (5), *Dolichoderus* (2), *Myrmelachista*

(3), *Nesomyrmex* (2), *Procryptocerus* (1), *Pseudomyrmex* (11), and *Technomyrmex* (1) (Philpott and Foster 2005, Livingston and Philpott 2010).

'Real-estate' experiments

We examined the relative competitive ability of twig-nesting ants by constructing dominance hierarchies based on 'real estate' experiments conducted in the lab. We collected ants during systematic field surveys in 2007, 2009, 2011, and 2012 in the two different areas of the farm, and then used ants in lab experiments.

Once in the lab, we selected two twigs, each hosting a different species, removed all ants (i.e. all workers, alates and brood) from the twigs and placed them into sealed plastic tubs with one empty artificial nest (15 cm high by 11 cm diameter cylindrical tubs). The artificial nest, or 'real estate', consisted of a bamboo twig, 120 mm long with a 2-4 mm opening. All trials started between 12-2 pm and after 24 hours, we opened the bamboo twigs to note which species had colonized the twig. All ants collected and brought to the lab were used in 'real estate' trials within two days of collection, or were otherwise discarded.

We conducted trials between pairs of the ten most common ant species encountered during surveys: *Camponotus abditus*, *Camponotus* (*Colobopsis*) sp. 1, *Myrmelachista mexicana*, *Nesomyrmex echinatinodis*, *Procryptocerus scabriusculus, Pseudomyrmex ejectus*, *Pseudomyrmex elongatus*, *Pseudomyrmex filiformis*, *Pseudomyrmex* PSW-53, and *Pseudomyrmex simplex*. We selected a priori to use the 10 most common species and did not run trials between other ant species. We replicated trials for each species pair on average 5.73 times (range: 1-18 trials per pairs of species); four species pairs were replicated once, nine species pairs were replicated twice, and 31 species pairs were replicated three or more times. Only one species pair (*M. mexicana* and *P. filiformis*) was not tested. We conducted 42 trials in 2007, 105 trials in 2009, 82 trials in 2011, and 30 trials in 2012 for a total of 259 trials (Supplementary Materials).

Dominance hierarchy

We used the trial outcomes to infer the dominance hierarchy ad estimate the level of uncertainty and steepness. All simulations were conducted in R version 3.3.3 (R Core Development Team 2017). We used the R package "aniDom" version 0.1.3 to infer dominance hierarchies using the randomized Elo-rating method (Farine and Sánchez-Tójar 2017, Sánchez-Tójar et al. 2018). To analyze competitive interactions we used the R package "compete" version 0.1 and graphics were completed in the "igraphs" package version 1.2.4.1(Csardi and Nepusz 2006, Curley 2016).

We subsampled the observed data to determine whether the population had been adequately sampled to infer reliable dominance hierarchies. The subsampling procedure consists of estimating the randomized Elo-rating repeatability values as more data is added to determine if the repeatability values remain stable or decline. Thus, the repeatability values provide insights into the steepness of the hierarchy(Sánchez-Tójar et al. 2018).

Additionally, we also calculated the ratio of interactions to species to determine sampling effort. An average sampling effort ranging from 10-20 interactions is sufficient to infer hierarchies in empirical networks (Sánchez-Tójar et al. 2018). We estimated the dominance hierarchy using the randomized Elo-rating method. The matrix of interactions was converted to a sequence of interactions 1000 times such that different species individual Elo-ratings were calculated each time to obtain mean rankings. We estimated uncertainty in the hierarchy by splitting our dataset into two halves and estimated whether the hierarchy in one half of the matrix correlated with the hierarchy of the other half of the matrix (Sánchez-Tójar et al. 2018).

In addition to examining the role of ant species attributes and levels of uncertainty in dominance hierarchies, we examined the formation of dominance hierarchies using motif analysis to identify network structures composed of transitive and cyclical triads (Faust 2007). Motif analysis is commonly used in social network analysis to detect emergent properties of the network structure by comparing the relative frequencies of motifs in the observed network to the expected value for the null hypothesis of a random network (Holland and Leinhardt 1972, Faust 2007). We carried out motif analysis with customized randomization procedures (McDonald and Shizuka 2013) to compare the structure of our network model against random network graphs. Species interaction data were represented as a network plot of the dominance interactions between the 10 species (Fig. 1). The nodes in the network represent ant species and the one-way directional arrows of the edges represent dominant-subordinate relationships. In the random networks, we maintained the same number of nodes and edges as in the observed network, but the directionality and placement of edges were generated randomly. Using the adjacency matrix, we calculated the triad census (Shizuka and McDonald 2012, McDonald and Shizuka 2013). The triad census allows us to examine directed species interactions (Pinter-Wollman et al. 2014). We used the seven possible triad configurations fully composed of three nodes that either have asymmetric or mutual edges (Holland and Leinhardt 1972).

Results

'Real estate' experiments.

Across the vast majority of the trials, there was a clear winner of the 'real estate' battle after 24 hours, meaning that one of the two species had occupied the artificial nest. From examining the wins and losses, a clear hierarchy emerged, with some species winning the vast majority of trials in which they were involved, and other species winning few trials. The ranking shows that the twig-nesting species *Myrmelachista mexicana* is the highest ranked species, while *Pseudomyrmex ejectus* is the lowest ranked species in the hierarchy (Table 1). The one trial that did not result in a winner was a trial involving *P. elongatus* and *P. ejectus*.

Dyadic interactions: Estimating Dominance Hierarchy Uncertainty

The total number of interactions among the 10 species was 258. The ratio of interactions to species (25.8) shows an adequate sampling effort beyond the 10-20 recommended range (Sánchez-Tójar et al. 2018). Using the randomized Elo-rating method, we found that the hierarchy was intermediate in steepness showing that rank in the hierarchy largely predicts the probability of winning an interaction (Fig 1). The Elo-rating repeatability was 0.578 which also indicates an intermediate level of uncertainty. We further estimated the uncertainty in the hierarchy by splitting the database into two, and estimating whether hierarchy from one half resembles the hierarchy estimated from the other half. We find that the degree of uncertainty/steepness in the hierarchy is intermediate (mean=0.43, 2.5 % and 97.5% quantile = (-0.12, 0.85)).

Triad census analysis.

The triad census analysis of the triad distribution showed that the observed network has a significant excess of transitive triads followed by a significant deficit of cyclical triads

(Ttri=0.66, p-value=0.002). Triad types that are positive (i.e. non-overlapping at 0) occurred in excess in the observed network, while triad types that are negative showed a deficit in the observed network as compared to the random null network (Fig. 2).

The remaining five triads in the network did not show any significant differences in the mean triad percentage rates between the observed and expected network. While the data showed a clear excess of transitive triangles (34.55 %) and deficit for cyclical triangles (3.6%), the distribution for pass-along triads shows a less typical pattern with the 95% confidence intervals crossing the zero line but the mean percentage still showing a deficit.

Discussion

In this study, we used a novel set of statistical approaches to determine that tropical twig-nesting ants competing for nesting resources are arranged in a linear dominance hierarchy. Although many studies have documented ant dominance hierarchies, it is important to note that ranking methods vary considerably among studies (Stuble et al. 2013). Traditionally, field studies have quantified dominance relationships on the basis of proportion of contests won. Other studies have use more sophisticated methods to account for competitive reversals (Vries 1998) or have updated rankings based on relative wins and losses during contests (Colley 2002). In this study, we used the randomized Elo-rating by calculating the mean of species Elo-ratings (Sánchez-Tójar et al. 2018). With this method, we find that the probability of a higher ranked species winning a contest against a lower ranked species is relatively high, which corroborates our finding that the hierarchy has intermediate steepness. Moving beyond simple pair-wise interactions, we used motif analysis of the network to infer a significant excess of transitive interactions. Transitive interactions were significantly over-represented in the network. Thus the combination of techniques allowed us to determine that the dominance hierarchy in this community is intermediate in steepness and transitive.

Dominance hierarchies over food resources have been commonly documented in ant communities in a variety of ecosystems, but may vary depending on environmental conditions or the amount of food resource provided. For instance, in Mediterranean ecosystems, dominant and subordinate ants are partitioned on the basis of their life-history traits (Arnan et al. 2012). Dominant ant species had more abundant colonies and displayed increased defense for resources in contrast to subordinate ant species. Meanwhile, subordinate ants exemplified greater tolerance to higher temperatures (Cros et al. 1997, Cerdá et al. 1998a). In addition, outcomes of interspecific interactions within the dominance hierarchy are contingent on environmental conditions (Arnan et al. 2012). In a temperate forest ecosystem of North Carolina, dominance was context dependent (Stuble et al. 2017). Rankings on the basis of food bait monopolization revealed that dominance correlated positively with relative abundance since the most abundant species were ranked higher in the dominance hierarchy. In contrast, rankings based on aggressive encounters did not correlate with abundance. In some habitats, dominance patterns are largely determined by the time of day that foraging occurs (Bestelmeyer 2000). In the North Carolina system, the most abundant ant species, *Aphaenogaster rudis*, was most active during the morning hours, whereas the cold-tolerant ant species, *Prenolepis imparis*, was dominant during the night hours (Stuble et al. 2017). Species rankings can also strongly depend on the size of food resources provided in trials. In an assemblage of woodland ants, smaller-sized ants were more efficient at acquiring and transporting fixed resources and larger-sized solitary ants excelled at retrieving smaller food that were mobile during competitive interactions (LeBrun 2005). However, the introduction of phorid parasitoids in this system reduced the transitive hierarchy facilitating the coexistence of subdominant ants (LeBrun 2005, LeBrun and Feener 2007). In our study on competition for nesting sites in the lab, we were able to use fixed resources and to a certain degree control variation in colony size.

Although the twig-nesting ant community that we studied here in lab experiments showed a strong dominance hierarchy, there were some factors that could not be explicitly considered. Species with larger colony sizes might have a competitive advantage over other species. For instance, large colony sizes of invasive Argentine ants are indicative of strong competitive abilities relative to native species (Holway 1999). However, smaller ant colonies can sometimes overtake larger colonies depending on competitive traits, such as chemical defenses in the example of African Acacia ants (Palmer 2004). Although there might be some colony to colony variation in the number of individuals used in each trial (unpublished data), the focus of our study did not involve ant colony size variation. Preferences for nest entrance sizes is another important consideration that can determine competitive outcomes (Powell et al. 2011, Jiménez-Soto and Philpott 2015). While it is certainly the case that ant species prefer different nest entrance sizes, the distribution of natural nest sizes for most of our species (7 out of 10) are statistically indistinguishable. One notable exception is the arboreal ant *P. scabriusculus* which tends to prefer slightly larger nest entrances (in the field) than we provided in the real estate experiments (Livingston and Philpott 2010). However, we have found that *P. scabriusculus* nests in twigs as small as 2-3 mm in diameter.

Dominance hierarchies are often highly context-dependent and species ranking may vary across geographical regions or disturbance regimes (Palmer 2004). Previous research involving ant competition for variable resources in temperate ecosystems showed that intransitive competitive interactions at local spatial scales mediates ant coexistence (Sanders and Gordon

2003). Microclimatic factors also disrupt dominance hierarchies. For instance, environmental variation in coffee systems is likely to influence dominance hierarchies (Philpott and Foster 2005, Perfecto and Vandermeer 2002, Perfecto and Vandermeer 2011)(Philpott and Foster 2005, Perfecto and Vandermeer 2011). Occurrence of fire can disrupt dominance hierarchies in specialist ants in *Acacia* trees resulting in increased abundance of subordinate ants (Sensenig et al. 2017). Top down processes such as predation and parasitism likely mediate twig-nesting ant competition in natural communities (Philpott et al. 2004, Feener et al. 2008, Hsieh and Perfecto 2012)(Philpott et al. 2004, Feener et al. 2008a, Hsieh and Perfecto 2012). In addition, competition and disturbance from ground- and arboreal carton-nesting ants may influence the colonization and community composition of arboreal twig-nesting ants (Philpott 2010, Ennis and Philpott 2018). Therefore, more comparative research is needed to examine how variable field conditions may affect the hierarchy and ultimately the distribution and relative abundance of different arboreal, twig-nesting ant species.

In addition to dominance hierarchies, there are other factors that can drive the distribution and co-existence patterns of arboreal ant communities (Yamaguchi 1992, Palmer et al. 2000)(Yamaguchi 1992, Palmer et al. 2000). For instance, variation in life-history trade-offs can influence dominance patterns. Competition-colonization trade-offs have been identified between competitive colonies expanding into nearby trees and foundress queens establishing new nest sites (Stanton et al. 2002). Twig-ant communities are strongly influenced by canopy structure and habitat complexity (Philpott et al. 2018). Tree size correlates positively with ant abundance (Yusah and Foster 2016), species richness (Klimes et al. 2015), and composition (Dejean et al. 2008). Canopy connectivity, in turn, impacts local species coexistence as lower connectivity decreases species richness and canopy connections augment access to tree resources (Powell et al. 2011). Limited access to cavity nesting sites hampers growth and reproduction of arboreal ants (Philpott and Foster 2005) and differences in nest entrance size can (Philpott and Foster 2005)affect abundance and richness of arboreal ant species competing for cavity resources (Powell et al. 2011, Jiménez-Soto & Philpott 2015). For some cavity-nesting ants (e.g. species in the genus *Cephalotes*), nest entrance size impacted survival and colony fitness (Powell 2009) with important implications for changes in relative abundance over time. Therefore translating lab competitive hierarchies for nesting sites to ant species co-existence and abundance patterns is not straightforward, but needs to be viewed while considering other factors that simultaneously drive patterns of distributions and diversity.

Conclusion

While we find that twig-nesting ants from this tropical agricultural system form a dominance hierarchy, it is likely that behavioral dominance will vary across ecosystems and habitats. Subsequent studies should link dominance patterns with relative abundance patterns in the field in order to assess if particular species traits are important in structuring local communities. While competitive outcomes in our experiment are static, dominance hierarchies exhibit considerable variation and field studies should therefore include spatial and temporal variation. Dominance hierarchy studies are typically designed to assess antagonistic interactions, but less focus has been placed on collecting data with neutral interactions (Stuble et al. 2017). Differences in food preference and temporal foraging patterns suggest that neither species alter their behavior in the presence of the other. Therefore, more studies noting neutral interactions will shed greater light on the prevalence of dominance hierarchies under natural conditions.

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Data Accessibility Twig-ant competition data and scripts to calculate dominance rankings and interaction network are made available on Dryad. doi:10.5061/dryad.1t0s20m

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Figures & Tables.

Table 1. Estimation of dominance hierarchy using Elo-rating method. The ranking shows that the twig-nesting species *Myrmelachista mexicana* is the highest ranked species, while *Pseudomyrmex ejectus* is the lowest ranked species in the hierarchy.

Species	Rankings
Myrmecalista mexicana	1.402
Pseudomyrmex (PSW-53)	3.833
Nesomyrmex echinatinodis	3.859
Camponotus abditus	5.008
Camponotus (Colobopsis) species 1	5.173
Pseudomyrmex filiformis	5.517
Procryptocerus scabriusculus	6.911
Pseudomyrmex simplex	7.091
Pseudomyrmex elongatus	7.903
Pseudomyrmex ejectus	8.303

Figure 1. Competitive network of arboreal ants. Network representing all 10 arboreal species. Directed edges with arrows represent asymmetrical relationships between species. Species are as follows: Myrm = *Myrmelachista mexicana*, Ps53 = *Pseudomyrmex PSW-53*, Neso = *Nesomyrmex echinatinodis*, Ca.ab. = *Camponotus abditus*, Ca.n. = *Camponotus* (*Colobopsis)* sp. 1, Psfili = *Pseudomyrmex filiformis*, Pssimp = *Pseudomyrmex simplex*, Procryp = *Procryptocerus scabriusculus*, Pselong = *Pseudomyrmex elongatus*, Psej = *Pseudomyrmex ejectus*.

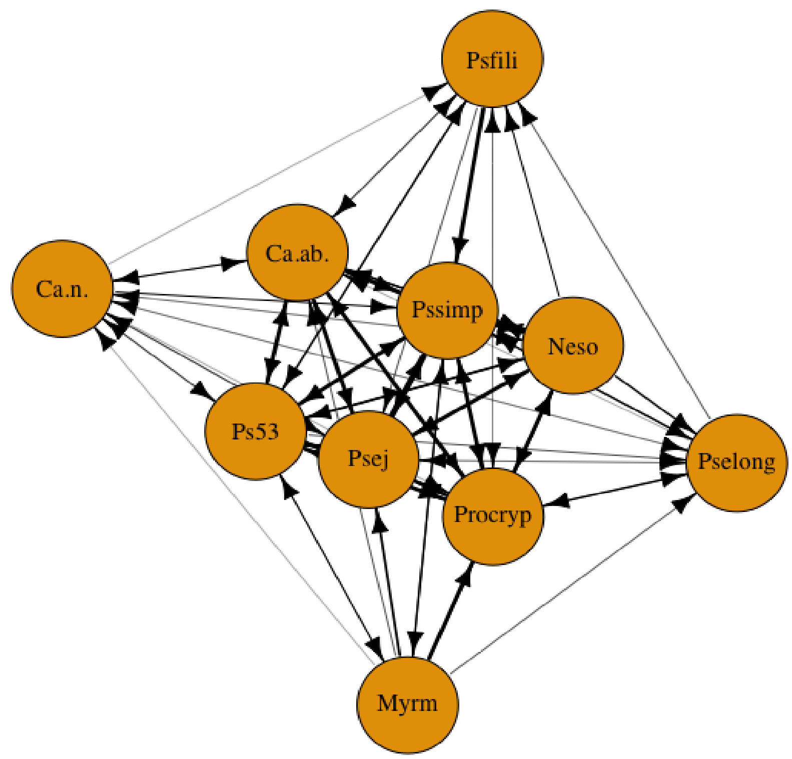

Figure 2. The probability of a higher ranked species winning. The shape of the hierarchy indicates that the rank is intermediate. We quantified the uncertainty/steepness of the hierarchy based on Elo-rating repeatability which is independent of group size and the ratio of interactions to species (Sánchez-Tójar et al. 2018). Based on the Elo-rating, we find that the value obtained is 0.578 which corroborates our qualitative results showing that the hierarchy is intermediate. Thus, rank in this network is a relatively good predictor that a higher ranked species is more like to win from lower-ranked species even though that is not always the case.

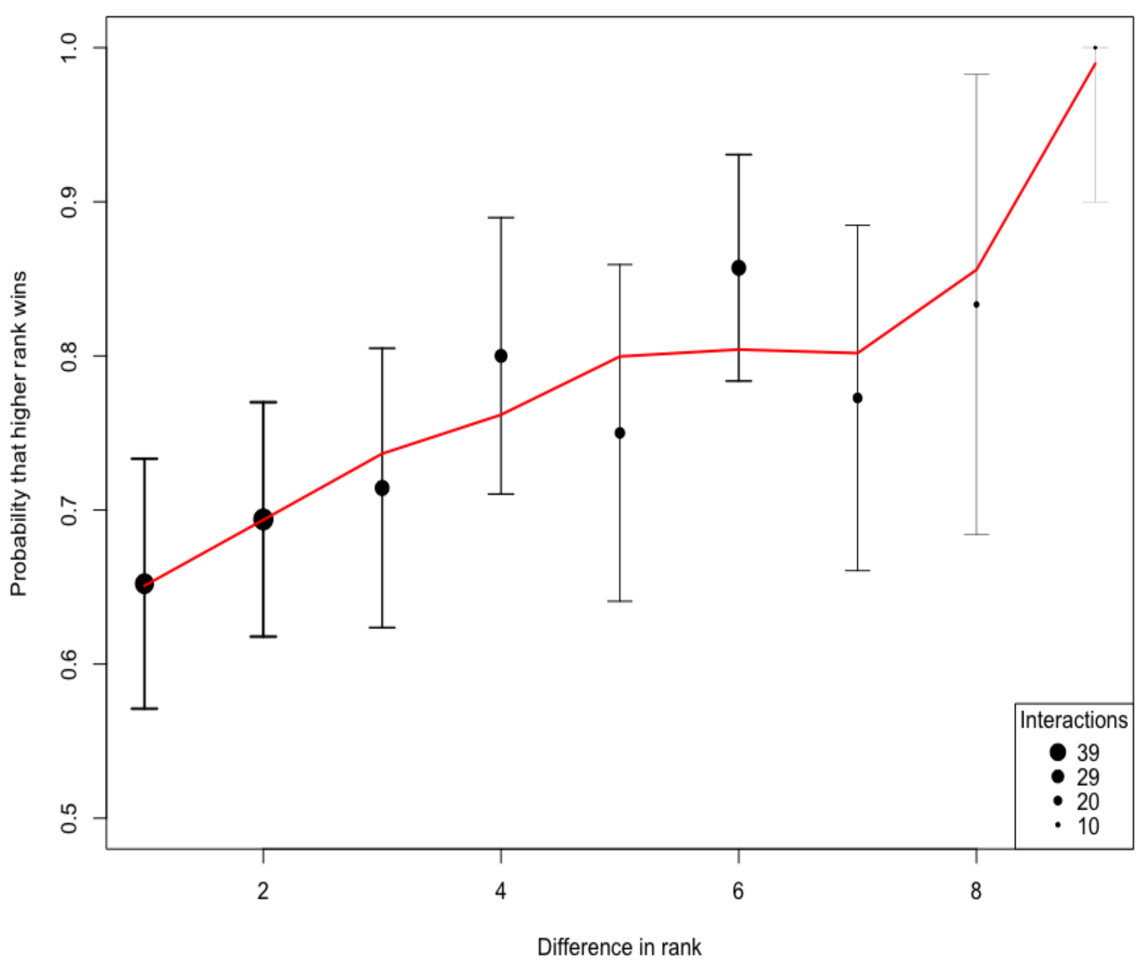

Figure 3. Triad census of twig-nesting arboreal ants. We determined the orderliness of hierarchy by estimating the transitivity of interactions. The y-axis represents the mean difference between the observed (ten ant species network) and expected (10,000 random networks) percentage of the triad subtypes (shown on the x-axis) and error bars show 95% confidence intervals. The twig-nesting ant data shows a significant excess of transitive triads (Tri=0.66, p-value=0.002) and a significant deficit of cyclical triads. All the other triad sub-types found were not significantly different from the expected random network (zero horizontal line). The following symbols define seven possible triad types: A= Null, B=Single-edge, C=Double-dominance, D=Double-subordinate, E=Pass-along, F=Transitive, G=Cycle.

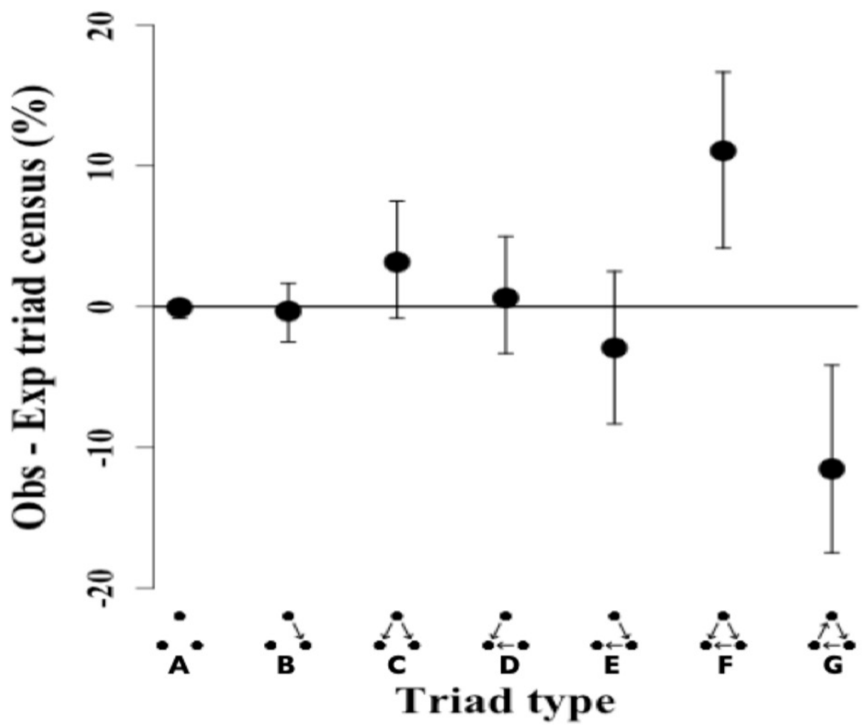

Table 1(on next page)

Estimation of dominance hierarchy using Elo-rating method.

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Figure 1

Competitive network of arboreal ants.

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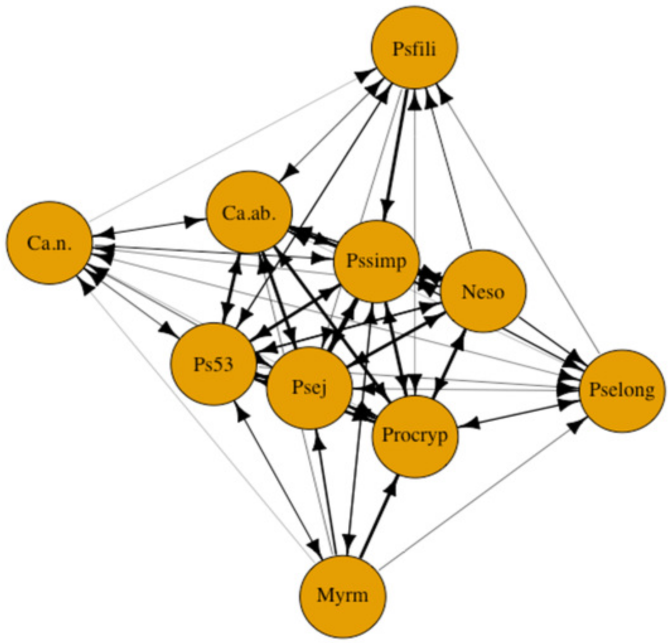

Psfili
Ca.ab.
Ca.n.
Pssimp
Neso
Ps53
Psej
Pselong
Procryp
Myrm

Figure 2

The probability of a higher ranked species winning.

The shape of the hierarchy indicates that the rank is intermediate. We quantified the uncertainty/steepness of the hierarchy based on Elo-rating repeatability which is independent of group size and the ratio of interactions to species (Sánchez-Tójar et al. 2018) . Based on the Elo-rating, we find that the value obtained is 0.578 which corroborates our qualitative results showing that the hierarchy is intermediate. Thus, rank in this network is a relatively good predictor that a higher ranked species is more like to win from lower-ranked species even though that is not always the case.

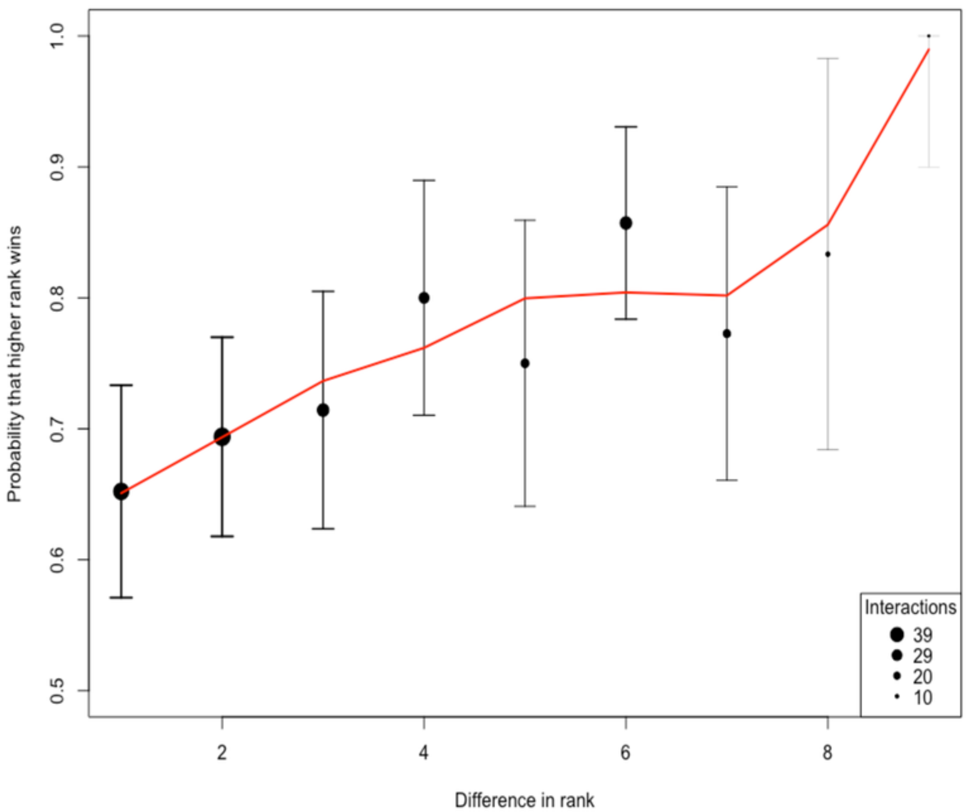
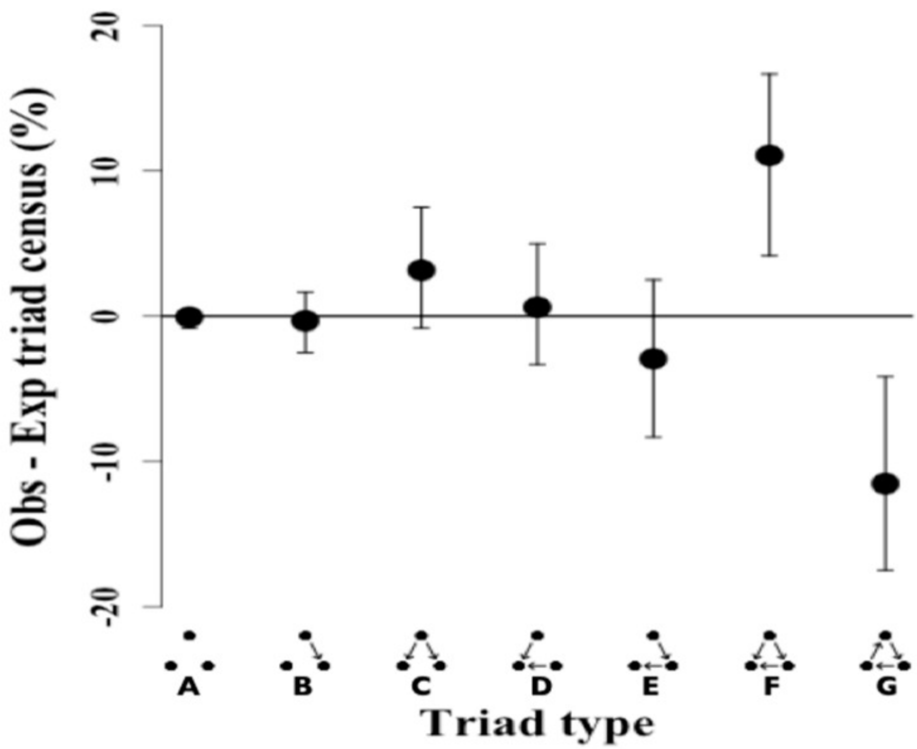

Probability that higher rank wins
0.5
0.6
0.7
0.8
0.9
1.0
2
4
6
8
Difference in rank
Interactions
39
29
20
10

Figure 3

Triad census of twig-nesting arboreal ants.

We determined the orderliness of hierarchy by estimating the transitivity of interactions. The y-axis represents the mean difference between the observed (ten ant species network) and expected (10,000 random networks) percentage of the triad subtypes (shown on the x-axis) and error bars show 95% confidence intervals. The twig-nesting ant data shows a significant excess of transitive triads (Tri=0.66, p-value=0.002) and a significant deficit of cyclical triads. All the other triad sub-types found were not significantly different from the expected random network (zero horizontal line). The following symbols define seven possible triad types: A= Null, B=Single-edge, C=Double-dominance, D=Double-subordinate, E=Pass-along, F=Transitive, G=Cycle.


Obs - Exp triad census (%)
20
10
0
-10
-20
A
B
C
D
E
F
G
Triad type