Arboreal twig-nesting ants form dominance hierarchies over nesting resources

Senay Yitbarek [Corresp., 1] , **Stacy Philpott** [2]

1 University of California, Berkeley, Berkeley, United States

2 University of California, Santa Cruz, Santa Cruz, United States

Corresponding Author: Senay Yitbarek
Email address: senay@berkeley.edu

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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2 **resources**

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4 Senay Yitbarek[1][§]

5 Stacy M. Philpott[2]

6

7 [1]Department of Integrative Biology

8 University of California, Berkeley

9 VLSB 5017, Berkeley, California 94720

10

11 [2]Environmental Studies Department

12 University of California, Santa Cruz

13 1156 High Street

14 Santa Cruz, CA 95064

15

16 Corresponding Author:

17 Senay Yitbarek

18 VLSB 5017, Berkeley, CA 94720. USA

19 Email address: senay@berkeley.edu

20

21

22 **Abstract**

23 Interspecific dominance hierarchies have been widely reported across animal systems. High-

24 ranking species are expected to monopolize more resources than low-ranking species via

25 resource monopolization. In some ant species, dominance hierarchies have been used to explain

26 species coexistence and community structure. However, it remains unclear whether or in what

27 contexts dominance hierarchies occur in tropical ant communities. This study seeks to examine

28 whether arboreal twig-nesting ants competing for nesting resources in a Mexican coffee

29 agricultural ecosystem are arranged in a linear dominance hierarchy. We described the

30 dominance relationships among 10 species of ants and measured the uncertainty and steepness of

31 the inferred dominance hierarchy. We also assessed the orderliness of the hierarchy by

32 considering species interactions at the network level. Based on the randomized Elo-rating

33 method, we found that the twig-nesting ant species *Myrmelachista mexicana* ranked highest in

34 the ranking, while *Pseudomyrmex ejectus* was ranked as the lowest in the hierarchy. Our results

35 show that the hierarchy was intermediate in its steepness, suggesting that the probability of

36 higher ranked species winning contests against lower ranked species was fairly high. Motif

37 analysis and significant excess of triads further revealed that the species networks were largely

38 transitive. This study highlights that some tropical arboreal ant communities organize into

39 dominance hierarchies.

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

42

43 **Introduction**

44   A long-standing goal in ecology has been to determine the underlying mechanisms that

45 give rise to species coexistence in local communities, especially in assemblages with multiple

46 competing species (MacArthur 1958, Hutchinson 1959). Numerous mechanisms have been

47 proposed for maintaining species coexistence (Wright 2002, Silvertown 2004). Interspecific

48 competitive trade-offs, whereby the dominance of a particular species in one environment is

49 offset by the dominance of another species in a different environment, can lead to spatial

50 segregation between species (Tilman 1994, Levine et al. 2004). These interspecific interactions

51 are thought to lead to the long-term stable coexistence of ecologically similar species (Levins

52 1979, Holt et al. 1994, Chesson 2000, Bever 2003, Rudolf and Antonovics 2005), and may also

53 be characterized by dominance hierarchies. Dominance hierarchies have been observed in a wide

54 range of taxa, from vertebrates to invertebrates (Chase and Seitz 2011). Species can be ranked

55 into a hierarchy based on their behavioral dominance during interspecific competitive encounters

56 for resources (Davidson 1998). For example, dominance ranking was positively associated with

57 body mass in bird species, with heavier species more likely to monopolize food sources in

58 contrast to lighter species(Francis et al. 2018). However, dominance rankings can be determined

59 by many other factors including age, sex, aggressiveness, and previous encounters(Haley et al.

60 1994, Zucker and Murray 1996). Furthermore, interspecific dominance hierarchies have been

61 used to understand patterns of local species coexistence in ecological communities (Morse 1974,

62 Schoener 1983).

63   In ant communities, dominance hierarchies have been used to examine interspecific

64 tradeoffs that may explain species coexistence patterns (Stuble et al. 2013). These trade-offs

65 include the discovery-dominance trade-off, the discovery-thermal tolerance tradeoff, and the

66   discovery-colonization trade-offs (Cerdá et al. 1998a, Stanton et al. 2002a, Lebrun and Feener

67   2007, Stuble et al. 2013). In addition to testing interspecific trade-offs, dominance hierarchies

68   have been used to understand the role of dominant species in structuring local communities and

69   species composition, such as partitioning dominant and subdominant species within guilds

70   (Baccaro et al. 2010, Arnan et al. 2012). Dominant ant species can play an important role in the

71   structuring of local communities. For example, *Formica* species dominating a boreal ecosystem

72   divert resources away from subdominant competitors (Savolainen and Vepsäläinen 1988). In

73   Mediterranean ecosystems, subdominant species forage at nearly lethal environmental conditions

74   while dominant species reduce their own mortality risk by foraging at more favorable

75   temperatures (Cerdá et al. 1998a, Castillo-Guevara et al. 2019). In tropical ecosystems,

76   competing arboreal ants can be structured into a dominance hierarchy with higher ranked ant

77   species having greater access to nesting sites and extrafloral nectaries (Blüthgen et al. 2004,

78   Díaz-Castelazo et al. 2004). However, levels of uncertainty associated with outcomes of

79   interspecific interactions between ants are often not quantified (Stuble et al. 2017). Furthermore,

80   its remains unclear how arboreal ants or tropical ants are structured at the community level, such

81   as when interspecific interactions are viewed as a network (Dáttilo et al. 2014).

82   In this study, we examine dominance hierarchies for a community of arboreal twig-

83   nesting ants in a coffee agroecosystem. Both arboreal and ground-dwelling twig-nesting ants in

84   coffee agroecosystems are nest-site limited in terms of number (Philpott and Foster 2005),

85   diversity (Armbrecht et al. 2004, Gillette et al. 2015), and size (Jiménez-Soto and Philpott 2015)

86   of nesting resources. For twig-nesting ants, nest takeovers are common, and therefore dominance

87   in this system is defined as competition for nest sites (Brian 1952), and in one case dominance

88   over nest sites has been experimentally demonstrated (Palmer et al. 2000).

89   This present study aims to describe dominance hierarchies for twig-nesting ants due to

90   competition for nest resources in a Mexican coffee agricultural ecosystem. Since competition is

91   thought to play an important role in the structuring of ant communities, we postulated that

92   resource competition among twig-nesting ants could contribute to the structure of ecological

93   networks involving arboreal ants and their nesting sites. Specifically, we hypothesized that

94   tropical arboreal twig-nesting ants form a linear dominance hierarchy for nesting sites, even

95   when accounting for uncertainties associated with intransitive interactions and sample size. We

96   overall predict that ranking-order remains relatively stable such that higher-ranked individuals

97   maintain their dominant position in the network.

98   We adopt statistical methods to infer a dominance hierarchy from competitive

99   interactions over nest resources and estimate uncertainty and steepness of that dominance

100   (Shizuka and McDonald 2012, Pinter-Wollman et al. 2014, Sánchez-Tójar et al. 2018).

101   Furthermore, we estimate the orderliness of the hierarchy within the community.

102

103   **Methods**

104   ***Study Site and System***

105   We conducted fieldwork at Finca Irlanda (15°20' N, 90°20' W), a 300 ha, privately owned

106   shaded coffee farm in the Soconusco region of Chiapas, Mexico with ~250 shade trees per ha.

107   The farm is located between 900-1100 m a.s.l (Perfecto et al. 2014). Between 2006-2011, the

108   field site received an average rainfall of 5726 mm per year with most rain falling during the rainy

109   season between May and October. The farm hosts ~50 species of shade trees that provide

110   between 30-75% canopy cover to the coffee bushes below. The farm has two distinct

111   management areas -- one that is a traditional polyculture and the other that is a mixture of

112   commercial polyculture coffee and shade monoculture coffee according to the classification

113   system of (Moguel and Toledo 1999).

114   The arboreal twig-nesting ant community in coffee agroecosystems in Mexico is diverse.

115   There are ~40 species of arboreal twig-nesting ants at the study site including *Brachymyrmex* (3

116   species), *Camponotus* (8), *Cephalotes* (2), *Crematogaster* (5), *Dolichoderus* (2), *Myrmelachista*

117   (3), *Nesomyrmex* (2), *Procryptocerus* (1), *Pseudomyrmex* (11), and *Technomyrmex* (1) (Philpott

118   and Foster 2005, Livingston and Philpott 2010).

119

120   ***'Real-estate' experiments***

121   We examined the relative competitive ability of twig-nesting ants by constructing

122   dominance hierarchies based on 'real estate' experiments conducted in the lab. We collected ants

123   during systematic field surveys in 2007, 2009, 2011, and 2012 in the two different areas of the

124   farm, and then used ants in lab experiments.

125   Once in the lab, we selected two twigs, each hosting a different species, removed all ants

126   (i.e. all workers, alates and brood) from the twigs and placed them into sealed plastic tubs with

127   one empty artificial nest (15 cm high by 11 cm diameter cylindrical tubs). The artificial nest, or

128   'real estate', consisted of a bamboo twig, 120 mm long with a 2-4 mm opening. All trials started

129   between 12-2 pm and after 24 hours, we opened the bamboo twigs to note which species had

130   colonized the twig. All ants collected and brought to the lab were used in 'real estate' trials

131   within two days of collection, or were otherwise discarded.

132   We conducted trials between pairs of the ten most common ant species encountered

133   during surveys: *Camponotus abditus*, *Camponotus* (*Colobopsis*) sp. 1, *Myrmelachista mexicana*,

134   *Nesomyrmex echinatinodis, Procryptocerus scabriusculus, Pseudomyrmex ejectus,*

135 *Pseudomyrmex elongatus*, *Pseudomyrmex filiformis*, *Pseudomyrmex* PSW-53, and

136 *Pseudomyrmex simplex*. We selected a priori to use the 10 most common species and did not run

137 trials between other ant species. We replicated trials for each species pair on average 5.73 times

138 (range: 1-18 trials per pairs of species); four species pairs were replicated once, nine species

139 pairs were replicated twice, and 31 species pairs were replicated three or more times. Only one

140 species pair (*M. mexicana* and *P. filiformis*) was not tested. We conducted 42 trials in 2007, 105

141 trials in 2009, 82 trials in 2011, and 30 trials in 2012 for a total of 259 trials (Supplementary

142 Materials).

143

144 ***Dominance hierarchy***

145   We used the trial outcomes to infer the dominance hierarchy ad estimate the level of

146 uncertainty and steepness. All simulations were conducted in R version 3.3.3 (R Core

147 Development Team 2017). We used the R package "aniDom" version 0.1.3 to infer dominance

148 hierarchies using the randomized Elo-rating method (Farine and Sánchez-Tójar 2017,

149 Sánchez-Tójar et al. 2018). To analyze competitive interactions we used the R package

150 "compete" version 0.1 and graphics were completed in the "igraphs" package version

151 1.2.4.1(Csardi and Nepusz 2006, Curley 2016).

152   We subsampled the observed data to determine whether the population had been

153 adequately sampled to infer reliable dominance hierarchies. The subsampling procedure consists

154 of estimating the randomized Elo-rating repeatability values as more data is added to determine

155 if the repeatability values remain stable or decline. Thus, the repeatability values provide insights

156 into the steepness of the hierarchy(Sánchez-Tójar et al. 2018).

157   Additionally, we also calculated the ratio of interactions to species to determine sampling

158   effort. An average sampling effort ranging from 10-20 interactions is sufficient to infer

159   hierarchies in empirical networks (Sánchez-Tójar et al. 2018). We estimated the dominance

160   hierarchy using the randomized Elo-rating method. The matrix of interactions was converted to a

161   sequence of interactions 1000 times such that different species individual Elo-ratings were

162   calculated each time to obtain mean rankings. We estimated uncertainty in the hierarchy by

163   splitting our dataset into two halves and estimated whether the hierarchy in one half of the matrix

164   correlated with the hierarchy of the other half of the matrix (Sánchez-Tójar et al. 2018).

165   In addition to examining the role of ant species attributes and levels of uncertainty in

166   dominance hierarchies, we examined the formation of dominance hierarchies using motif

167   analysis to identify network structures composed of transitive and cyclical triads (Faust 2007).

168   Motif analysis is commonly used in social network analysis to detect emergent properties of the

169   network structure by comparing the relative frequencies of motifs in the observed network to the

170   expected value for the null hypothesis of a random network (Holland and Leinhardt 1972, Faust

171   2007). We carried out motif analysis with customized randomization procedures (McDonald and

172   Shizuka 2013) to compare the structure of our network model against random network graphs.

173   Species interaction data were represented as a network plot of the dominance interactions

174   between the 10 species (Fig. 1). The nodes in the network represent ant species and the one-way

175   directional arrows of the edges represent dominant-subordinate relationships. In the random

176   networks, we maintained the same number of nodes and edges as in the observed network, but

177   the directionality and placement of edges were generated randomly. Using the adjacency matrix,

178   we calculated the triad census (Shizuka and McDonald 2012, McDonald and Shizuka 2013). The

179   triad census allows us to examine directed species interactions (Pinter-Wollman et al. 2014). We

180   used the seven possible triad configurations fully composed of three nodes that either have

181   asymmetric or mutual edges (Holland and Leinhardt 1972). The triad census can be used to

182   formalize competitive networks into transitive triads (e.g. species A dominates both species B

183   and C.) versus cyclic triads (e.g. species A dominates species B, species B dominates species C,

184   and species C dominates species A). The triads are then compared to the null model of random

185   networks.

186

187   **Results**

188   ***'Real estate' experiments.***

189   Across the vast majority of the trials, there was a clear winner of the 'real estate' battle

190   after 24 hours, meaning that one of the two species had occupied the artificial nest. From

191   examining the wins and losses, a clear hierarchy emerged, with some species winning the vast

192   majority of trials in which they were involved, and other species winning few trials. The ranking

193   shows that the twig-nesting species *Myrmelachista mexicana* is the highest ranked species, while

194   *Pseudomyrmex ejectus* is the lowest ranked species in the hierarchy (Table 1). The one trial that

195   did not result in a winner was a trial involving *P. elongatus* and *P. ejectus*.

196

197

198   ***Dyadic interactions: Estimating Dominance Hierarchy Uncertainty***

199   The total number of interactions among the 10 species was 258. The ratio of interactions

200   to species (25.8) shows an adequate sampling effort beyond the 10-20 recommended range

201   (Sánchez-Tójar et al. 2018). Using the randomized Elo-rating method, we found that the

202   hierarchy was intermediate in steepness showing that rank in the hierarchy largely predicts the

203   probability of winning an interaction (Fig 2). The Elo-rating repeatability was 0.578 which also

204   indicates an intermediate level of uncertainty. We further estimated the uncertainty in the

205   hierarchy by splitting the database into two, and estimating whether hierarchy from one half

206   resembles the hierarchy estimated from the other half. We find that the degree of

207   uncertainty/steepness in the hierarchy is intermediate (mean=0.43, 2.5 % and 97.5%

208   quantile = (-0.12, 0.85)).

209

210   ***Triad census analysis.***

211   The triad census analysis of the triad distribution showed that the observed network has a

212   significant excess of transitive triads followed by a significant deficit of cyclical triads

213   (Ttri=0.66, p-value=0.002). Triad types that are positive (i.e. non-overlapping at 0) occurred in

214   excess in the observed network, while triad types that are negative showed a deficit in the

215   observed network as compared to the random null network (Fig 3).

216   The remaining five triads in the network did not show any significant differences in the

217   mean triad percentage rates between the observed and expected network. While the data showed

218   a clear excess of transitive triangles (34.55 %) and deficit for cyclical triangles (3.6%), the

219   distribution for pass-along triads shows a less typical pattern with the 95% confidence intervals

220   crossing the zero line but the mean percentage still showing a deficit.

221

222   **Discussion**

223   In this study, we used a novel set of statistical approaches to determine that tropical twig-

224   nesting ants competing for nesting resources are arranged in a linear dominance hierarchy.

225   Although many studies have documented ant dominance hierarches, it is important to note that

226 ranking methods vary considerably among studies (Stuble et al. 2013). Traditionally, field

227 studies have quantified dominance relationships on the basis of proportion of contests won.

228 Other studies have use more sophisticated methods to account for competitive reversals (Vries

229 1998) or have updated rankings based on relative wins and losses during contests (Colley 2002).

230 In this study, we used the randomized Elo-rating by calculating the mean of species Elo-ratings

231 (Sánchez-Tójar et al. 2018). With this method, we find that the probability of a higher ranked

232 species winning a contest against a lower ranked species is relatively high, which corroborates

233 our finding that the hierarchy has intermediate steepness.

234

235

236   Moving beyond simple pair-wise interactions, we used motif analysis of the network to

237 infer a significant excess of transitive interactions. Transitive interactions were significantly

238 over-represented in the network. Thus the combination of techniques allowed us to determine

239 that the dominance hierarchy in this community is intermediate in steepness and transitive.

240   Dominance hierarchies over food resources have been commonly documented in ant

241 communities in a variety of ecosystems, but may vary depending on environmental conditions or

242 the amount of food resource provided. For instance, in Mediterranean ecosystems, dominant and

243 subordinate ants are partitioned on the basis of their life-history traits (Arnan et al. 2012).

244 Dominant ant species had more abundant colonies and displayed increased defense for resources

245 in contrast to subordinate ant species. Meanwhile, subordinate ants exemplified greater tolerance

246 to higher temperatures (Cros et al. 1997, Cerdá et al. 1998a) . In addition, outcomes of

247 interspecific interactions within the dominance hierarchy are contingent on environmental

248 conditions (Arnan et al. 2012). In a temperate forest ecosystem of North Carolina, dominance

249   was context dependent (Stuble et al. 2017). Rankings on the basis of food bait monopolization

250   revealed that dominance correlated positively with relative abundance since the most abundant

251   species were ranked higher in the dominance hierarchy. In contrast, rankings based on aggressive

252   encounters did not correlate with abundance. In some habitats, dominance patterns are largely

253   determined by the time of day that foraging occurs (Bestelmeyer 2000). In the North Carolina

254   system, the most abundant ant species, *Aphaenogaster rudis*, was most active during the morning

255   hours, whereas the cold-tolerant ant species, *Prenolepis imparis*, was dominant during the night

256   hours (Stuble et al. 2017). Species rankings can also strongly depend on the size of food

257   resources provided in trials. In an assemblage of woodland ants, smaller-sized ants were more

258   efficient at acquiring and transporting fixed resources and larger-sized solitary ants excelled at

259   retrieving smaller food that were mobile during competitive interactions (LeBrun 2005).

260   However, the introduction of phorid parasitoids in this system reduced the transitive hierarchy

261   facilitating the coexistence of subdominant ants (LeBrun 2005, LeBrun and Feener 2007). In our

262   study on competition for nesting sites in the lab, we were able to use fixed resources and to a

263   certain degree control variation in colony size.

264   It has been suggested that ant dominance hierarchies may be limited in their ability to

265   provide insights into community structure and species coexistence because ranking methods

266   might not be directly related to resource acquisition (Gordon 2011, Cerdá et al. 2013).

267   Furthermore, dominance ranking methods can lead to variation in hierarchies due to inadequate

268   sample sizes (Stuble et al. 2017). To account for steepness/uncertainty associated with our

269   ranking methods, we estimated the sampling effort by determining the ratio of species

270   interactions to individuals (Sánchez-Tójar et al. 2018). The average sampling effort that we

271   found falls within the recommended range reported in the literature(McDonald and Shizuka

272 2013). The steepness/uncertainty in the hierarchy, independent of both group size and ratio of

273 interactions to individuals, indicates that our ranking approach is robust and representative of the

274 underlying community structure. However, species coexistence can be maintained because

275 subordinate individuals can occasionally outcompete higher-ranked individuals over resources.

276   Although the twig-nesting ant community that we studied here in lab experiments showed

277 a strong dominance hierarchy, there were some factors that could not be explicitly considered.

278 Species with larger colony sizes might have a competitive advantage over other species. For

279 instance, large colony sizes of invasive Argentine ants are indicative of strong competitive

280 abilities relative to native species (Holway 1999). However, smaller ant colonies can sometimes

281 overtake larger colonies depending on competitive traits, such as chemical defenses in the

282 example of African Acacia ants (Palmer 2004). Although there might be some colony to colony

283 variation in the number of individuals used in each trial (unpublished data), the focus of our

284 study did not involve ant colony size variation. Preferences for nest entrance sizes is another

285 important consideration that can determine competitive outcomes (Powell et al. 2011,

286 Jiménez-Soto and Philpott 2015). While it is certainly the case that ant species prefer different

287 nest entrance sizes, the distribution of natural nest sizes for most of our species (7 out of 10) are

288 statistically indistinguishable. One notable exception is the arboreal ant *P. scabriusculus* which

289 tends to prefer slightly larger nest entrances (in the field) than we provided in the real estate

290 experiments (Livingston and Philpott 2010). However, we have found that *P. scabriusculus* nests

291 in twigs as small as 2-3 mm in diameter.

292   Dominance hierarchies are often highly context-dependent and species ranking may vary

293 across geographical regions or disturbance regimes (Palmer 2004). Previous research involving

294 ant competition for variable resources in temperate ecosystems showed that intransitive

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295   competitive interactions at local spatial scales mediates ant coexistence (Sanders and Gordon

296   2003). Microclimatic factors also disrupt dominance hierarchies. For instance, environmental

297   variation in coffee systems is likely to influence dominance hierarchies (Philpott and Foster

298   2005, Perfecto and Vandermeer 2011, Castillo-Guevara et al. 2019). Occurrence of fire can

299   disrupt dominance hierarchies in specialist ants in *Acacia* trees resulting in increased abundance

300   of subordinate ants (Sensenig et al. 2017). Top down processes such as predation and parasitism

301   likely mediate twig-nesting ant competition in natural communities (Philpott et al. 2004, Feener

302   et al. 2008, Hsieh and Perfecto 2012). In addition, competition and disturbance from ground- and

303   arboreal carton-nesting ants may influence the colonization and community composition of

304   arboreal twig-nesting ants (Philpott 2010, Ennis and Philpott 2018). Therefore, more

305   comparative research is needed to examine how variable field conditions may affect the

306   hierarchy and ultimately the distribution and relative abundance of different arboreal, twig-

307   nesting ant species.

308   In addition to dominance hierarchies, there are other factors that can drive the distribution

309   and co-existence patterns of arboreal ant communities (Yamaguchi 1992, Palmer et al. 2000).

310   For instance, variation in life-history trade-offs can influence dominance patterns. Competition-

311   colonization trade-offs have been identified between competitive colonies expanding into nearby

312   trees and foundress queens establishing new nest sites (Stanton et al. 2002). Twig-ant

313   communities are strongly influenced by canopy structure and habitat complexity (Philpott et al.

314   2018). Tree size correlates positively with ant abundance (Yusah and Foster 2016), species

315   richness (Klimes et al. 2015), and composition (Dejean et al. 2008). Canopy connectivity, in

316   turn, impacts local species coexistence as lower connectivity decreases species richness and

317   canopy connections augment access to tree resources (Powell et al. 2011). Limited access to

318   cavity nesting sites hampers growth and reproduction of arboreal ants (Philpott and Foster 2005)

319   and differences in nest entrance size can (Philpott and Foster 2005) affect abundance and

320   richness of arboreal ant species competing for cavity resources (Powell et al. 2011, Jiménez-Soto

321   & Philpott 2015). For some cavity-nesting ants (e.g. species in the genus *Cephalotes*), nest

322   entrance size impacted survival and colony fitness (Powell 2009) with important implications for

323   changes in relative abundance over time. Therefore, translating lab competitive hierarchies for

324   nesting sites to ant species co-existence and abundance patterns is not straightforward, but needs

325   to be viewed while considering other factors that simultaneously drive patterns of distributions

326   and diversity. Subsequent studies should link dominance patterns with relative abundance

327   patterns in the field in order to assess if particular species traits are important in structuring local

328   communities. While competitive outcomes in our experiment are static, dominance hierarchies

329   exhibit considerable variation and field studies should therefore include spatial and temporal

330   variation. Dominance hierarchy studies are typically designed to assess antagonistic interactions,

331   but less focus has been placed on collecting data with neutral interactions (Stuble et al. 2017).

332   Differences in food preference and temporal foraging patterns suggest that neither species alter

333   their behavior in the presence of the other. Therefore, more studies noting neutral interactions

334   will shed greater light on the prevalence of dominance hierarchies under natural conditions.

335

336

337   **Conclusion**

338   Interspecific dominance hierarchies have been used to explain species coexistence and

339   community structure. One major challenge in the study of ant communities is that different

340   ranking methods have been used to construct dominance hierarchies. In particular, uncertainties

341 associated with species interactions and sampling size are often not quantified. The present study

342 corroborates the existence of dominance hierarchies among tropical arboreal twig-nesting ants.

343 Our study quantified the uncertainty associated with competitive interactions for nesting sites.

344 We show that the shape of the hierarchy is intermediate in steepness, with *Myrmelachista*

345 *mexicana* ranked highest in the ranking, while *Pseudomyrmex ejectus* was ranked as the lowest

346 in the hierarchy. While lower-ranked individuals can sometimes overtake nesting sites from

347 higher-ranked individuals, the ranking order remains relatively stable. Our analysis of the

348 competition network finds that the hierarchy at the community level is overwhelmingly

349 transitive, suggesting that intransitive interactions are less important in this system. This study

350 contributes to our understanding of the role of competition on the structure of ant communities

351 and dominance hierarchies.

352

353 **Acknowledgements**

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

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581 **Figures & Tables.**

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583 **Table 1. Estimation of dominance hierarchy using Elo-rating method.** The ranking shows

584 that the twig-nesting species *Myrmelachista mexicana* is the highest ranked species,

585 while *Pseudomyrmex ejectus* is the lowest ranked species in the hierarchy.

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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

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591 **Figure 1. Competitive network of arboreal ants.** The nodes in the network represent all 10
592 arboreal ant species and the one-way directional arrows of the edges represent dominant-
593 subordinate relationships. Species are as follows: Myrm = *Myrmelachista mexicana*, Ps53 =
594 *Pseudomyrmex PSW-53*, Neso = *Nesomyrmex echinatinodis*, Ca.ab. = *Camponotus abditus*,
595 Ca.n. = *Camponotus (Colobopsis)* sp. 1, Psfili = *Pseudomyrmex filiformis*, Pssimp =
596 *Pseudomyrmex simplex*, Procryp = *Procryptocerus scabriusculus*, Pselong = *Pseudomyrmex*
597 *elongatus*, Psej = *Pseudomyrmex ejectus*.

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599 **Figure 2. The probability of a higher ranked species winning.** The shape of the hierarchy

600 indicates that the rank is intermediate. We quantified the uncertainty/steepness of the hierarchy

601 based on Elo-rating repeatability which is independent of group size and the ratio of interactions

602 to species (Sánchez-Tójar et al. 2018). Based on the Elo-rating, we find that the value obtained is

603 0.578 which corroborates our qualitative results showing that the hierarchy is intermediate. Thus,

604 rank in this network is a relatively good predictor that a higher ranked species is more like to win

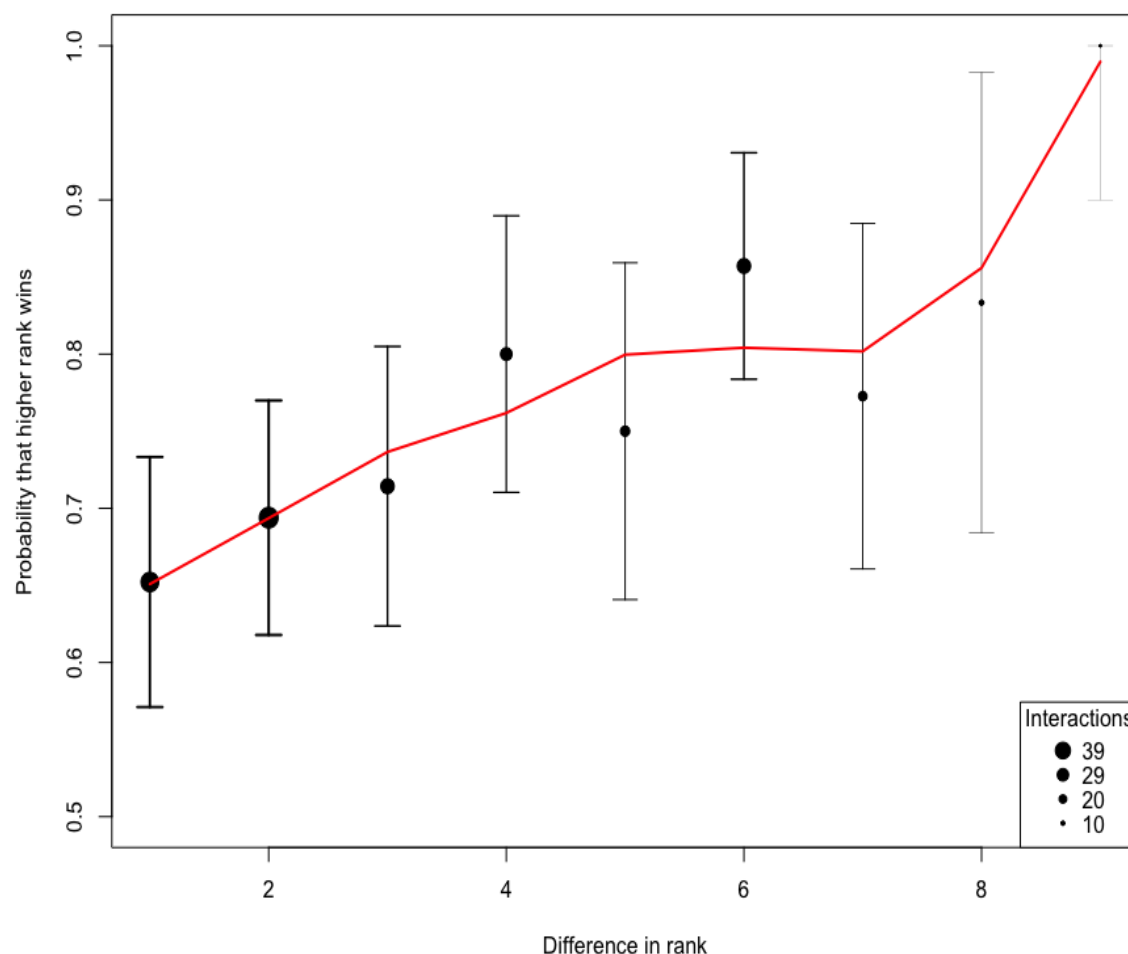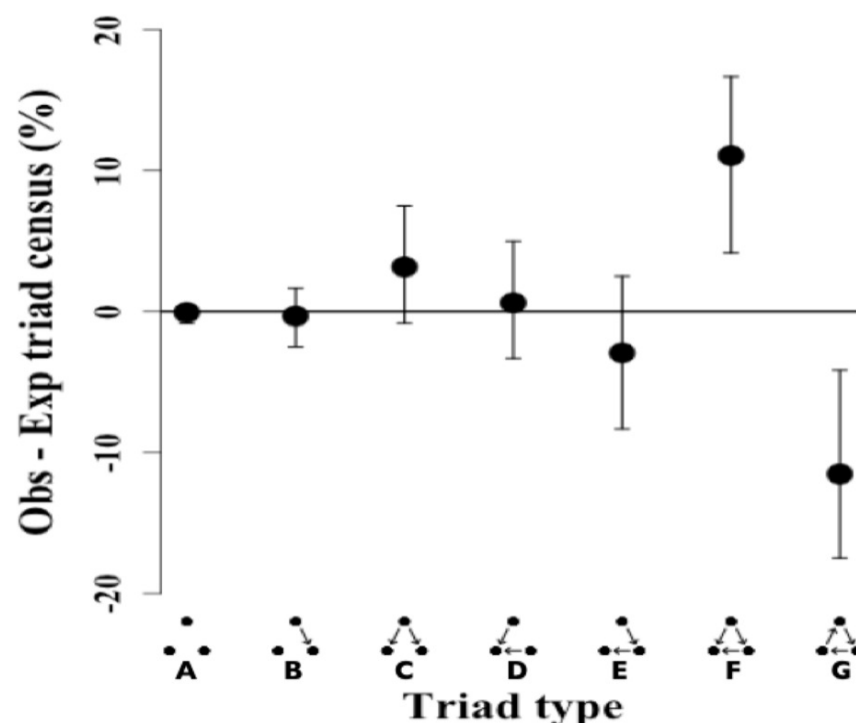605 from lower-ranked species even though that is not always the case.

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608 **Figure 3. Triad census of twig-nesting arboreal ants.** We determined the orderliness of

609 hierarchy by estimating the transitivity of interactions. The y-axis represents the mean difference

610 between the observed (ten ant species network) and expected (10,000 random networks)

611 percentage of the triad subtypes (shown on the x-axis) and error bars show 95% confidence

612 intervals. The twig-nesting ant data shows a significant excess of transitive triads (Tri=0.66, p-

613 value=0.002) and a significant deficit of cyclical triads. All the other triad sub-types found were

614 not significantly different from the expected random network (zero horizontal line). The

615 following symbols define seven possible triad types: A= Null, B=Single-edge, C=Double-

616 dominant, D=Double-subordinate, E=Pass-along, F=Transitive, G=Cycle. The classic transitive

617 triads are represented by the Double-dominant, Double-subordinate, and Transitive triangles.

618 The Pass-along triad can either turn transitive or cyclical if the third edge becomes established.

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Table 1(on next page)

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
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Figure 1

Competitive network of arboreal ants

The nodes in the network represent all 10 arboreal ant species and the one-way directional arrows of the edges represent dominant-subordinate relationships. 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*.
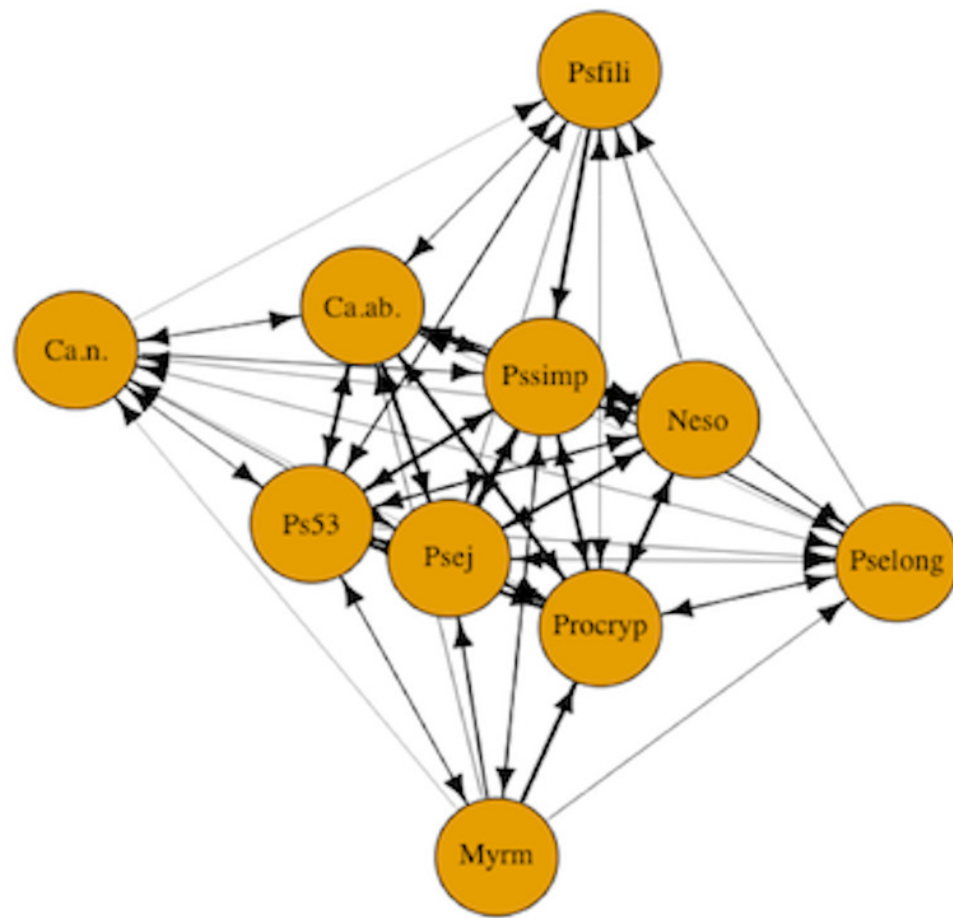
Figure 2

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.
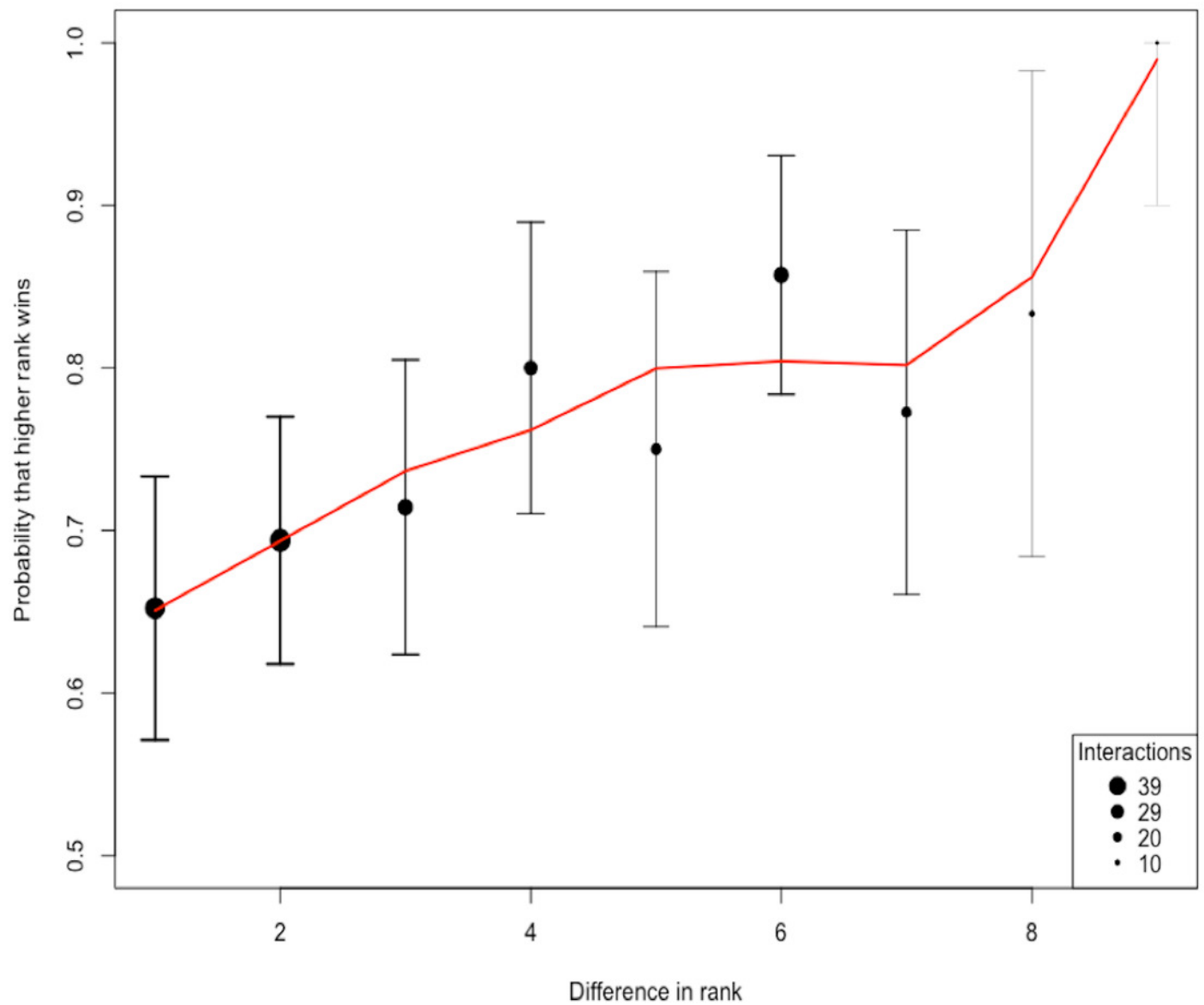
Figure 3

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-dominant, D=Double-subordinate, E=Pass-along, F=Transitive, G=Cycle. The classic transitive triads are represented by the Double-dominant, Double-subordinate, and Transitive triangles. The Pass-along triad can either turn transitive or cyclical if the third edge becomes established.