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The evolution of foraging behavior in ants (Hymenoptera: Formicidae)

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Abstract. Cooperative foraging behavior is a key characteristic of ants. A variety of foraging behaviors are present across this animal family, but little is known of how these behavioral traits evolved and differentiated. In addition, classification of these foraging behaviors has been inconsistent across the literature. Using four classification methods, we infer the ancestral foraging states across the Formicidae, as well as test the transitions between and resulting speciation due to foraging behavior. Our study reinforces the hypothesis that solitary foraging behaviors are ancestral to cooperative foraging behaviors, with strong support for solitary foraging at the root of the phylogeny. We find that cooperative foraging behaviors rarely revert to solitary, and that cooperative behaviors do not often transition between one another. While our findings are consistent across all four classification methods, they are limited by a small behavioral dataset relative to the number of living ant species—we therefore assert that behavioral data are as important as genetic data, and that further effort for detailed, published observations be maintained.

Key words. Macroevolution, phylogenetics, Formicidae.

1. Introduction

Ants (Family: Formicidae) are an exceptionally diverse and widespread group of arthropods, containing over 13,000 extant species estimated to comprise up to 20% of animal biomass (Bolton 2018; Schultz 2000). The sheer number of ant species lends itself to a variety of morphologies and behaviors. Of these behaviors, foraging is considered one of the most charismatic and best documented. The foraging strategies of ants are complicated by obligate eusociality within the group, as foraging workers must forage for the benefit of the entire colony rather than the individual (Traniello 1989). As a result, foraging methods range in efficiency, from individuals foraging solitarily to entire colonies acting as a collective, predatory unit (Rettenmeyer 1963). However, despite the popularity of observing and documenting the presence of foraging strategies, the classification of these behaviors has proven to be a source of difficulty. Early descriptions of foraging ecology classify foraging strategies into three categories: "individual" foraging, in which the foraging worker leaves the colony alone, then locates and retrieves a food item independent of other workers; "recruit" foraging, in which a foraging worker acts as a scout that locates food items independently, then recruits other workers for food retrieval; and "group" foraging, wherein workers follow foraging trails to a food item, retrieve it independently, and reinforce the trail as they return to the nest (Bernstein 1975; Carroll & Janzen 1973). However, these descriptions have been critiqued as too general (Hölldobler & Möglich 1980). Subsequent descriptions therefore do not follow a strict classification scheme: Jaffe (1984) classifies foraging into four categories, whereas Beckers et al. (1989) defines four categories and three subcategories, and Baroni Urbani (1993) five categories. Recently, Lanan (2014) classifies foraging methods into ten distinct subcategories within three overarching categories (see Table 1). This range of classification is due to dividing "recruit" and "group" foraging into subcategories, discovering and classifying rare behaviors, and redefining previ-

Table 1. Foraging method classifications and definitions.

Jaffe (1984)	
Individual foraging: individuals foragers leave the nest, forage, and transport food without any aid from other workers. No information is transmitted between foragers, although the arrival of food may excite other individual foragers to leave the nest.	
Tandem running: A foraging ant scout attracts a single nestmate using antennal contact and then physically leads the nestmate in tandem to the food source. Physical contact is often maintained between the scout and the nestmate, and chemical signals are not used.	
Group recruitment: A scout recruits "up to thirty nestmates" and physically leads them to a food source. Chemical signals are often used but physical contact between the scout and the group is also used.	
Chemical mass recruitment: Groups are guided via chemical means only.	
Beckers et al. (1989)	
Solitary: same as "individual foraging" as in Jaffe.	
Recruitment: a scout discovers a food item and communicates its location to other nestmates	
	Tandem: a leading scout physically leads one recruit at a time to a food source. Trails may or may not be laid.
	Mass: a trail is laid from the food source back to the nest by a scout. Other workers may follow this trail of their own accord or via invitation by the scout, and may reinforce it as they bring food back.
	Group: a trail is usually laid from the food source back to the nest, a scout must also lead a group of foragers (not an individual at a time) to the food source; group recruitment may appear similar to group hunting but is differentiated by scout recruitment. Beckers et al. claim that most ants that use group recruitment also use mass recruitment—nevertheless, group recruitment is used as a separate classification in our dataset and polymorphisms are coded as necessary.
Group hunting: a swarm of foragers leave the nest collectively, they may reinforce a "well-defined trail system" or it may be short-lived; "army ant" behavior	
Trunk trails: trails are close to permanent and often lead to permanent food sources, individual foragers follow them and may reinforce.	
Baroni Urbani (1993)	
Solitary: same definition as in Beckers et al.	
Tandem running: same definition as in Beckers et al.	
Group recruitment ("trail following"): same definition as in Beckers et al., with the presence of a leader (or scout) being required. While Baroni Urbani calls this behavior strictly "trail following", he states nothing on trail following behavior.	
Mass recruitment: same as in Beckers et al., however a scout is not involved. Trunk trails are included in this category.	
Army ant behavior: this is assumed to mean the same as "group hunting" in Beckers et al., as Baroni Urbani does not explicitly define this behavior.	
Lanan (2014)	
No recruitment:	
	Solitary: same definitions as above
Recruitment of groups:	
	Social carrying (tandem carrying): a scout physically carries a forager to the food source
	Tandem running: same definitions as above
	Group recruitment: same definitions as in Baroni Urbani
	Group raiding: Behavior that is akin to group hunting/army ant behavior, but a scout is necessary to lead a group in this manner.
Chemical mass recruitment:	
	Short-term trails: same definition as "mass recruitment" in Beckers et al.
	Volatile alarm recruitment: a worker discovers a food source and releases a volatile chemical signal that alerts other foragers; often described as "short-range recruitment"
	Trunk trails, foraging columns, and fans: similar to the definition of Beckers et al., with the exception that these near-permanent trails have a clear dendritic pattern
	Long-term trail network: similar to "trunk trails, foraging columns, and fans" but lacking the dendritic pattern
	Column and swarm raids: same definition as in "group hunting" via Beckers et al.

ous classifications. To further complicate matters, species have shown to be labile in their behaviors depending on ecological conditions, and often display polymorphism in these behavioral traits (Schatz et al. 1997; Mercier & Lenoir 1999; Sanders & Gordon 2002). While a greater, detailed classification method seems suitable (as in Lanan 2014), such datasets provide too many parameters to be suitable for statistical testing in most cases.

Perhaps due to this inconsistency in classification, no recent studies have utilized modern phylogenetic comparative methods to study the origins and diversification of ant foraging behavior. Despite the lack of explicit tests, it is generally accepted or implied that ancestral ants lived in small family groups and foraged solitarily (Hölldobler & Wilson 1990; Baroni Urbani 1993; Bourke & Franks 1995). It then follows that more cooperative forms of foraging are all derived from a solitary foraging state (Traniello 1989; Schatz et al. 1997). Prior speculation as to how foraging evolved and differentiated suggests that, ultimately, there exists no correlation between phylogeny and foraging method (Jaffe 1984; Baroni Urbani 1993). However, these studies are based on minimal data and outdated taxonomic and phylogenetic information. Recently, colony size and resource preference – traits that are theoretically associated with foraging method – have been shown to have some de-

gree of phylogenetic relationship (Lanan 2014; Burchill & Moreau 2016). New molecular phylogenies for the ants have provided a reliable foundation for these studies (Brady et al. 2006; Moreau et al. 2006; LaPolla et al. 2010; Mehdiabadi & Schultz 2010; Ward et al. 2010; Schmidt 2013; Moreau & Bell 2013).

In this study, we leverage two recent species-level phylogenies (Blanchard & Moreau 2017; Nelsen et al. 2018) and a comparative methods approach to study the evolution of foraging behavior across the family Formicidae. We explore the evolution of foraging behavior, inferring the ancestral foraging state as well as the origins of multiple foraging behaviors. We also test for bias in increasing foraging method complexity. The classifications used in the works of Jaffe (1984), Beckers et al. (1989), Baroni Urbani (1993), and Lanan (2014) are used to test the consistency of classification and infer broad results, and from here onward we shall use these names to refer to their respective publications. These four classification methods do not differ significantly – rather, they vary in putting particular weight on certain behaviors. For example, Jaffe's classification defines tandem running as a distinct category, whereas Baroni Urbani includes this behavior in group recruitment. Our goal in using four different means of classification is not necessarily to determine an ideal classification method, but to rather tease apart potential relationships and avoid potential biases that may arise when strictly using one means of classification.

2. Material and methods

2.1. Foraging method literature search

We collected data on the foraging methods of the Formicidae via an extensive search of published scientific literature. The foraging behavior for each genus was individually searched for via online databases and primary literature. We recorded species for which foraging data were available, either through recorded observation or controlled tests. Older synonyms of currently valid genera were also researched, and species data were recorded for the appropriate valid genus. Data were coded as multistate discrete traits – as well as polymorphic where applicable – according to the foraging method classifications of Jaffe, Beckers et al., Baroni Urbani, and Lanan. As our data sampling does not contain all species of Formicidae (3.6%), the subcategories of Beckers et al. and Lanan classifications were not utilized in order to reduce parameters. Rather, the corresponding primary categories of the two classifications were used to classify behaviors (see Table 1).

Due to the lack of an extensive species-level phylogeny, we performed phylogenetic analyses at the level of the genus, and coded genera according to species-level data of each genus. This method has been utilized successfully by Burchill & Moreau (2016) to investigate the evolution of ant colony size and in Blanchard & Moreau (2017) to investigate the evolution of ant defensive traits. Two datasets per classification method were created for use in analysis, one in which all genera were included and coded as polymorphic as necessary (e.g., a genus displaying foraging methods 1 and 2 was coded as "1&2", regardless of representation in the dataset); the second in which genera were coded as monomorphic when applicable. Monomorphism was determined by classifying a genus by its predominant state (e.g., a genus with a majority of species, for which data was available, displaying foraging method 1 was coded as "1", despite other species in the genus displaying other methods). If no predominant state was apparent, the genus was trimmed from the monomorphic dataset.

2.2. Phylogenetic comparative methods

We modified the latest species-level phylogeny (Nelsen et al. 2018) for use in all subsequent analyses. This phylogeny incorporates 1730 ant species, with representatives across all extant subfamilies and 317 of the 334 extant genera. Species for which no foraging data are available were trimmed using the drop.tip function in the R package ape v5.1 (Paradis 2004). Constraints were placed on the tree to resolve instances of inferred non-monophyly. *Camponotus*, *Colobopsis*, and *Nylanderia* were separated into distinct monophyletic clades despite the phylogeny inferring otherwise (see Ward et al. 2015; Ward et al. 2016). Other instances of inferred non-monophyly were accounted for by separating genera into monophyletic groups with distinct identifying names (e.g. *Acromyrmex Group A*, *Acromyrmex Group B*, etc.).

Ancestral state reconstruction (ASR) for our polymorphic datasets were performed using the function rayDISC within the R package corHMM v1.22 (Beaulieu et al. 2012; Beaulieu et al. 2017), which estimates transition rates and ancestral states for multistate, polymorphic characters using a maximum likelihood (ML) approach. We utilized both marginal and joint reconstruction of ancestral states. Marginal reconstruction returns matrices of likelihood, joint reconstruction returns the likeliest states at internal nodes. Although more computationally complex than the alternative marginal reconstruction, joint reconstruction is less likely to fix on local optima that may potentially deviate from a global optimum (Yang et al. 1995). Three commonly-used transition rate models were analyzed: "equal rates" (ER), "symmetrical rates" (SYM), and "all rates different" (ARD), with titles referring to the transition rates between each state. Results were visualized by mapping results onto the phylogeny with the function plotRECON. As plotRECON requires matrices of likelihood, only marginal reconstruction results could be visualized.

The ancestral states of foraging behavior for our monomorphic datasets were examined using both a ML

approach using the ace function within the R package ape v5.1 (Paradis 2004), and a stochastic character mapping (SCM) approach using the make.simmap and describe.simmap functions within the R package phytools v0.6-44 (Revell 2012). The ace function utilizes marginal reconstruction, and returns marginal ancestral state likelihood of all nodes within a phylogeny. The make.simmap function utilizes joint reconstruction; describe.simmap returns posterior probabilities of all nodes and provides the number of changes between each state. As with the polymorphic data, the same three transition rate models – ER, SYM, and ARD – were analyzed. Each model in make.simmap was set to run for 500 simulations. The resulting states from both methods were mapped onto the existing phylogeny using the ape v5.1 function nodelabels.

For all analyses conducted, the Akaike information criterion (AIC) values corrected for small sample size (AICc values) and the weighted AICc values (AICc weights) of the three transition rate models were compared in order to select the most appropriate model. AICc are useful in instances where AIC may incorrectly select a parameter-heavy model. In the case that the sample sizes are sufficient to accommodate AIC values, both AIC and AICc values will be similar (Cavanaugh 1997). AICc weight can be directly interpreted as the conditional probability per model, allowing otherwise similar AICc values to be directly compared (Wagenmakers & Farrell 2004).

Based on the best fitting transition rate model for the Jaffe, Beckers et al., Baroni Urbani, and Lanan monomorphic datasets, transition and speciation rates were estimated and visualized using a pure-birth Multiple State Speciation and Extinction (MuSSE) method (FitzJohn 2010) and Markov chain Monte Carlo (MCMC) Bayesian analysis via the functions make.musse and mcmc in diversitreev0.9-9 (FitzJohn 2012). We used an exponential prior with rate 1/(2r), with r as a character independent diversification rate. Chains were run for 50,000 iterations, discarding the first 10% as burn-in. This method was utilized by Burchill & Moreau (2016) to infer genus-level rates.

3. Results

3.1. Foraging method literature search

In total, 485 species (representing 3.6% of extant species) across 177 monophyletic groups (171 genera, representing 51% of extant genera) had available foraging data (Table S1). Of these monophyletic groups, 172 were represented in our phylogeny. When trimmed for monomorphy, the Jaffe, Beckers et al., Baroni Urbani, and Lanan datasets represented 138, 140, 137, and 138 monophyletic groups respectively. State distributions for both the polymorphic and monomorphic datasets are presented in Tables S2 & S3.

3.2. Evolution of foraging method

Our ASR results, with inferred ancestral foraging methods mapped onto our phylogeny of 171 genus groups, are visualized in Figs. 1–4. The log likelihood values, AIC values, AICc values, and calculated AICc weights for each transition rate model, as well as number of parameters per model, are presented in Table 2. Comparisons of AICc values reveal that simple ER models were rejected in favor of models with a greater number of parameters (SYM, ARD). In all ASR analyses, Jaffe and Lanan classifications favor the ARD model; Beckers et al. and Baroni Urbani classifications favor the SYM model. AICc weights reveal high levels of fit for Beckers et al. and Baroni Urbani.

Across all datasets, the majority of ASR analyses infer a solitary foraging method at the root of the phylogeny (see Table 3). Conversely, Jaffe classification inferred a group recruitment foraging method for two of the three ASR analyses. The majority of internal nodes for the subfamilies Amblyoponinae, Ectatomminae, Myrmeciinae, Paraponerinae, Ponerinae, and Proceratiinae also infer a solitary foraging method. Internal nodes for the Dorylinae and Dolichoderinae subfamilies, the Plagiolepidini tribe of subfamily Formicinae, and the Attini, Crematogastrini, and Solenopsidini tribes of subfamily Myrmicinae are dominated by an inferred cooperative (non-solitary) foraging method. Solitary foraging is inferred at internal nodes for the remaining tribes of Formicinae and Myrmicinae. Cooperative foraging has evolved independently in all subfamilies. Clades for which cooperative foraging is an inferred ancestral state rarely display solitary foraging behavior at the tips.

The majority of changes inferred from SCM are from a solitary to a cooperative foraging state: 56.5%, 35.6%, 47.9%, and 58.8% of changes for Jaffe, Beckers et al., Baroni Urbani, and Lanan respectively. Rarer are reversions from cooperative to solitary foraging: 13.3%, 34.1%, 17.5%, and 14%; rarer still are reversions from behaviors relying on chemical communication to those that do not: 6.06%, 9.03%, 28.3%, and 5.35%. All transitions and corresponding percentages are presented in Table 4. Visualizing the transition rates from our MuSSE and MCMC analyses supports the results from SCM, revealing that transitions between solitary and cooperative foraging behavior occur more often for SYM models (i.e. Beckers et al. and Baroni Urbani), and transitions from solitary to cooperative behavior occur more often in ARD models. Transitions between cooperative behaviors occur less often than those from/to solitary foraging behavior, although both Jaffe and Beckers et al. yield high transition rates between tandem running/recruitment and chemical mass recruitment/trunk trails (Figs. S1–S4). The speciation rates from our MuSSE and MCMC analyses each yield different conclusions: for Jaffe's classifications, tandem running allows for higher speciation; for Beckers et al., recruitment has the highest speciation rate followed by group hunting; for Baroni Urbani, solitary foraging followed by group hunting; and for Lanan, soli-

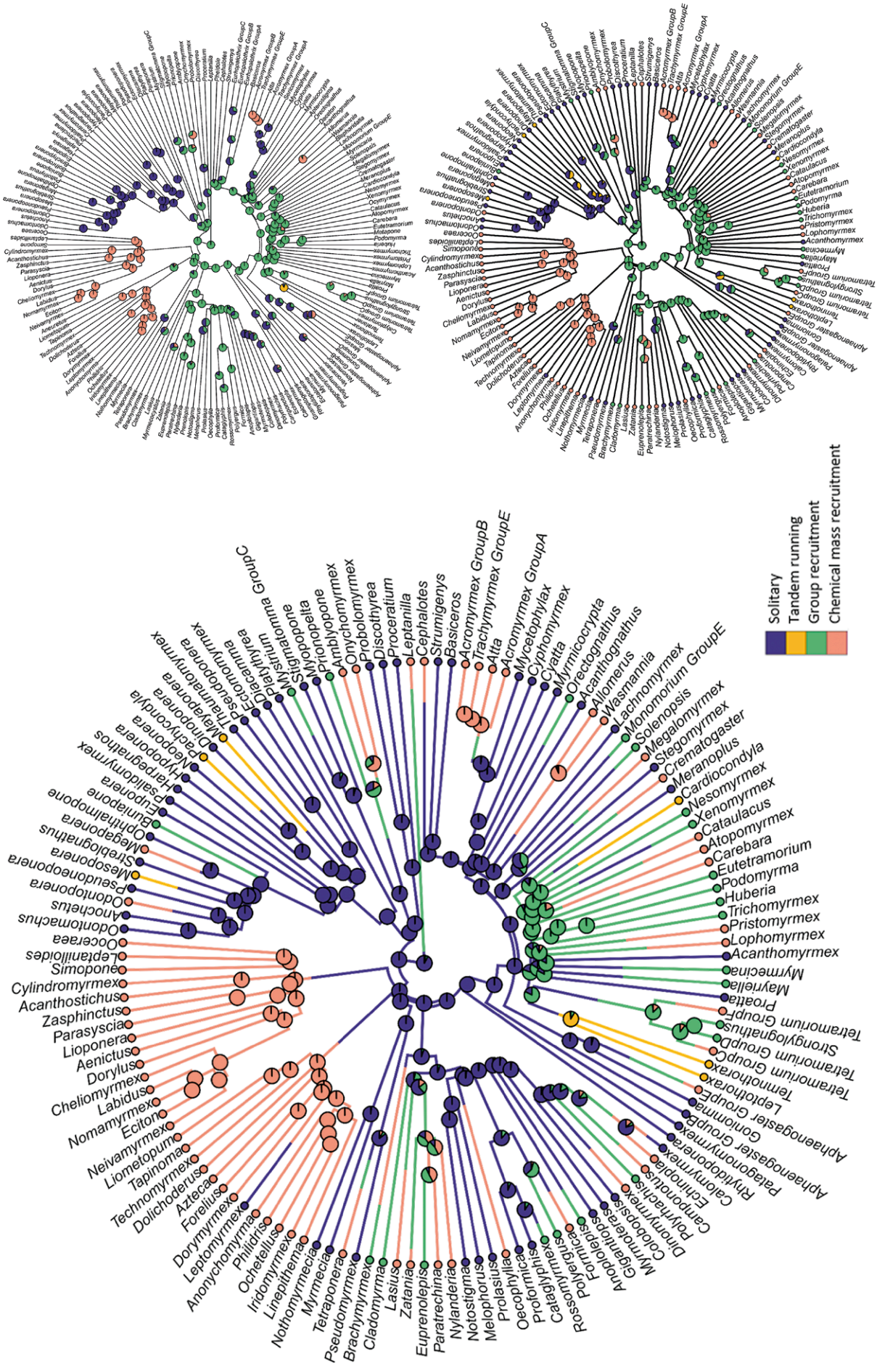

Fig. 1. Ancestral state reconstruction of JAFFE (1984) foraging classifications. Clockwise from left: SCM; ML (polymorphic data); ML (monomorphic data).

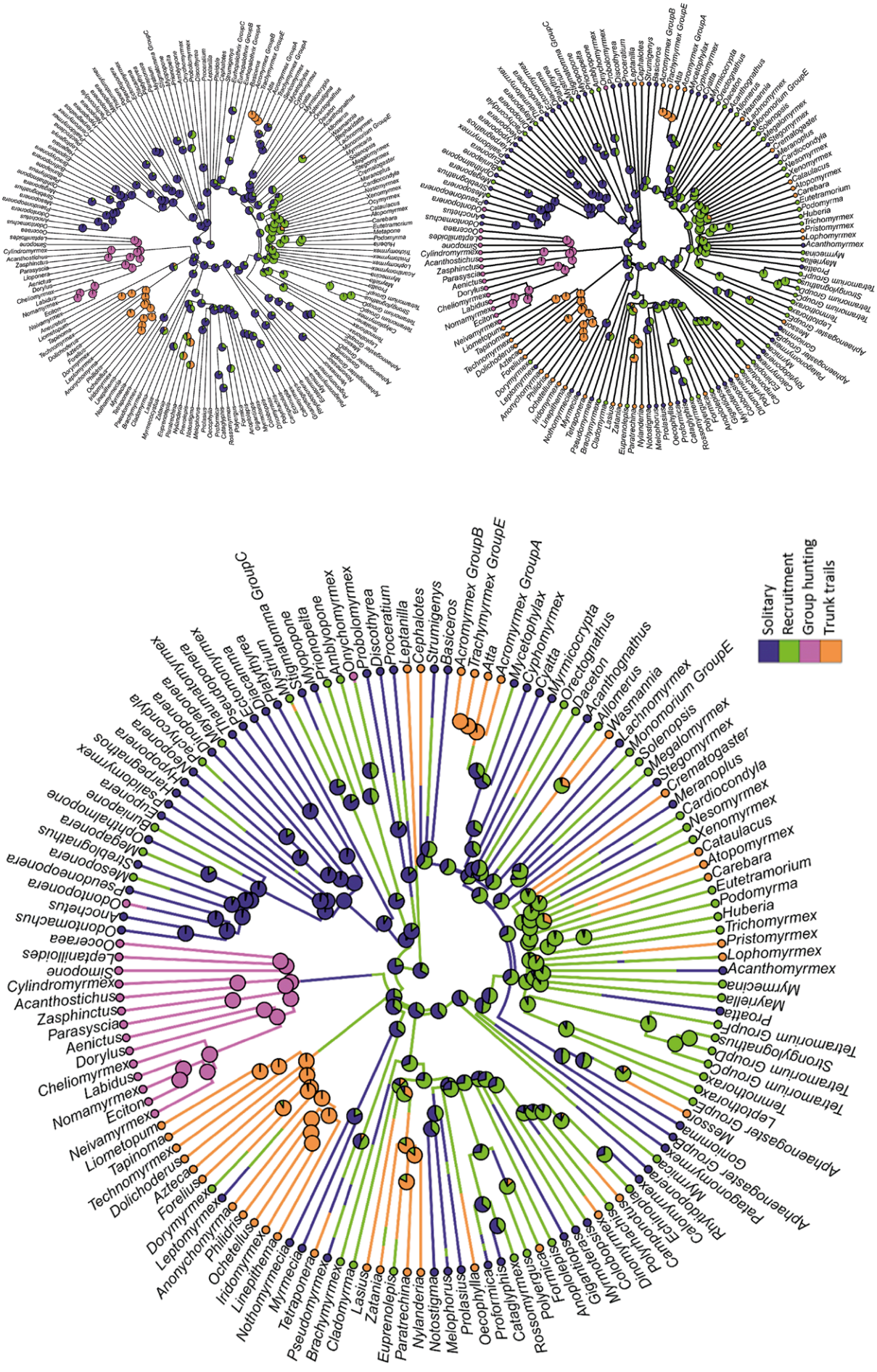

Fig. 2. Ancestral state reconstruction of Beckers et al. (1989) foraging classifications. Clockwise from left: SCM; ML (polymorphic data); ML (monomorphic data).

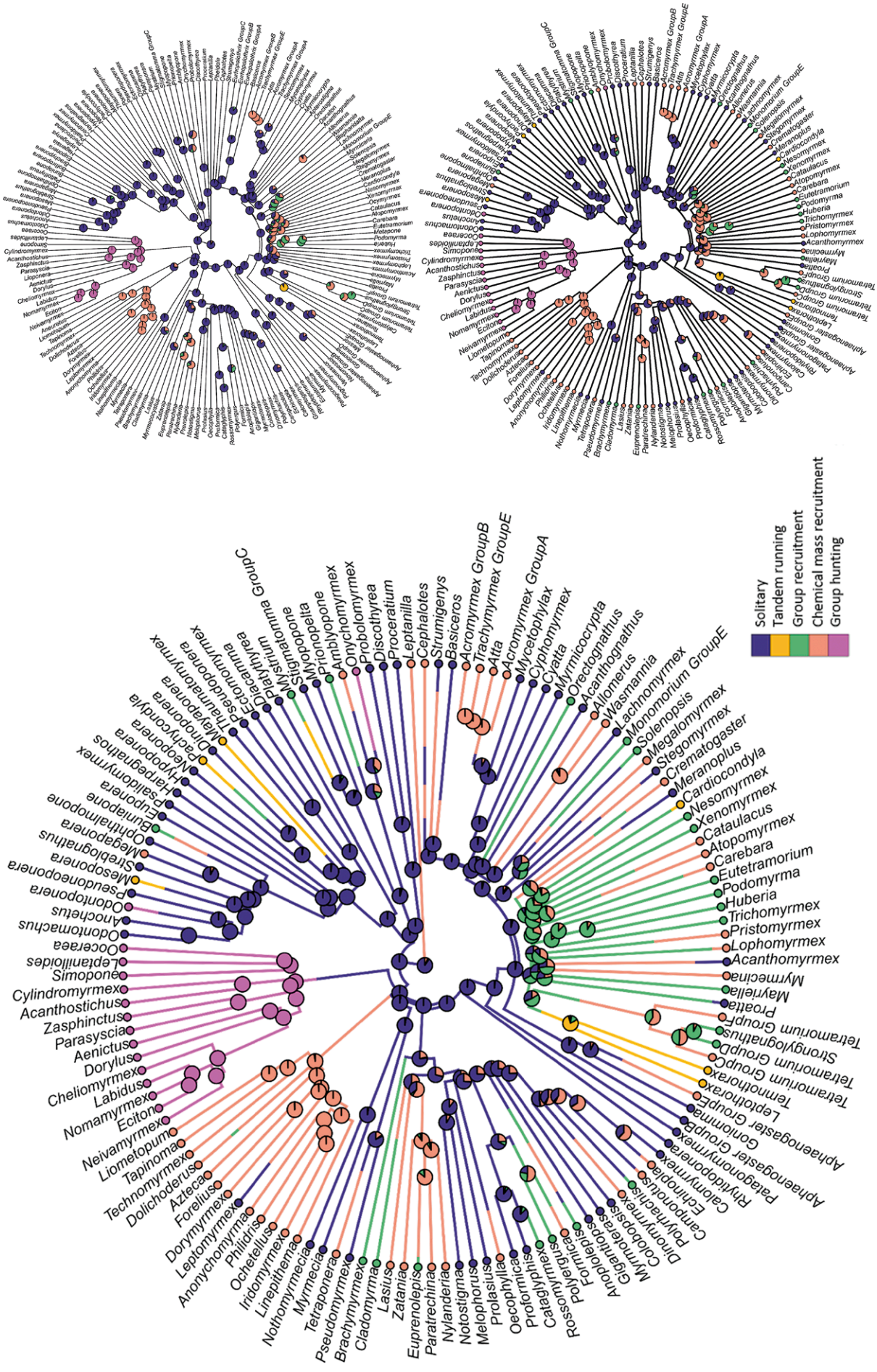

Fig. 3. Ancestral state reconstruction of Baroni Urbani (1993) foraging classifications. Clockwise from left: SCM; ML (polymorphic data); ML (monomorphic data).

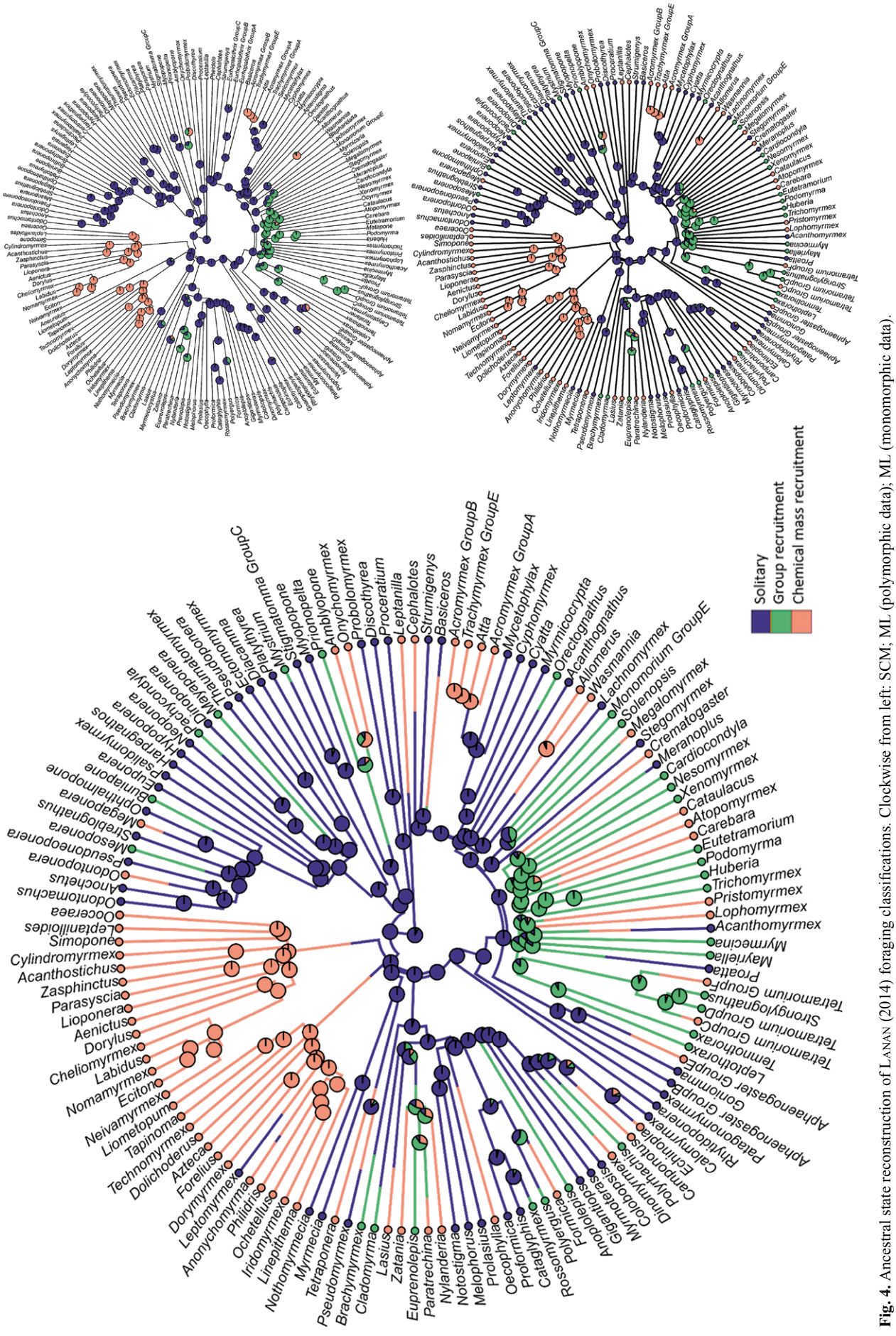

Fig. 4. Ancestral state reconstruction of Lanan (2014) foraging classifications. Clockwise from left: SCM; ML (polymorphic data); ML (monomorphic data).

Table 2. Log likelihoods, Akaike information criterion values, and number of parameters per transition rate model. Chosen models and related values are bolded.

	Polymorphism; ML (*rayDISC*)				Monomorphism; ML (*ace*)				Monomorphism; SCM (*make.simmap*)				
	Model	logL	AIC	AICc	AICcW	Model	logL	AIC	AICc	AICcW	Model	logL	AIC	AICc	AICcW	# Param
Jaffe (1984)	ER	-155	311.3	311.3	0.00956	ER	-156	314.1	314.1	0.0112	ER	-161	323.2	323.2	0.0004105	1
	SYM	-146	303.5	304.1	0.35046	SYM	-147	306.3	306.9	0.4123	SYM	-149	309.8	310.3	0.2524625	6
	ARD	**-138**	**300.4**	**302.9**	**0.63998**	**ARD**	**-140**	**303.7**	**306.2**	**0.5765**	**ARD**	**-141**	**306.2**	**308.2**	**0.747127**	12
Beckers et al. (1989)	ER	-156	314	314.1	9.50E-07	ER	-157	316.8	316.8	1E-06	ER	-158	317.1	317.1	8E-08	1
	SYM	**-137**	**285.7**	**286.4**	**1**	**SYM**	**-138**	**288.5**	**289.1**	**0.9955**	**SYM**	**-136**	**284**	**284.5**	**0.9975893**	6
	ARD	-148	319.2	321.7	2E-08	ARD	-137	297.5	299.9	0.0045	ARD	-135	294.6	296.5	0.0024107	12
Baroni Urbani (1993)	ER	-169	340	340	2.53E-04	ER	-171	343.2	343.2	0.0002	ER	-177	356.9	357	2.88E-06	1
	SYM	**-151**	**321.7**	**323.7**	**0.99975**	**SYM**	**-152**	**324.7**	**326.4**	**0.9995**	**SYM**	**-155**	**330.1**	**331.4**	**0.9995864**	10
	ARD	-188	416.9	424.1	0	ARD	-148	335.5	342.8	0.0003	ARD	-151	341.5	347	0.0004107	20
Lanan (2014)	ER	-132	266	266	0.17111	ER	-152	305.2	305.2	0	ER	-136	273.9	273.9	0.1090185	1
	SYM	-132	269.9	270.1	0.02249	SYM	-152	309.2	309.4	0	SYM	-136	277.5	277.7	0.01628	3
	ARD	**-125**	**262.3**	**262.9**	**0.8064**	**ARD**	**-126**	**264.5**	**265.1**	**1**	**ARD**	**-129**	**269.2**	**269.7**	**0.8747015**	6

tary foraging. Speciation rates for other behaviors are close to or at zero (see Figs. S5–S8). Significant speciation rates are visualized in Fig. 5.

4. Discussion

In this study, we compile a dataset of foraging behaviors of ants, classifying them according to the works of Jaffe (1984), Beckers et al. (1989), Baroni Urbani (1993), and Lanan (2014). Although our species representation is small in relation to extant diversity (3.6% of described extant species), our dataset represents over half of all current extant genera (51%) and 13 of the 17 extant subfamilies. Our subsequent analyses give strong support to the theory that solitary foraging is the ancestral foraging behavior of the Formicidae, and that cooperative behaviors have arisen independently multiple times within each subfamily. These patterns are consistent across each classification method, and are maintained even when comparing our polymorphic and monomorphic datasets.

Our results suggest that many cooperative foraging behaviors arise from solitary foraging behavior and stabilize. Reversions from cooperative foraging to solitary are rare, and these inferred reversions may be due to gaps in our dataset. For instance, the genus *Leptomyrmex* is classified as a solitary forager within the cooperative-dominated subfamily Dolichoderinae, yet the only published account of *Leptomyrmex* foraging behavior is from 1916 (Wheeler 1916). As behavior is more labile than physical traits, cooperative foraging behaviors may be mistakenly reported as solitary if single workers are in the process of recruitment, reported behaviors may be biased towards those that are more conspicuous, or a given species might exhibit unreported polymorphic behaviors. Solitary foraging could also result from ecological context and environmental stressors, rather than physical incapability (Traniello 1989; Jaffe 1984; Baroni Urbani 1993; Torres-Contreras et al. 2007). Such constraints may be the spatial and temporal distribution of food sources (Carroll & Janzen 1973; Sundström 1993), size of food source (Hölldobler et al. 1992), the quality or type of the food source (Cogni & Oliveira 2004), prey weight and size (Schatz et al. 1997), predation by other organisms (Hunt 1983), substrate surface temperature (Ruano et al. 2000; Van Oudenhove et al. 2012), season (Judd 2005; Heller & Gordon 2006), and innumerable other factors. Therefore, while a species might have the morphological capability for complex cooperative foraging behaviors, solitary foraging may be the most efficient within a given environment.

In addition, our results suggest that once a chemical-based cooperative behavior evolves, transitions to other methods of cooperative foraging rarely occur. Traniello (1977) and Hölldobler & Wilson (1990) hypothesize that foraging behaviors follow a stepwise means of evolution, transitioning from less efficient to more efficient foraging methods along a phylogeny – for example: solitary, to tandem running, to group recruitment, to chemical mass recruitment. Further analyses of foraging behavior may be able to test an irreversible transition rate model, as it is suggested by our analysis that more complex transition rate models better reflect the evolution of foraging behavior. Wilkins et al. (2006) suggests that recruitment behaviors evolved primarily as a means for nest relocation, and were secondarily applied to foraging. This hypothesis is

Table 3. Likelihoods and posterior probabilities for the root state of our ant phylogeny. Highest likelihood/probability states are bolded.

	Character states	Scaled root likelihood (*rayDISC*)	Scaled root likelihood (*ace*)	Posterior probability at root (*describe.simmap*)
Jaffe (1984)	Solitary	0.0182	0.044	**0.914**
	Tandem running	0	0.004	0
	Group recruitment	**0.97**	**0.918**	0.064
	Chemical mass recruitment	0.0118	0.034	0.022
Beckers et al. (1989)	Solitary	**0.775**	**0.651**	**0.664**
	Recruitment	0.1812	0.304	0.296
	Group hunting	0.0003	0	0
	Trunk trails	0.0435	0.045	0.04
Baroni Urbani (1993)	Solitary	**0.897**	**0.895**	**0.9**
	Tandem running	0	0.002	0.002
	Group recruitment	0.03	0.026	0.022
	Chemical mass recruitment	0.073	0.077	0.074
	Group hunting	0	0	0.002
Lanan (2014)	Solitary	**0.918**	**0.929**	**0.912**
	Group recruitment	0.0566	0.047	0.064
	Chemical mass recruitment	0.0254	0.024	0.024

Table 4. Changes inferred from SCM. S = solitary, TR = tandem running, GR = group recruitment, CMR = chemical mass recruitment, R = recruitment, GH = group hunting, TT = trunk trails.

Jaffe (1984)	Total changes:	64.322											
	Type:	S->TR	S->GR	S->CMR	TR->S	TR->GR	TR->CMR	GR->S	GR->TR	GR->CMR	CMR->S	CMR->TR	CMR->GR
	Number:	2.61	19.567	14.152	0	0	0	6.144	2.476	15.464	2.394	0	1.506
	Percentage:	4.1%	30.4%	22.0%	0.0%	0.0%	0.0%	9.6%	3.8%	24.0%	3.7%	0.0%	2.3%
Beckers et al. (1989)	Total changes:	100.742											
	Type:	S->R	S->GH	S->TT	R->S	R->GH	R->TT	GH->S	GH->R	GH->TT	TT->S	TT->R	TT->GH
	Number:	31.586	2.624	1.642	33.616	0.442	21.73	0.06	0.012	0	0.71	8.32	0
	Percentage:	31.4%	2.6%	1.6%	33.4%	0.4%	21.6%	0.1%	0.0%	0.0%	0.7%	8.3%	0.0%
Baroni Urbani (1993)	Total changes:	74.796											
	Type:	S->TR	S->GR	S->CMR	S->GH	TR->S	TR->GR	TR->CMR	TR->GH	GR->S	GR->TR	GR->CMR	GR->GH
	Number:	3.214	10.944	18.942	2.722	0.176	0.268	0	0	3.894	2.344	11.084	0
	Percentage:	4.3%	14.6%	25.3%	3.6%	0.2%	0.4%	0.0%	0.0%	5.2%	3.1%	14.8%	0.0%
	Type:	CMR->S	CMR->TR	CMR->GR	CMR->GH	GH->S	GH->TR	GH->GR	GH->CMR				
	Number:	8.996	0	11.834	0.322	0.052	0	0	0.004				
	Percentage:	12.0%	0.0%	15.8%	0.4%	0.1%	0.0%	0.0%	0.0%				
Lanan (2014)	Total changes:	62.742											
	Type:	S->GR	S->CMR	GR->S	GR->CMR	CMR->S	CMR->GR						
	Number:	23.372	13.508	6.206	16.302	2.558	0.0796						
	Percentage:	37.3%	21.5%	9.9%	26.0%	4.1%	0.1%						

supported by the fact that mobile colonies, such as the nomadic army ants, also display highly cooperative, chemical-based group hunting behavior. Likewise, a number of publications mention recruitment observed solely for nest relocation, with foragers only occasionally using recruitment for foraging for food (Abe & Uezu 1977; Freitas 1995; McGlynn et al. 2003). A thorough collection of nest relocation data may reveal a relationship between nest relocation and tendency for cooperative foraging behaviors, or reveal nest relocation as a transitional step between solitary and cooperative foraging.

While all classification methods reveal similar patterns when comparing the results of ASR, the speciation rates from MuSSE and MCMC analyses yield more dissimilar results. We presume that bias in dataset representation for each classification scheme can at least partially explain the disparity. For example, both Beckers et al. (1989) and Baroni Urbani (1993) devote a category to group hunting behavior, a behavior characteristic of the Dorylinae subfamily. Because group hunting is a highly specialized behavior, high speciation is not unprecedented; yet other classification methods do not devote a category to group hunting. The high speciation rate due to tandem running could result from the seemingly necessary transitions between solitary foraging and tandem running, and chemical mass recruitment and tandem run-

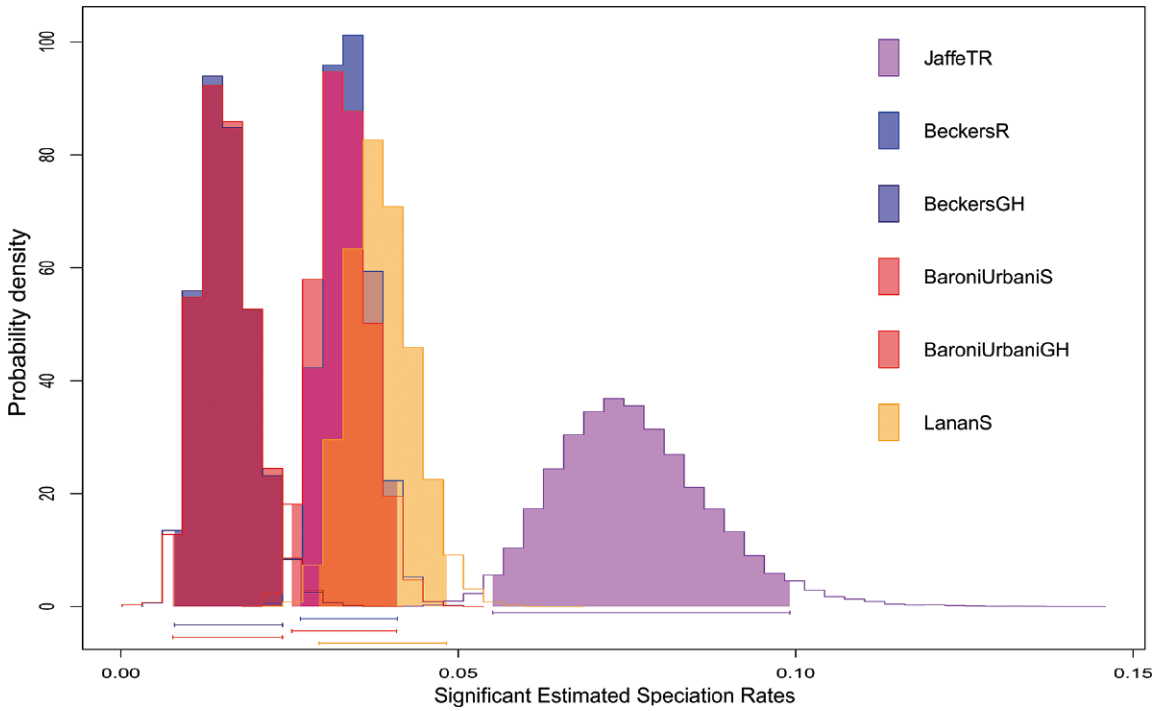

Fig. 5. Significant (non-zero) speciation rates from each analysis. TR = tandem running; R = recruitment; GH = group hunting; S = solitary. High speciation rates for group hunting may be due to the fact that the entirety of Dorylinae data were classified "group hunting" by Beckers et al. and Baroni Urbani classifications. The high speciation for tandem running is likely due to high transition rates for the behavior.

ning inferred for Jaffe (1984) classifications (see Fig. S1). It is also likely that these methods of analysis are less robust with our genus-level data.

The low AICc weights resulting from the Jaffe (1984) and Lanan (2014) classification methods suggest that while an ARD model is preferable, the amount of data available do not support the numerous parameters of an ARD model (Table 2). While our results provide insight into how foraging behavior has evolved across the ants, we are limited by the number of published detailed observations of foraging behavior for many species of ants. Incorporating additional species foraging behaviors will allow more conclusive transition and speciation rates, as well as otherwise ambiguous internal node states, to be inferred. While grouping behaviors into broad categories reduces the number of parameters, there is the possibility that similar, yet convergent, behaviors may be grouped together. In the ants, trail and recruitment pheromones originate from several different glands; the gland of origin is often related to the subfamily (David Morgan 2009), suggesting that otherwise similar recruitment behaviors are convergent in morphological origin as well.

Therefore, while we applaud the advances in molecular research regarding the ants, more data are needed on their behaviors; we therefore agree with past authors that detailed observations on behavior should be included in publications whenever possible. In addition, as of now, we lack a well-supported means of inferring the correlation between multiple discrete, multistate traits. Foraging behavior is assumed to be influenced by a number of ecological and behavioral factors, yet there have yet to be any published, modern analyses of correlation. Given the complexity of foraging behavior and what influences it, as computation methods improve so will our understanding of this charismatic, significant trait of the Formicidae.

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Electronic Supplement Files

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File 1: reeves&moreau-antforaging-asp2019-electronicsupplement-1 — **Fig. S1.** Transition rates for an ARD model. A transition from tandem running to chemical mass recruitment has a notably higher rate than any other transitions. Transitions between solitary and tandem running, and chemical mass recruitment and tandem running, are close to 0. Numbers: 1 = Solitary foraging, 2 = tandem running, 3 = group recruitment, 4 = chemical mass recruitment. — **Fig. S2.** Transition rates for a SYM model. Half of transition rates are close to 0; transitions between solitary and recruitment foraging, and recruitment and trunk trails have notably higher rates than other transitions. The high spread for the transition between solitary and trunk trails is likely due to these rates not actually being symmetrical. Numbers: 1 = Solitary foraging, 2 = recruitment, 3 = group hunting, 4 = trunk trails. — **Fig. S3.** Transition rates for a SYM model. Transitions between solitary foraging and group hunting, and between solitary foraging and chemical mass recruitment, occur at a higher rate than others; however, high spread is likely due to these rates not being truly symmetrical. Low probability density is likely due to the high number of parameters. Numbers: 1 = Solitary foraging, 2 = group recruitment, 3 = chemical mass recruitment, 4 = group hunting. — **Fig. S4.** Transition rates from an ARD model. A transition from solitary foraging to chemical mass recruitment has a notably higher rate than any other transitions. Transitions from chemical mass recruitment to group recruitment, chemical mass recruitment to solitary foraging, and group recruitment to solitary foraging have non-zero rates. Numbers: 1 = Solitary foraging, 2 = group recruitment, 3 = chemical mass recruitment. — **Fig. S5.** Speciation rates from an ARD model. Lambda 1 = solitary; lambda 2 = tandem running; lambda 3 = group recruitment; lambda 4 = chemical mass recruitment. — **Fig. S6.** Speciation rates from a SYM model. Lambda 1 = solitary; lambda 2 = recruitment; lambda 3 = group hunting; lambda 4 = trunk trails. — **Fig. S7.** Speciation rates from a SYM model. Lambda 1 = solitary; lambda 2 = tandem running; lambda 3 = group recruitment; lambda 4 = chemical mass recruitment, lambda 5 = group hunting. — **Fig. S8.** Speciation rates from an ARD model. Lambda 1 = solitary; lambda 2 = group recruitment; lambda 3 = chemical mass recruitment. — DOI: 10.26049/ASP77-2-2019-10/1

File 2: reeves&moreau-antforaging-asp2019-electronicsupplement-2.xlsx — **Table S1.** Monomorphic and polymorphic foraging classifications for ant species. — DOI: 10.26049/ASP77-2-2019-10/2

File 3: reeves&moreau-antforaging-asp2019-electronicsupplement-3.docx — **Table S2.** State distributions for our polymorphic datasets. S = solitary; TR = tandem running; CMR = chemical mass recruitment; GR = group recruitment; GH = group hunting; R = recruitment; TT = trunk trails — **Table S3.** State distributions for our monomorphic datasets. S = solitary; TR = tandem running; CMR = chemical mass recruitment; GR = group recruitment; GH = group hunting; R = recruitment; TT = trunk trails — **Table S4.** Results of the joint reconstruction with rayDISC. Jaffe: 1 = Solitary foraging, 2 = tandem running, 3 = group recruitment, 4 = chemical mass recruitment; Beckers et al.: 1 = Solitary foraging, 2 = recruitment, 3 = group hunting, 4 = trunk trails; Baroni Urbani: 1 = Solitary foraging, 2 = group recruitment, 3 = chemical mass recruitment, 4 = group hunting; Lanan: 1 = Solitary foraging, 2 = group recruitment, 3 = chemical mass recruitment. — DOI: 10.26049/ASP77-2-2019-10/3