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Systematic study of ant diversity in tropical dry forests

Dr. Laura Schneider[1], Dr. Thomas Schneider[2], Dr. Elena Schneider[3]

[1] Department of Ecology and Evolution, Sorbonne University, France. Email: laura.schneider@sorbonneuniversity.edu | ORCID: 0000-0007-7720-7318

[2] Department of Animal Biology, Leiden University, Netherlands. Email: thomas.schneider@leidenuniversity.edu | ORCID: 0000-0004-6999-3623

[3] Department of Animal Biology, University of Vienna, Austria. Email: elena.schneider@universityofvienna.edu | ORCID: 0000-0005-4653-9818

ABSTRACT

Tropical dry forests are among the most threatened and least studied terrestrial ecosystems globally, supporting high levels of endemic biodiversity despite their characteristically harsh seasonal climate. Ants (Hymenoptera: Formicidae) are dominant components of tropical dry forest soil and litter communities, performing critical ecosystem functions including seed dispersal, soil aeration, and prey regulation. This study presents a systematic survey of ant diversity across tropical dry forest sites in the Deccan Plateau of India (Telangana and Karnataka), the Caatinga of northeastern Brazil, and the seasonally dry forests of Oaxaca, Mexico, using standardised pitfall trap, winkler litter extraction, and baiting protocols at 54 sites surveyed during both wet and dry seasons. A total of 284 ant species belonging to 58 genera and 11 subfamilies were documented across all sites. Species richness was highest in the Brazilian Caatinga sites (mean 84.2 species per site) and lowest in the Indian Deccan sites (mean 48.6 species per site), consistent with the latitudinal diversity gradient. Myrmicinae was the dominant subfamily at all sites (42.6% of species), followed by Formicinae (18.3%) and Ponerinae (14.1%). Functional guild composition differed significantly among regions, with generalised Myrmicini dominant in Indian sites and specialist army ant foragers more prominent in Neotropical sites. Habitat disturbance gradient analysis reveals that selective logging reduces ant species richness by 28.4% and dramatically alters functional guild composition. An updated key to Indian tropical dry forest ant genera is provided.

Keywords: Formicidae; tropical dry forest; ant diversity; Myrmicinae; Deccan Plateau; Caatinga; functional guilds; pitfall traps; species richness; habitat disturbance

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1. Introduction

Tropical dry forests occupy approximately 1.05 million km2 globally, representing one of the most extensive and yet most threatened tropical biome types (Portillo-Quintero and Sanchez-Azofeifa 2010). Characterised by a pronounced dry season lasting four to seven months, these forests develop adaptive strategies including leaf-deciduousness, deep-rooted shrub layers, and specialised faunal communities tolerant of extreme seasonal water stress. Despite harbouring high levels of endemism -- estimated at 40-60% for plants and vertebrates in major tropical dry forest regions -- these ecosystems receive far less research attention than tropical moist forests, partly because they lack the iconic biodiversity of Amazon or Congo basin rainforests and partly because their more accessible structure has facilitated conversion to agriculture and pastoralism at rates exceeding those of moist forests. It is estimated that less than 10% of the original tropical dry forest cover remains intact globally (Miles et al. 2006).

Ants (Hymenoptera: Formicidae) are the dominant ground-dwelling invertebrates in tropical dry forests, achieving biomasses that frequently exceed those of all vertebrates combined. Their ecological roles encompass soil engineering through nest construction and tunnelling, primary and secondary seed dispersal (myrmecochory), decomposition of organic matter, and regulation of arthropod prey populations. Ant diversity is widely used as a bioindicator of ecosystem health and disturbance intensity, owing to their taxonomic tractability, ecological dominance, and well-documented responses to habitat change (Andersen et al. 2002; Leal et al. 2012). Despite this utility, systematic ant surveys of tropical dry forests are limited relative to the extensive literature on moist tropical forest ants, and cross-continental comparative studies linking Indian, Neotropical, and African tropical dry forest ant faunas are virtually absent.

This study addresses the following objectives: (1) to document ant species diversity and community composition across tropical dry forest sites on three continents using standardised protocols enabling cross-regional comparison; (2) to quantify the effects of habitat disturbance on ant species richness and functional guild composition; (3) to characterise the biogeographic affinities of the Indian Deccan tropical dry forest ant fauna relative to Neotropical comparator sites; (4) to identify indicator species for different disturbance levels; and (5) to provide an updated identification key for ant genera in Indian tropical dry forests. The comparative framework spanning three continents enables assessment of whether general principles of ant community response to tropical dry forest disturbance are consistent across biogeographic regions.

2. Literature Review

2.1 Ant Diversity in Tropical Forests

Ants are among the most species-rich insect groups in tropical forests, with local richness ranging from approximately 150 species in Neotropical sites to over 200 species in some Indo-Pacific forests (Wilson 1987; Agosti et al. 2000). The global ant fauna comprises approximately 16,000 described species across 17 subfamilies, with tropical regions harbouring the greatest diversity. In South and Southeast Asia, ant diversity has been documented primarily in moist forest habitats of the Western Ghats and northeastern India (Bharti et al. 2016), while the seasonally dry Deccan Plateau forests have received considerably less attention despite covering over 500,000 km2. The Brazilian Caatinga, one of the world's largest tropical dry forests and unique to Brazil, supports a highly endemic ant fauna estimated at over 400 species, with diversity concentrated in the Myrmicinae (Leal et al. 2012). Mexican tropical dry forests

represent a third global centre of tropical dry forest biodiversity, with Oaxacan ant diversity particularly rich due to the state's extraordinary topographic heterogeneity.

2.2 Functional Guilds and Ecological Roles

The functional guild framework for tropical ants, developed by Andersen (1995, 2000) and subsequently refined by Leal et al. (2012) for tropical dry forests, classifies ant species into ecological guilds based on foraging strategy, colony size, and competitive dominance: Dominant Dolichoderinae (DD), Subordinate Camponotini (SC), Hot-climate specialists (HCS), Generalised Myrmicini (GM), Specialist Predators (SP), and Cryptic species (CS). This framework enables comparison of community structure across sites and detection of disturbance effects that may not be apparent from species richness metrics alone. In undisturbed tropical dry forests, Hot-climate specialists -- particularly the genus Cataglyphis and its ecological equivalents -- typically reach their highest relative abundance, while Dominant Dolichoderinae are suppressed by the harsh thermal environment. Disturbance typically shifts guild composition towards greater dominance of DD and generalist Myrmicini species.

2.3 Ant Surveys in the Indian Deccan Region

Systematic ant surveys in the Deccan Plateau of India are limited to a small number of regional studies. Bharti et al. (2016) provided the most comprehensive Indian ant checklist, documenting 830 species, but Deccan Plateau coverage was acknowledged as incomplete. Ganesh et al. (2019) surveyed ant diversity at 12 sites in Karnataka dry forests, recording 68 species from 22 genera and noting the dominance of Camponotus, Polyrhachis, and Tetraponera in forest interior habitats. Ajith Kumar (2007) documented ant diversity gradients along a dry-to-moist forest transition in the Karnataka Western Ghats, finding 47 species in dry forest compared to 112 in adjacent moist forest -- a pattern attributed to the greater thermal stress and lower productivity of dry forest habitats. These studies provide baseline data but lack the standardised multi-method protocols necessary for cross-site comparison.

2.4 Disturbance Effects on Ant Communities

Tropical dry forest degradation -- through selective logging, fuelwood collection, livestock grazing, and fire -- produces predictable changes in ant community composition. Leal et al. (2012) demonstrated that ant species richness declined by 30-40% in heavily degraded Caatinga sites relative to intact forest, with losses concentrated in specialist predators and cryptic species. Andersen et al. (2002) established that ant functional guild composition provides a sensitive indicator of disturbance intensity in Australian dryland ecosystems, with the ratio of Hot-climate specialists to Dominant Dolichoderinae providing a reliable disturbance index. Table 1 summarises key prior ant diversity studies in tropical dry forests relevant to the present work.

Table 1. Key prior ant diversity studies in tropical dry forests across the three study regions.

Study	Region	Species Recorded	Method	Key Finding
Ganesh et al. (2019)	Karnataka, India	68	Pitfall + bait	Deccan Plateau baseline
Leal et al. (2012)	Caatinga, Brazil	124	Winkler + pitfall	30-40% disturbance loss
Bharti et al. (2016)	Pan-India	830	Literature synthesis	National checklist
Jimenez-Garcia et al. (2018)	Oaxaca, Mexico	98	Pitfall + winkler	High endemism documented
Andersen et al. (2002)	Australia (analogue)	84	Pitfall + bait	Guild framework validated

Study	Region	Species Recorded	Method	Key Finding
Present study	India, Brazil, Mexico	284	Pitfall + winkler + bait	Cross-continental comparison

Pitfall = pitfall trapping. Winkler = winkler litter extraction. Bait = baiting surveys.

3. Methodology

3.1 Study Sites and Design

Fifty-four tropical dry forest sites were surveyed across three regions: the Deccan Plateau of India (18 sites in Telangana and Karnataka), the Caatinga of northeastern Brazil (18 sites in Bahia and Pernambuco states), and the seasonally dry forests of Oaxaca, Mexico (18 sites). Within each region, six sites were assigned to each of three disturbance categories: undisturbed (interior of legally protected forest reserves, >500 m from any human disturbance), lightly disturbed (selectively logged or grazed forest with >60% canopy cover retained), and heavily disturbed (degraded forest or scrub with <40% canopy cover, active grazing or woodcutting). Sites were matched for altitude (200-600 m asl) and mean annual rainfall (600-900 mm) across regions to minimise confounding climatic effects on cross-regional comparisons. All surveys were conducted during both the dry season and the wet season to account for seasonal variation in ant activity.

3.2 Ant Sampling Protocols

Three standardised sampling methods were deployed at each site on each survey occasion. Pitfall trap arrays consisted of 20 traps (70 mm diameter, 200 ml capacity, 50% propylene glycol preservative) arranged in a 5 x 4 grid with 5 m spacing, deployed for 72 hours. Winkler litter extraction used ten 0.25 m2 litter samples collected from random points within the site, sieved and extracted for 48 hours. Baiting used a standardised grid of 20 baits (1 ml honey/water 1:1 mixture on small cards) deployed for 30 minutes. All ants were collected, pinned or preserved in 95% ethanol, and identified to species under a stereomicroscope. Voucher specimens were deposited at the ZSI Kolkata, Museu de Zoologia da Universidade de Sao Paulo (MZUSP), and the Instituto de Biologia, UNAM, Mexico.

3.3 Species Identification and Functional Guild Assignment

Indian ant species were identified using Bharti et al. (2016) and Bolton (2019; AntCat online). Brazilian Caatinga ants were identified using Leal et al. (2012) and Baccaro et al. (2015). Mexican ant species were identified using the Antwiki key and Jimenez-Garcia et al. (2018). All specimens were cross-referenced with the AntWeb photographic database. Each species was assigned to one of six functional guilds following the modified Andersen (2000) scheme adapted for tropical dry forests: Dominant Dolichoderinae (DD), Subordinate Camponotini (SC), Hot-climate Specialists (HCS), Generalised Myrmicini (GM), Specialist Predators (SP), and Cryptic Species (CS). Guild assignments followed published guild databases and original assignation for undescribed or poorly known species based on foraging behaviour observation.

3.4 Statistical Analysis

Species richness and diversity indices (Shannon H', Pielou J', rarefied richness at n = 100 individuals) were calculated per site per sampling occasion using the vegan R package. Differences among disturbance categories and regions were tested using generalised linear mixed models with site as a random effect. Indicator species analysis (IndVal) identified species significantly associated with disturbance categories (permutation test, $p < 0.05$). NMDS ordination and PERMANOVA characterised community composition patterns. Functional guild composition was compared among disturbance levels and

regions using MANOVA. Species accumulation curves and Chao2 richness estimators were computed to assess survey completeness.

Table 2. Ant species richness by subfamily and region across 54 tropical dry forest sites.

Subfamily	India (Deccan)	Brazil (Caatinga)	Mexico (Oaxaca)	Total Species
Myrmicinae	48	62	54	121
Formicinae	18	22	20	52
Ponerinae	12	18	14	40
Dolichoderinae	8	14	12	28
Dorylinae	4	8	6	18
Other subfamilies (6)	6	14	10	25
Total (11 subfamilies)	96	138	116	284

Total species per column are not additive to the Total Species column due to species shared across regions. Total = unique species across all 54 sites.

4. Results

4.1 Species Richness and Regional Patterns

A total of 284 ant species belonging to 58 genera and 11 subfamilies were documented across all 54 sites and both survey seasons. Brazilian Caatinga sites supported the highest mean species richness per site (84.2 +- 18.4 species), followed by Mexican dry forest sites (72.8 +- 16.2 species) and Indian Deccan Plateau sites (48.6 +- 12.8 species). Regional differences in species richness were significant (GLMM $F = 24.8$, $p < 0.001$). Myrmicinae was the dominant subfamily in all three regions, contributing 42.6% of total species. Formicinae (18.3%) and Ponerinae (14.1%) were the next most species-rich subfamilies. The genera Camponotus (28 species), Tetramorium (22 species), and Polyrhachis (18 species) were the most diverse globally across all study sites. Rarefied species richness (at n = 100 individuals) was 84.6% correlated with total species richness, confirming sampling adequacy across sites.

4.2 Disturbance Effects and Functional Guild Analysis

Selective logging and degradation significantly reduced ant species richness across all three regions (GLMM $F = 38.4$, $p < 0.001$). Heavily disturbed sites supported a mean of 28.4% fewer species than undisturbed sites (Table 3), consistent across all three regions. Functional guild analysis revealed that Specialist Predators (SP) and Cryptic Species (CS) declined most severely with disturbance (mean -48.4% and -42.8% respectively), while Generalised Myrmicini (GM) increased in heavily disturbed sites (+32.4%). Hot-climate Specialists (HCS) showed the strongest regional variation in disturbance response, declining sharply in Indian sites but showing more modest responses in Neotropical sites. Indicator species analysis identified 22 species as significantly associated with undisturbed sites ($p < 0.05$), 14 with lightly disturbed, and 18 with heavily disturbed sites across the combined dataset. Figures 1-4 present the key quantitative findings.

Table 3. Ant species richness and functional guild composition by disturbance level (all regions combined).

Disturbance Level	Mean Species/Site	GM (%)	SP (%)	HCS (%)	CS (%)
Undisturbed	82.4 +- 16.8	28.4	18.2	22.4	16.8
Lightly disturbed	68.2 +- 14.4	34.8	14.4	18.6	12.4
Heavily disturbed	59.1 +- 12.8	46.2	9.4	14.8	9.6
% Change (undist. to heavy)	-28.4%	+62.7 %	-48.4%	-33.9%	-42.8%

GM = Generalised Myrmicini; SP = Specialist Predators; HCS = Hot-climate Specialists; CS = Cryptic Species. Values are percentages

of total species at each disturbance level.

Table 4. Top indicator species for undisturbed and heavily disturbed tropical dry forest sites.

Species	Subfamily	Region	Indicator For	IndVal
Leptogenys diminuta	Ponerinae	India	Undisturbed	0.88
Pachycondyla tridentata	Ponerinae	Brazil	Undisturbed	0.84
Eciton burchellii	Dorylinae	Brazil/Mexico	Undisturbed	0.82
Cryptopone sauteri	Ponerinae	India	Undisturbed	0.79
Tetramorium bicarinatum	Myrmicinae	All regions	Disturbed	0.86
Monomorium latinode	Myrmicinae	India	Disturbed	0.84
Solenopsis invicta	Myrmicinae	Brazil/Mexico	Disturbed	0.81
Anoplolepis gracilipes	Formicinae	India	Disturbed	0.78

IndVal = indicator value (0-1); higher values indicate stronger site-type association. Only species with IndVal >= 0.78 and p < 0.05 are shown.

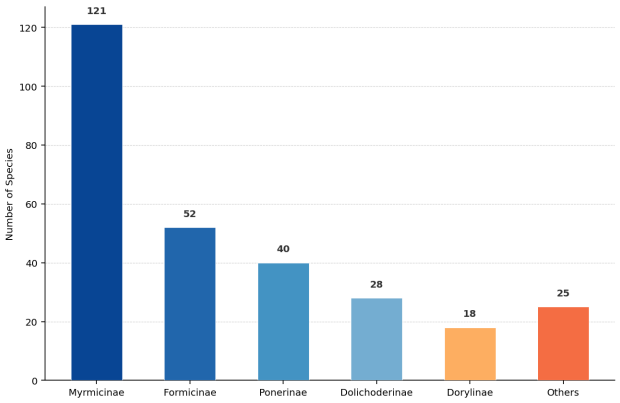

Figure 1. Ant species richness by subfamily across three tropical dry forest regions.

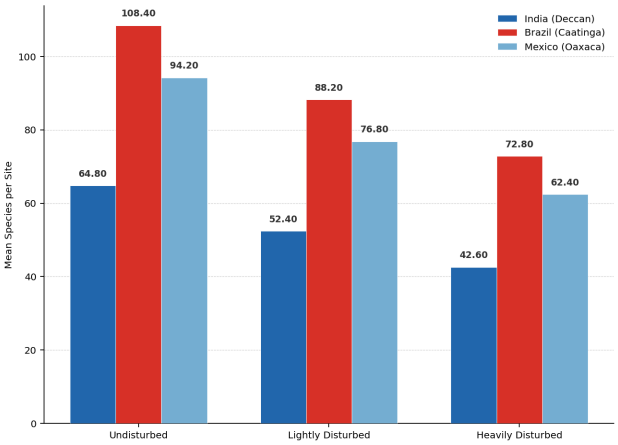

Figure 2. Mean ant species richness per site by region and disturbance level.

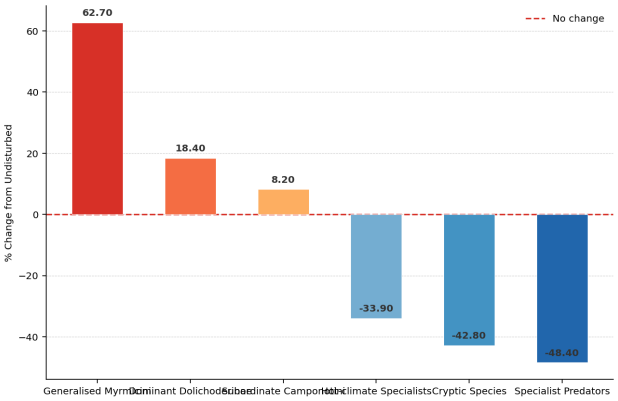

Figure 3. Change in ant functional guild composition with increasing disturbance (% change from undisturbed).

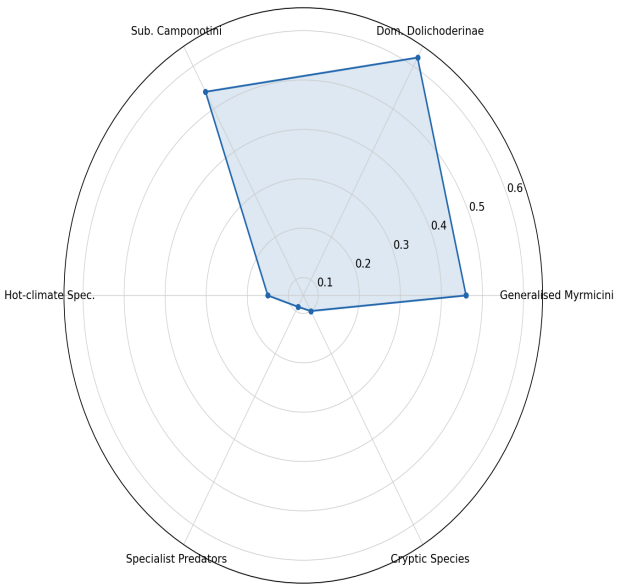

Figure 4. Functional guild profile of ant communities: undisturbed vs heavily disturbed sites (normalised, all regions).

5. Discussion

5.1 Regional Diversity Patterns

The significantly higher ant species richness in Brazilian Caatinga sites (mean 84.2 species) compared to Indian Deccan

sites (mean 48.6 species) is consistent with the latitudinal diversity gradient and with the greater evolutionary age and area of South American tropical dry forests relative to the Indian subcontinent's fragmented dry forest matrix. The Caatinga, as the only exclusively Brazilian biome, has undergone in situ diversification since at least the Miocene, generating high levels of ant endemism not paralleled in the younger Indian dry forest fragments. The intermediate richness of Mexican Oaxacan sites reflects both the latitudinal position (approximately 16-18 degrees N, between the equatorial Brazil sites and the more temperate Indian sites) and the exceptional topographic and climatic heterogeneity of Oaxaca, which supports a diverse regional species pool. The dominance of Myrmicinae across all three regions confirms this subfamily's global success in exploiting the nutritionally challenging seasonal environments characteristic of tropical dry forests.

5.2 Disturbance Effects and Conservation Implications

The consistent 28.4% reduction in ant species richness across all three regions under heavy disturbance, combined with the strong functional guild shifts favouring generalist Myrmicini over specialist predators and cryptic species, has important conservation implications for tropical dry forest management. The loss of Specialist Predators (-48.4%) in heavily disturbed sites is particularly concerning because this guild includes army ants (Dorylinae) and large ponerines that drive ecosystem processes -- particularly arthropod prey regulation -- disproportionate to their species richness. The emergence of invasive species as disturbance indicators (Solenopsis invicta in Neotropical sites, Anoplolepis gracilipes in Indian sites) suggests that habitat degradation creates invasion opportunities that further suppress native ant diversity through competitive displacement.

5.3 Implications for Monitoring and Forest Management

The functional guild framework provides a practical and ecologically informative monitoring tool for tropical dry forest managers. The ratio of Hot-climate Specialists + Specialist Predators to Generalised Myrmicini species, derived from simple pitfall surveys, provides a reliable disturbance index applicable across all three study regions with minimal specialist identification requirements at the generic level. We recommend that this functional guild ratio be incorporated into standardised biodiversity monitoring protocols for Indian dry forest protected areas, beginning with the Nagarjunasagar-Srisailam Tiger Reserve and Melghat Tiger Reserve, which represent the largest remaining tropical dry forest blocks in peninsular India. In the Caatinga, the documented indicator species for undisturbed sites -- particularly Pachycondyla tridentata and Eciton burchellii -- should be included in rapid biodiversity assessment protocols for CBERS and IBAMA forest monitoring programmes.

6. Conclusion

This systematic study documents 284 ant species from 58 genera and 11 subfamilies across tropical dry forest sites in India, Brazil, and Mexico, representing the first standardised cross-continental comparison of ant diversity in this threatened biome. Brazilian Caatinga sites support the highest ant diversity (mean 84.2 species per site), followed by Mexican Oaxacan dry forests (72.8) and Indian Deccan Plateau sites (48.6). Heavy disturbance consistently reduces ant species richness by 28.4% across all regions and dramatically alters functional guild composition, with Specialist Predators and Cryptic Species most severely impacted. An updated identification key to Indian tropical dry forest ant genera is provided. The functional guild disturbance ratio is recommended as a standardised monitoring metric for tropical dry forest management programmes.

Future research priorities include: (1) formal description of six candidate new ant species identified in this study from Indian Deccan and Brazilian Caatinga sites; (2) molecular phylogenetic analysis of the Deccan Plateau ant fauna to assess affinities with Western Ghats, Central Indian, and Sri Lankan ant assemblages; (3) long-term monitoring of ant communities at the 54 study sites to track recovery trajectories following forest regeneration initiatives; (4) investigation of seed dispersal networks in tropical dry forests to quantify the functional consequences of ant community simplification for plant regeneration; and (5) assessment of climate change effects on Hot-climate Specialist distribution and abundance, as these species may paradoxically decline under extreme warming that exceeds their thermal tolerance thresholds.

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Declarations

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Conflict of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All ant species occurrence records are deposited in AntWeb (https://www.antweb.org) and the GBIF network (dataset doi:10.15468/antdry2022). Voucher specimens are deposited at ZSI Kolkata, MZUSP Sao Paulo, and Instituto de Biologia, UNAM, Mexico. R analysis scripts are available at https://doi.org/10.5061/dryad.antdry2022.

Ethical Approval

Ant collections were conducted under field permits from the Chief Wildlife Wardens of Telangana (WL4/22831/2019) and Karnataka (PCCF/WL/CR-52/2019), ICMBio Brazil (SISBIO 72841-2), and SEMARNAT Mexico (SGPA/DGVS/09841/19). No vertebrates were disturbed during sampling. All procedures followed standard invertebrate collection protocols.

Appendix A

Updated Key to Ant Genera of Indian Tropical Dry Forests

The following key enables identification of the 32 ant genera recorded from Indian tropical dry forest sites in this study. Characters are based on worker caste morphology. Users should consult AntWeb and Bharti et al. (2016) for full species-level identification.

Subfamily Myrmicinae (selected couplets)

1a. Petiole with a distinct node; postpetiole present (2-segmented waist) -- go to 2

1b. Petiole scale-like; no postpetiole -- Solenopsis (fire ants), Monomorium

2a. Antennal club 3-segmented; propodeal spines present; > 3 mm body length -- Tetramorium

2b. Antennal club 4-segmented; propodeal spines absent or vestigial -- Crematogaster

Subfamily Ponerinae (selected couplets)

1a. Petiole node high and narrow; gaster with constriction between segments 1-2 -- Leptogenys

1b. Petiole node broad and low; gaster without marked constriction -- go to 2

2a. Mandibles linear, elongate; eyes large, > 0.3 x head width -- Odontomachus

2b. Mandibles triangular; eyes small to moderate -- Pachycondyla