



# Structure of ant assemblages in Western Ghats, India: role of habitat, disturbance and introduced species

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**Abstract.** 1. Habitat fragmentation, anthropogenic disturbance and the introduction of invasive species are factors thought to structure ant assemblages. To understand responses of the ant community to changes in the environment, ants are commonly categorised into functional groups, a scheme developed and based on Australian ants.

2. Behaviourally dominant and aggressive ants of the dominant dolichoderinae functional group have been suggested to structure the ant assemblages in arid and semi-arid habitats of these regions. Given the limited geographical distribution of dominant dolichoderinae, it is crucial to determine the responses of the ant community to changes in the environment in their absence.

3. This study addresses this less studied aspect by considering the associations of ants of Western Ghats, India, with habitat, anthropogenic disturbance and introduced ants. We determined how ant functional groups respond to these factors in this region, where dominant dolichoderines are naturally absent, and whether responses are consistent with predictions derived from the ant functional group scheme.

4. This study provides new information on ant assemblages in a little-studied region. As in other parts of the world, ant assemblages in Western Ghats were strongly influenced by habitat and disturbance, with different functional groups associated with different habitats and levels of disturbance.

5. No functional group showed evidence of being influenced by the abundance of introduced species. In addition, predictions of negative interactions between functional groups were not supported. Our findings suggest that abiotic factors are universal determinants of ant assemblage structure, but that competitive interactions may not be.

**Key words.** Abiotic factors, Formicidae, functional groups, Sharavathi river basin.

## Introduction

The ecological importance and diversity of ants (Redford, 1987; Folgarait, 1998; Agosti & Johnson, 2005; Rico-Gray & Oliveira, 2007) has led community ecologists to study patterns of ant distribution and species composition throughout the globe. Ant

composition and species richness differ between habitats (Andersen, 1995), climatic zones (Dunn *et al.*, 2009) and altitudes (Sanders *et al.*, 2003). However, very little is known about the factors that affect the composition of ant assemblages. Ants in Central Asia in particular, have been neglected, with few studies considering the Indian ant fauna and factors that determine its composition.

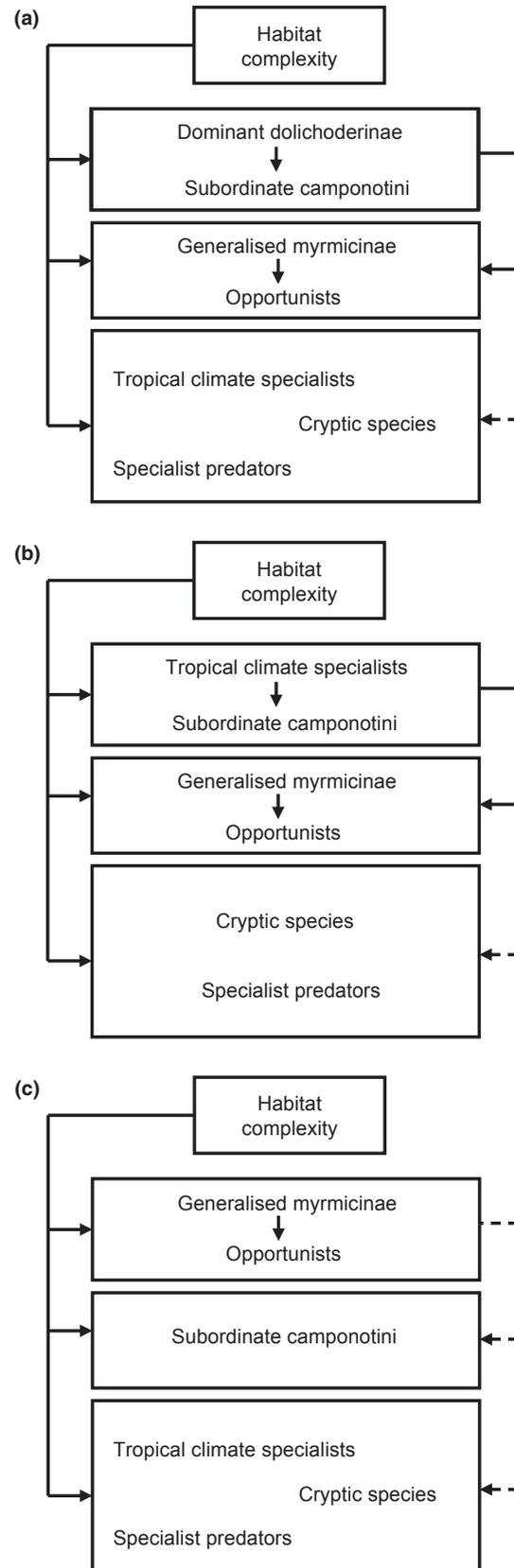
Anthropogenic drivers such as habitat disturbance and the introduction of invasive ants are thought to be important in structuring ant assemblages (McGlynn, 1999; Gibb & Hochuli, 2002) and may be of similar importance to natural drivers at a

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local scale. Anthropogenic disturbance tends to favour species that prefer simplified habitats (Gibb & Hochuli, 2003). Invasive species are associated with lower abundance and species richness of ants in assemblages worldwide (Carpintero *et al.*, 2005). However, presence of opportunistic and invasive species is also commonly associated with anthropogenic disturbance (Bolger *et al.*, 2000; King & Tschinkel, 2006, 2008), at least in the early stages of invasion, suggesting that these factors may easily be confounded.

To better understand community responses to the environment, organisms are commonly categorised into functional groups. The ant functional group scheme classifies ants according to biogeographical-scale responses to environmental stress and disturbance and was developed based on Australian ant assemblages (Greenslade, 1978; Andersen, 1990, 1995) (Fig. 1a). Many Australian studies have used this scheme to examine functional groups as bioindicators of anthropogenic disturbances at local scales (Hoffmann & Andersen, 2003). More recently, studies have attempted to extend this classification to other parts of the world (Andersen, 1997; Gómez *et al.*, 2003; Pfeiffer *et al.*, 2003; Vineesh *et al.*, 2007). However, problems are encountered in interpreting predictions from the scheme because of the limited geographic distribution of the functional group dominant dolichoderinae. This functional group is predicted to be competitively dominant in Australian ecosystems characterised by hot, open habitats, but not in other types of ecosystems. The dominant dolichoderinae group comprises of *Anonychomyrma*, *Froggattella*, *Iridomyrmex* (some species groups), *Papyrius* and *Philidris* in Australia and *Azteca*, *Forelius*, *Linepithema* and *Liometopum* in the New World (Andersen, 1997; Brown, 2000). In the absence of the desired habitat of this group, different ant groups are predicted to dominate, depending on the climatic zone (Andersen, 1986; Reichel & Andersen, 1996).

In this study, we revisit the functional group scheme (Greenslade, 1978; Andersen, 1990) and determine how functional groups respond in the natural absence of dominant dolichoderines, which are highly active and aggressive ants (Brown, 2000). Here, we test local-scale responses to habitat, disturbance and introduced species. In the functional group model proposed by Andersen, interacting groups of ants were classified into three tiers (Model I, Fig. 1a). Environmental stress and disturbance were thought to influence all groups. Habitat type was used as an indicator of environmental stress in this study because ants are considered to reach their maximum productivity in warm, open habitats, suggesting that more complex habitats are less favourable (Andersen, 1995). Competition from dominant ants is also hypothesised to regulate the responses of some functional groups. In Andersen's (1990) functional group model (Model I, Fig. 1a), dominant dolichoderines were suggested to influence subordinate camponotini in the first tier. These groups together



**Fig. 1.** Predicted responses of functional groups to habitat and competition (modified from Andersen, 1990) in (a) the presence of dominant dolichoderines; and the absence of dominant dolichoderines with replacement by: (b) tropical climate specialists and (c) generalised myrmicinae. Complete lines represent strong interactions, while dashed lines represent weak interactions.

regulate the second tier groups, the generalised myrmicinae and the opportunists. Within the second tier, generalised myrmicinae were suggested to regulate opportunists. Other functional groups, including climate specialists (hot, cold and tropical), cryptic species and specialist predators were grouped into a third tier, which was influenced mainly by habitat structure. In the absence of dominant dolichoderines, we propose that two alternatives are possible for this model in tropical climates. Firstly, they may be replaced by tropical climate specialists, which thrive in tropical climates (Model II, Fig. 1b). In this case, the combined tropical climate specialists and subordinate camponotini would be expected to suppress the combined group of generalised myrmicinae and opportunists. Alternatively, generalised myrmicinae may take a dominant role, in which case, subordinate camponotini would interact only weakly with other levels of the hierarchy (Model III, Fig. 1c; weak interactions represented with dashed lines). We propose that both scenarios will occur, depending on habitat structure.

We aim to address the gaps in the literature, by considering the associations of ants from the Western Ghats, India, with habitat, anthropogenic disturbance and introduced ants. We hypothesise that ant functional groups respond to the presence of introduced ants and to the characteristics of their habitat that are indicative of disturbance and habitat complexity. We also hypothesise that correlations between functional groups will be consistent with predictions derived from the ant functional group scheme (Andersen, 1990), when modified to account for the natural absence of dominant dolichoderines in this geographical region.

## Materials and methods

### Study area

This study was carried out at the Sharavathi River Basin (13°43'24N–14°11'57N, and 74°40'58E–75°18'34E) in Western Ghats, Shimoga, India (Fig. 2a). The Linganamakki dam (north of the study area) built on the Sharavathi river created a large man-made water reservoir and a 1991.43 km<sup>2</sup> river basin or catchment area. Mean annual rainfall in the region ranges from 6000 mm in the western side to 1700 mm in the eastern side of the river basin and temperature varies from a maximum of 35 °C in April to a minimum of 16 °C in December. Though ants are abundant in this region (Ali & Ganeshiah, 1998; Narendra & Kumar, 2006), they are mostly known from surveys and not standardised sampling (but see Gadagkar *et al.*, 1993; Basu, 1997; Narendra & Ramachandra, 2008; Sabu *et al.*, 2008).

Nearly 60% of the river basin is covered by vegetation, of which 15% is deciduous forest habitat (Narendra & Ramachandra, 2008). Canopy in both deciduous (e.g. species of *Lagerstroemia*, *Terminalia*, *Xylia*) and evergreen forests (e.g. species of *Dipterocarpus*, *Ficus*, *Garcinia*, *Myristica*) reached a height of about 40 m and was dense and closed. Leaf litter in such habitats was dense and about 25 cm thick. Plantations were primarily monocultures of *Acacia*, *Casuarina* with trees about 15–20 m tall. Canopy cover in plantations was sparse and leaf litter was about 5–10 cm thick. Scrub jungle was characterised by thorny

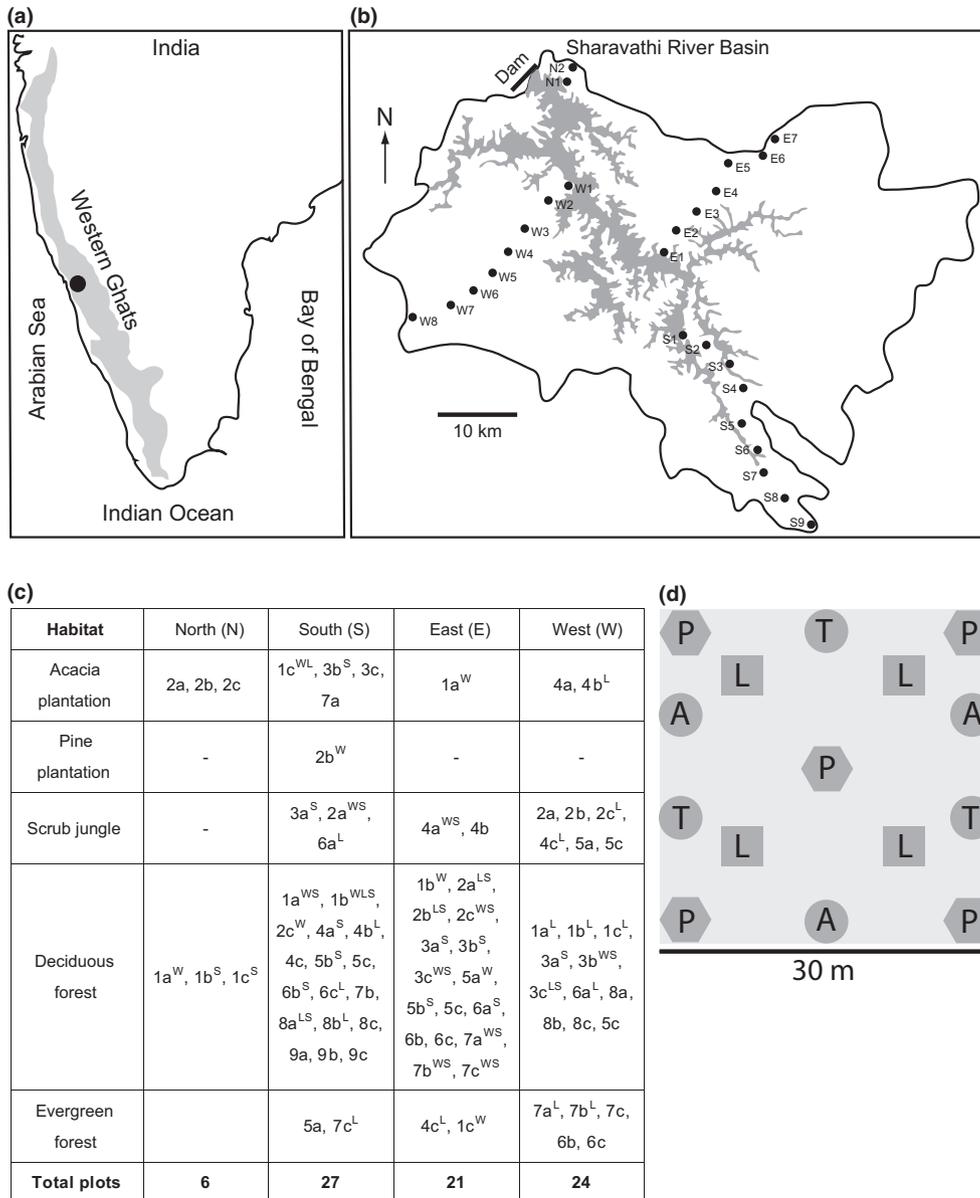
bushes and shrubs that were less than a metre in height. Scrub jungles were devoid of any significant leaf litter.

### Sampling methods

We established transects in four directions of the reservoir: north (4 km in length), south (32 km), east (24 km) and west (28 km) (Fig. 2b). Transects were measured from the bank of the reservoir. At every 4 km along these transects, an 800 m mini-transect was laid out such that it was perpendicular to the main transect. A snap-shot survey was carried out in a 30 m × 30 m plot along the mini-transect at forest fringes (0 m), middle of the forest (400 m) and forest interiors (800 m). We identified the tree species and assigned a habitat type at each plot. This resulted in a total of 78 plots classified as *Acacia* plantations (10 plots), Pine plantations (1 plot), Scrub jungles (11 plots), Deciduous forests (47 plots) and Evergreen forests (nine plots; Fig. 2b,c). Pine plantation habitat was excluded from the analyses. We determined the type of disturbance in each plot by identifying the presence of walking tracks, logging, or if the plots were within a 500-m radius of settlements. At each plot we also identified the latitude and longitude, measured the depth of the leaf litter, the greenness of the region [Normalised Difference Vegetation Index (NDVI)], and the distance from the reservoir. We used a measuring tape to determine the depth of the leaf litter and classified it into four categories, 0–10, 10–20, 20–30 and > 30 cm. The vegetation status of this region was recently determined using the vegetation index NDVI computed from satellite imageries (Narendra & Ramachandra, 2008). NDVI values range from +1 to –1; negative or near-zero values indicate non-vegetated area (e.g. soil, water), whereas positive values indicate vegetated areas (Lillesand *et al.*, 2004). We used NDVI as one of the variables. We used coordinates from a GPS receiver to determine the distance from the sampling site to the reservoir.

### Sampling technique

At each 30 m × 30 m plot, a suite of sampling methods were used to collect ants: bait traps, pitfall traps, Berlese leaf litter sampling and hand collection (Fig. 2d). Sampling was carried out once at each plot. Baits were provided as both terrestrial and arboreal and consisted either of honey, tuna or fried coconut. Terrestrial baits were placed on the ground and arboreal baits were tied to a tree 2 m above the ground. Bait trap collections were carried out between 0700 and 1700 hours. Traps were checked regularly every 1 h, during which ants at the bait were collected and the baits were replenished if required. For pitfall traps a 15-cm long cylindrical jar with a mouth diameter of 10 cm was used. Five pitfall traps were laid at every plot for a 24-h period. Each of these traps contained 90% ethyl alcohol. Leaf litter ants were extracted using the Berlese leaf litter technique in four, 1 × 1 m quadrats at each plot, once at 0900 and 1800 hours. Hand collection was also conducted using a sweep net, checking under tree bark, rotting logs and on leaves. Hand sampling was restricted for a period of an hour at each plot. Ants collected from the different methods were sorted, cleaned



**Fig. 2.** Location of the study area and sampling strategy. (a) Location of the study area (black circle) in the biodiversity hotspot, Western Ghats (shaded region) in South India. (b) The study area, Sharavathi river basin. Shaded grey region represents the reservoir. The Linganamakki Dam is to the North of the study area. An 800 m mini-transect was established at 4 km interval (filled circle) along North (N), South (S), East (E) and West (W) transects from the reservoir and sampling was carried out at 0, 400 and 800 m in 30 m × 30 m plots. (c) Distribution of habitats: *a* = 0 m, *b* = 400 m, and *c* = 800 m along the mini-transect; and the type of disturbance: W = walking tracks, L = logging, and S = within 500 m radius of settlements. In total, 29 of the 78 sampled plots were undisturbed. (d) Sampling strategy at each plot. Four samples of leaf litter (L); five pitfall traps (P); baits provided as arboreal (A) and terrestrial (T) traps ensuring that adjacent traps had different baits.

and preserved in 70% ethyl alcohol. Ants were cleaned in salt-water solution, mounted and identified using keys provided by Bingham (1903) and Bolton (1994). Scientific names are updated according to the current nomenclature (Agosti & Johnson, 2005). Data reported here are from worker ants. Data were pooled from a range of different sampling methods, making it impossible to obtain a measure of occurrence for this study. We

used abundance as a measure instead of the frequently used occurrence data. Occurrence data fails to account for greater mobility of larger species, which can lead to individuals from the same nest being collected across a long transect. For all ant data, we used a fourth-root transformation, which reduces the weighting of abundant species but preserves relative abundance information (Clarke, 1993).

*Data analyses*

Ants collected from each trapping method were pooled to determine the species richness in each habitat per 30 m<sup>2</sup>. We estimated the species richness for the study area and for each habitat using Chao2 estimator in EstimateS, v.7.5 (Colwell, 2004). Ants were classified into functional groups based on the generic level classification (Andersen, 1990; Brown, 2000) and introduced species were identified (McGlynn, 1999). As we know little about the behaviour of tramp species we have classified tramp species as introduced species. For the functional group categorisation, we classified *Anoplolepis gracilipes* (Smith) as an opportunist (A. Andersen, pers. comm.) as this species is a renowned invasive species and *Myrmicaria brunnea* Saunders as a generalised myrmicinae based on recent findings (Vineesh *et al.*, 2007) and our own observations.

*Effects of habitat and disturbance on ant assemblage composition*

We tested the hypothesis that ant species composition differs between habitat types and disturbance levels using analysis of similarities (ANOSIM) (Clarke, 1993) in the program PRIMER (Primer-E Ltd, 2009) with a maximum of 5000 permutations. A crossed design could not be analysed as a result of a lack of balance in the data, hence habitat type and disturbance were tested separately. PRIMER constructs a similarity matrix between samples using the Bray–Curtis similarity measure, which is not affected by joint absences. This similarity measure also gives more weight to abundant than to rare species. When the ANOSIM was significant, similarity percentage (SIMPER) breakdowns (Clarke, 1993) were conducted to determine which species were primarily responsible for the differences between habitat types or disturbance levels. SIMPER breaks down the contribution of each species to the observed similarity or dissimilarity between samples. It allows one to identify the species most important in creating the observed pattern of similarity.

*Effects of environmental variables on species richness and abundance of ant functional groups*

We tested the effects of the environmental variables (categorical variables: habitat and disturbance; continuous variables: latitude, longitude, litter, distance to reservoir, NDVI and the abundance of introduced species) on the abundance and species richness of each of the common ant functional groups using two different approaches, ensuring that interpretations were not limited by slight differences in the fit of different models. Latitude and longitude were used in the models to better account for any spatial autocorrelation in our results. In the first approach, we tested all possible models (including from one to all factors) to find the model with the lowest Akaike Information Criterion (Akaike, 1974) i.e. the ‘best fit model’ in JMP (SAS Institute Inc., 2007), using a linear response in the generalised linear model module.

To determine whether multicollinearity amongst predictor variables which model we selected as the best model, we used a second statistical approach, hierarchical partitioning analysis (Chevan & Sutherland, 1991; MacNally & Walsh, 2004), in the R computing environment (R Foundation For Statistical Computing, 2005). The analysis estimates the increase in model fit associated with each predictor variable by averaging its additional explanatory power in all models (i.e. all possible combinations of the predictor variables) in which that variable appears (MacNally, 2000). The explanatory power of each predictor variable is segregated into independent effects (I), i.e. those associated with that variable independently of other predictor variables and joint effects (J), attributable to the joint action of that variable with other predictors. Here, we present only results for independent effects and I is presented as the % contribution across all possible models. For all approaches, all sites with any disturbances (logging, settlements and walking tracks) were considered ‘disturbed’. For opportunist species, which are thought to be associated with disturbance, we further investigated the relationship between abundance and species richness and disturbance level (divided now into four categories, in order of most to least disturbed: settlements, walking tracks, logged areas and undisturbed areas) using ANOVA. In addition, ‘introduced species’ was included as a predictor for all groups, except opportunists, which included all the introduced species.

*Functional group models*

We used a simple model to test how well the data fitted the functional group models (Model I, Fig. 1). A general linear model with ‘habitat’, ‘disturbance’, ‘habitat x disturbance’ and ‘abundance of predictor taxon’ was used to test relationships with the abundance of response taxa. Habitat and disturbance are predicted to influence the abundance of ants in particular functional groups, but their effects are predicted to be mediated by the abundance of other ants. The predictor taxon refers to the specific taxon or set of taxa that are predicted to influence the response taxa. All abundances were ln-transformed. Specifically, both models predict that the abundance of generalised myrmicinae affects the abundance of opportunists. From Model II (Fig. 1b), tropical climate specialists are predicted to affect subordinate camponotini and the combined abundance of tropical climate specialists and subordinate camponotini is predicted to affect the combined abundance of generalised myrmicinae and opportunistic species. Only weak effects on the remaining functional groups are expected from the models, so these effects were not tested.

**Results***Overview*

A total of 84 species, representing 30 genera and five subfamilies, were collected during this sampling (Appendix S1). The most widely represented subfamily was Myrmicinae known by 44 species and 11 genera. The most species rich genus was

*Monomorium* represented by 12 species and the most abundant species was *Pheidole* sp. 1. *Camponotus compressus* (Fabricius) and *Diacamma rugosum* (Le Guillou) were the most frequently occurring species, found in 46.15% of the 78 sampled plots. The behaviourally dominant group of ants, dominant dolichoderines were absent in this geographical region. The only dolichoderine ants found in this study were the opportunists *Tapinoma* and *Technomyrmex* and cold climate specialists *Bothriomyrmex* and *Dolichoderus*. A comparison of the observed and estimated species for the entire study area indicates that the estimated species richness is quite close to the observed species richness. However, the difference between observed and estimated species richness varied within each habitat (Appendix S1).

### Species assemblages

ANOSIM showed that the composition of ant assemblages in evergreen habitats differed from those in scrub and *Acacia* habitats, while assemblages in scrub and *Acacia* also differed from one another (Table 1). Deciduous forest did not differ from any other habitat type. In the disturbance comparison, settlements and walking tracks differed significantly from logged sites (Table 1). Undisturbed sites did not differ from the more disturbed sites, although  $P < 0.10$  for comparisons with settlements and walking tracks.

SIMPER revealed that differences between evergreen and other habitats were driven by high abundances of *Pheidole* sp. 1 and 2, while scrub habitats were characterised by high abun-

dances of *Crematogaster wroughtonii* Forel and *Lophomyrmex quadrispinosus* (Jerdon). *Acacia* habitats had low abundances of most species. Differences between logged sites and walking tracks were due to greater abundances of *Tetramorium* sp. 1, *Monomorium indicum* Forel and *Pheidole* sp. 1 in the latter. *Tetramorium* sp. 1, *Pheidole* sp. 2, *Crematogaster* sp. 2 and *L. quadrispinosus* drove differences between logging and settlement sites, the former three being more common in settlement sites and the latter in logging sites.

### Functional groups

The two different approaches to examining the relationship between the environmental predictor variables and the abundance and species richness of ant functional groups showed similar results for most groups (Table 2). Results for species richness and abundance were similar for most groups. Habitat, disturbance and leaf litter were the main contributing environmental predictors across all groups. The variables 'distance to reservoir', 'NDVI' and 'introduced species abundance' were not strong contributors to any of the models.

For all ants, hierarchical partitioning analysis suggested that habitat and disturbance made the highest independent contributions to all models, with disturbance significant in the best models for species richness and abundance (Table 2). Total abundance was also greater in sites with more leaf litter and significant in the best model. Patterns were very similar for opportunists, which made up 19% of all species, although this group tended to be less common in sites with more leaf litter and more common in disturbed sites and less affected by habitat (Table 2). The positive association with disturbance was in accordance with predictions. More detailed analysis showed a significant effect of disturbance ( $F_{(3,73)} = 6.75$ ,  $P = 0.0004$ ), with significantly greater abundance near the more disturbed areas, i.e. settlements and walking tracks, than in undisturbed areas. Logged areas were intermediate. Differences were also significant for species richness ( $F_{(3,73)} = 5.48$ ,  $P = 0.0019$ ), which was greatest near walking tracks and in logged areas.

No significant environmental predictors were found for subordinate camponotini or tropical climate specialists. Hierarchical partitioning analysis suggested that habitat and disturbance made the greatest independent contributions to all models for subordinate camponotini abundance and species richness (Table 2). They were also the only factors to appear in the best models. Predictions for this group in the absence of dominant dolichoderines are relatively unclear, except that they should be 'comparatively dominant' and relatively sparse. Best fit models for tropical climate specialists were not significant, although habitat made the greatest independent contribution to both species richness and abundance while disturbance also made a strong contribution to species richness.

The best fit model for the species richness of generalised myrmicinae was not significant, with hierarchical partitioning analysis suggesting that latitude and longitude made the greatest independent contribution to responses (Table 2). Longitude was significant in the best fit model for generalised myrmicinae

**Table 1.** Results of analysis of similarities (ANOSIM) on the relationship between assemblage composition and habitat, disturbance and disturbance within each habitat type.

| Comparison                          | Global <i>R</i> | <i>P</i> -value |
|-------------------------------------|-----------------|-----------------|
| Test of habitat                     | 0.047           | 0.154           |
| <i>Post hoc</i> comparisons         |                 |                 |
| Evergreen vs. scrub                 | 0.330           | <b>0.006</b>    |
| Evergreen vs. deciduous             | -0.030          | 0.645           |
| Evergreen vs. <i>Acacia</i>         | 0.167           | <b>0.024</b>    |
| Scrub vs. deciduous                 | 0.045           | 0.257           |
| Scrub vs. <i>Acacia</i>             | 0.198           | <b>0.009</b>    |
| Deciduous vs. <i>Acacia</i>         | 0.068           | 0.149           |
| Test of disturbance                 | 0.068           | <b>0.018</b>    |
| <i>Post hoc</i> comparisons         |                 |                 |
| Undisturbed, logging                | -0.038          | 0.862           |
| Undisturbed, settlements            | 0.099           | 0.098           |
| Undisturbed, walking tracks         | 0.057           | 0.060           |
| Logging, settlements                | 0.311           | <b>0.002</b>    |
| Logging, walking tracks             | 0.197           | <b>0.002</b>    |
| Settlements, walking tracks         | -0.006          | 0.494           |
| Test of disturbance within habitats |                 |                 |
| Evergreen                           | 0.225           | 0.095           |
| Scrub                               | 0.060           | 0.335           |
| Deciduous                           | 0.081           | 0.075           |
| <i>Acacia</i>                       | 0.200           | 0.084           |

Global *R* is the test statistic used for ANOSIM and ranges from 1 to -1. Significant differences between habitats or disturbance levels ( $P < 0.05$ ) are represented in bold.

**Table 2.** Best models and results of hierarchical partitioning analysis of the relationship between the environmental variables and the abundance of invasive ants on ant functional groups, in terms of species richness and abundance.

|                         | Total        |                 | Opportunist  |                 | Subordinate camponotini |                 | Tropical climate specialist |                 | Generalised myrmicinae |                 | Cryptic species |                 | Specialist predator |                 |
|-------------------------|--------------|-----------------|--------------|-----------------|-------------------------|-----------------|-----------------------------|-----------------|------------------------|-----------------|-----------------|-----------------|---------------------|-----------------|
|                         | <i>I</i> (%) | <i>F</i> -value | <i>I</i> (%) | <i>F</i> -value | <i>I</i> (%)            | <i>F</i> -value | <i>I</i> (%)                | <i>F</i> -value | <i>I</i> (%)           | <i>F</i> -value | <i>I</i> (%)    | <i>F</i> -value | <i>I</i> (%)        | <i>F</i> -value |
| <b>Species richness</b> |              |                 |              |                 |                         |                 |                             |                 |                        |                 |                 |                 |                     |                 |
| X                       | 2.23         |                 | 2.97         |                 | 5.71                    |                 | 6.51                        | 0.98            | 24.09                  |                 | 18.48           | 2.36            | 11.48               | 5.51*           |
| Y                       | 9.46         | 3.35            | 4.13         |                 | 13.73                   |                 | 2.95                        |                 | 38.00                  | 1.94            | 14.37           | 2.09            | 8.54                |                 |
| Litter                  | 3.44         |                 | 9.07         |                 | 2.31                    |                 | 5.65                        |                 | 2.71                   | 1.85            | 15.20           | 5.94*           | 6.14                |                 |
| Reservoir               | 3.70         | 1.77            | 7.16         |                 | 27.52                   |                 | 3.17                        |                 | 4.19                   |                 | 11.38           |                 | 4.09                |                 |
| Habitat                 | 20.75        | 2.06            | 5.03         |                 | 20.86                   | 1.21            | 37.90                       | 0.58            | 8.95                   | 0.91            | 16.13           | 1.76            | 54.76               | 5.77**          |
| NDVI                    | 5.15         |                 | 2.99         |                 | 8.38                    |                 | 3.03                        |                 | 1.88                   |                 | 2.83            |                 | 13.84               |                 |
| Disturbance             | 53.25        | 16.07***        | 68.66        | 16.43***        | 17.56                   | 2.06            | 37.82                       | 0.76            | 18.99                  | 2.72            | 1.36            | 0.01            | 0.57                |                 |
| Invasive species        | 2.03         |                 |              |                 | 3.92                    |                 | 2.98                        |                 | 1.19                   |                 | 20.26           |                 | 0.59                |                 |
| <b>Abundance</b>        |              |                 |              |                 |                         |                 |                             |                 |                        |                 |                 |                 |                     |                 |
| X                       | 1.02         |                 | 21.19        | 1.86            | 3.52                    |                 | 4.28                        | 0.83            | 21.00                  | 5.97*           | 17.00           | 2.69            | 15.26               | 3.31            |
| Y                       | 3.51         |                 | 1.85         | 0.04            | 6.32                    |                 | 15.77                       |                 | 8.97                   |                 | 17.99           | 2.78            | 6.69                |                 |
| Litter                  | 19.21        | 6.03*           | 18.28        | 4.91*           | 9.61                    |                 | 20.13                       |                 | 13.24                  |                 | 30.92           | 8.48**          | 8.56                |                 |
| Reservoir               | 11.69        | 2.2             | 9.58         |                 | 14.92                   |                 | 4.30                        |                 | 6.79                   |                 | 8.31            |                 | 0.97                |                 |
| Habitat                 | 27.13        | 2.38            | 6.04         |                 | 32.16                   | 2.37            | 33.00                       | 0.70            | 17.49                  |                 | 7.07            |                 | 55.84               | 3.28*           |
| NDVI                    | 0.83         |                 | 8.48         | 3.18            | 8.96                    |                 | 5.86                        |                 | 0.94                   |                 | 3.44            | 1.69            | 9.37                |                 |
| Disturbance             | 35.13        | 5.76*           | 34.57        | 9.83**          | 15.05                   | 2.49            | 8.25                        |                 | 24.01                  | 3.91            | 1.36            |                 | 2.74                |                 |
| Invasive species        | 1.49         |                 |              |                 | 9.46                    |                 | 8.42                        |                 | 7.57                   |                 | 13.90           |                 | 0.58                |                 |

*T* is the % independent contribution of each predictor in the hierarchical partitioning analysis.

\**P* < 0.05; \*\**P* < 0.01; \*\*\**P* < 0.001.

abundance. In accordance with predictions, the species richness and abundance of cryptic species was positively affected by higher quantities of leaf litter (Table 2). This predictor was significant in best fit models and made a strong independent contribution to all models. Best fit models for specialist predators suggested that habitat and longitude were important in determining both abundance and species richness, with habitat making a very high independent contribution to all models (55%) (Table 2).

#### Functional group models

Functional groups did not respond as predicted when the abundance of other functional groups was incorporated into simple models including habitat, disturbance and habitat × disturbance (Table 3). Habitat and disturbance behaved as in previous models.

## Discussion

#### Role of habitat and disturbance

The composition of ant assemblages responded strongly to habitat and disturbance. Although most habitats supported very different ant assemblages, deciduous forests supported assemblages intermediate to all other habitat types. It is perhaps due to the characteristics of this habitat such as the broken canopy cover and sparse leaf litter, which is intermediate between closed

canopy and dense litter of evergreen forests and the open canopy and bare ground of scrub jungles. Specificity of ant species to both habitats and microhabitats has been reported in regions worldwide (Brühl *et al.*, 1998), with few studies showing ant composition in different habitats to be similar (Belshaw & Bolton, 1993; Estrada & Fernández, 1999). Ant species richness commonly differs between monocultures and native forests (Cerdá *et al.*, 2009) and our study too shows that ant composition differs between plantations of introduced *Acacia* and most native habitats. Although habitat was a significant predictor of abundance and species richness only for specialist predators, it made the greatest or next-greatest independent contribution to all possible models for most functional groups and total species richness and abundance. In agreement with previous studies, we suggest that habitat is a key determinant of ant community structure in tropical climates.

Assemblages exposed to different levels of disturbance also differed significantly in both species and functional group composition. As predicted, opportunists showed the most pronounced response to habitat disturbance, although strong responses were evident for many other functional groups. In particular, selectively logged habitats differed from habitats disturbed by walking tracks and settlements. Although undisturbed sites were intermediate in species composition, they were most similar to sites disturbed by selective logging. Selectively logged sites had relatively closed canopies and were rich in leaf litter and thus resembled undisturbed sites in species composition. Their greater divergence from disturbed sites may be because they represent sites selected for logging due to their higher quality wood. Vasconcelos *et al.* (2000) also found that ant species

**Table 3.** Summary of the outcome of general linear models testing the predictions of Models II and III (Fig. 1b & c). Crosses show which taxa/taxon was used as the predictor in each of the models.

| Predicted by   | Subordinate camponotini |                 | Generalised myrmicinae<br>+ opportunist |                 | Opportunist       |                 |
|--|-------------------------|-----------------|---|-----------------|-------------------|-----------------|
|  | <i>F</i> -ratio         | <i>P</i> -value | <i>F</i> -ratio                         | <i>P</i> -value | <i>F</i> -ratio   | <i>P</i> -value |
|  | Model II                |                 | Model II                                |                 | Models II and III |                 |
| Habitat  | 2.63                    | 0.057           | 0.85                                    | 0.470           | 0.60              | 0.619           |
| Disturbance  | 2.99                    | 0.088           | 3.67                                    | 0.060           | 9.32              | 0.003**         |
| Habitat × Disturbance                                    | 0.44                    | 0.722           | 1.19                                    | 0.322           | 0.96              | 0.417           |
| Predictor taxon/taxa                                     | 2.27                    | 0.137           | 0.25                                    | 0.617           | 1.89              | 0.174           |
| Tropical climate specialist                              | x                       |                 |   |                 |                   |                 |
| Tropical climate specialist<br>+ subordinate camponotini |                         |                 | x                                       |                 |                   |                 |
| Generalised myrmicinae                                   |                         |                 |   |                 | x                 |                 |

\*\* $P < 0.01$ .

richness and abundance in unlogged forests of the Amazon were similar to the sites that had been selectively logged. However, it is important to note that, in contrast to selective felling, clear-cutting or deforestation reduces ant diversity in both temperate and tropical forests (Watt *et al.*, 2002).

Leaf litter depth significantly affected the abundance and species richness of opportunists and cryptic species, with the latter positively related to increasing depth and the former negatively related. A comparison between deciduous and shola forests in lower regions of Western Ghats has previously shown cryptic species to be the most abundant leaf litter group in deciduous forests (Vineesh *et al.*, 2007). Leaf litter also made a large contribution to the abundance of tropical climate specialists, a group that consisted of *Oecophylla* and *Polyrhachis* species. This was likely a result of the high correlation between leaf litter depth and greenness of the region measured as NDVI from satellite data, with these taxa relying more on broad-leaved trees.

#### Role of introduced species

We recorded a significant number of introduced species in this study region, all of which were classified as opportunists. It is clear from our models that the abundance of introduced species is not an important predictor of the abundance or species richness of any functional group, in contrast to Lessard *et al.* (2009). We found no evidence for negative effects of competition by introduced species in our study. Some of the introduced species are invasive and are thought to displace native ants (McGlynn, 1999). But since invasive species are mostly common in disturbed areas (Bolger *et al.*, 2000), many previous studies have confounded the effects of disturbance on native assemblages with the presence of invasive species. Recent experimental evidence (King & Tschinkel, 2008) suggests that invasive species cause less damage than human induced disturbance. Our records of numerical abundance of *Oecophylla smaragdina* (Fabricius) decreasing and *A. gracilipes* increasing in cleared forests compared to before clearing (A.

Narendra, pers. obs.) suggests that human induced disturbance might play a significant role in the replacement of native ant species by invasives. Another possibility for the relatively minor effect of introduced species could be because some of these ants in our study may behave as 'tramp' species and may not displace the local ant fauna (Appendix S1). Observations of food resources being shared by ants from different functional groups (including some introduced species) indicate this might be the case, but will require experimental evidence to be confident.

#### Functional composition in the absence of dominant dolichoderines

In the study area, tropical climate specialists were numerically dominant in deciduous and evergreen forests and generalised myrmicinae dominate in all other regions. This is similar to the organisation of the functional groups in the hot and humid tropics of Queensland (King *et al.*, 1998) and the rain forests of the Australian Northern Territory (Reichel & Andersen, 1996), where dominant dolichoderines are absent. This is also consistent with the hypothesis (Model 1, Fig. 1a, Andersen, 1990) that generalised myrmicinae occur in most habitats in the absence of competition from dominant dolichoderines. Generalised myrmicinae coexisted with opportunists in disturbed habitats, and with subordinate camponotini in undisturbed habitats. Elsewhere, in Mongolia where dominant dolichoderinae are naturally absent, cold climate specialists dominated in the steppe habitat, opportunists in semi-desert and hot climate specialists in deserts (Pfeiffer *et al.*, 2003). In Polynesian islands where dominant dolichoderinae are also absent, two species of *Pheidole* (generalised myrmicinae) and *Solenopsis geminata* (Fabricius) (opportunist and invasive species) are behaviourally dominant (Morrison, 1996).

If the functional group model represents a globally applicable model of responses of ant assemblages to habitat, disturbance and interactions with other ant taxa, removal of the dominant

dolichoderinae from the model should result in testable hypotheses on how assemblages will change. Responses of most functional groups to habitat were in accordance with those predicted, so global associations of functional groups with habitat and disturbance were supported. However, interactions between functional groups in accordance with our predictions (based on Andersen, 1990) could not be detected. The prediction that competitive interactions between functional groups are important in structuring ant assemblages thus does not appear to be globally applicable.

## Conclusions

This study provides new information on ant assemblages in a little-studied region. As in other parts of the world, ant assemblages in the Western Ghats were strongly influenced by habitat and disturbance, with different functional groups associated with different habitats and levels of disturbance. No functional group showed evidence of being influenced by the abundance of introduced species. In addition, predictions of negative interactions between functional groups were not supported. This suggests that, although functional groupings may predict habitat use, they are not helpful in predicting species interactions in this system. Our findings suggest that abiotic factors are more important determinants of ant assemblage structure than competitive interactions.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: doi: 10.1111/j.1752-4598.2010.00113.x:

**Appendix S1.** Ant abundance at the Sharavathi river basin, Western Ghats. (-) indicates absence of species. \* indicates introduced species. Functional groups are: cryptic species (CS), cold climate specialists (CCS), hot climate specialists (HCS), generalised myrmicinae (GM), opportunist species (OS), specialist predators (SP), subordinate camponotini (SC) and tropical climate specialists (TCS).

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