



RESEARCH ARTICLE - ANTS

Disturbance-Driven Patterns of Ant Diversity, Functional Composition, and Biogeographic Affiliation in a Rapidly Urbanizing Himalayan Landscape

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Abstract

This study assessed ant diversity and functional group distribution across forest, agricultural, and urban habitats in Dehradun (30.31650° N, 78.03220° E) under varying levels of anthropogenic disturbance. Sampling was conducted from August 2020 to February 2023 using three transects per habitat, each comprising twenty sampling units. Ants were collected through a combination of active and passive methods, including pitfall traps, leaf litter extraction, baiting, and hand collection. A total of 42 species belonging to 23 genera and 6 subfamilies (*Formicinae*, *Dolichoderinae*, *Myrmicinae*, *Ponerinae*, *Aenictinae*, and *Pseudomyrmicinae*) were recorded. Species richness was highest in forest habitats (36 species), followed by agricultural (21 species) and urban (19 species) habitats. Functional group analysis revealed clear effects of disturbance gradients, with Generalized *Myrmicinae* dominating across all habitats (30.01% in forest, 29.34% in agriculture, and 49.44% in urban areas). Opportunist species were most abundant in agricultural habitats (25.41%), while invasive species also showed the highest prevalence in these areas (26.22%), indicating strong anthropogenic influence. Overall, the study highlights the impact of urbanization and land-use change on ant community structure and emphasizes the importance of conserving less disturbed habitats to maintain biodiversity and ecological balance.

Introduction

Like most animal species, invertebrates are essential to the health and services of ecosystems. Ants have an unparalleled influence on other biota across Earth's surface, surpassing that of other animal clades. Ants have developed relationships ranging from metabolic mutualisms to exploitation by social parasites through their contacts with other animals, plants, fungi, and microorganisms. Given this diversity of interactions, ants likely serve as keystone taxa across diverse habitats, providing direct or indirect support to a wide range of species. Beyond these interactions, however, lies a less evident but no less substantial effect: ants, as a collective ecological force, have imposed survivorship bias on the species we see living in terrestrial habitats. It is critical to understand how ants have shaped and are embedded in

ecological communities, as terrestrial life may have undergone a selective filter imposed by ants (Parker & Kronauer, 2021).

Understanding an organism's position in an ecosystem and its ecological significance for other taxa requires knowledge of its distribution and abundance. Insects, long considered "the little things that run the world," currently lack such information. There is no accurate estimate of the total number of insects on Earth or of their abundance across biomes or habitats, even for ubiquitous insects like ants, which are of enormous ecological relevance (Schultheiss et al., 2022).

Land-use intensification has been identified as a primary driver of declining biodiversity, as evidenced by recent reports of huge decreases in arthropod biomass and local extinctions of arthropod species. However, there are no multisite time series of arthropod occurrences that we are aware of that span gradients in land-use intensity and may be used to



verify causal links. Furthermore, it remains unknown which arthropod groups and land-use types are affected, as well as whether the reported decreases in diversity and biomass are related (Seibold et al., 2019).

Understanding animal relationships is crucial to comprehending ecological systems. The nature and strength of these interactions influence how an organism affects its surroundings. Despite the recognized ecological importance of ants and their widespread use as bioindicators, integrative assessments that simultaneously examine taxonomic diversity, functional restructuring, and invasive-endemic dynamics across multiple land-use types remain scarce, particularly in Himalayan foothill landscapes undergoing rapid anthropogenic transformation.

Approximately 4,907 species of fauna are present in the state of Uttarakhand, out of which 3,984 are invertebrates and the remaining 959 are vertebrates. The Himalayas and Western Ghats are two biogeographically consequential regions of India that harbor a large number of ant species. The present study can be extended to assess the ecological status of the Himalayan foothills (Shivalik) using ants as ecological indicators.

Although ants have been widely employed as bioindicators across disturbance gradients, much of the existing literature emphasizes patterns in species richness or single-habitat comparisons, often in tropical lowland forests or managed agroecosystems. Comparatively fewer studies have examined ant communities in the Himalayan foothill landscapes, where rapid urban expansion, agricultural intensification, and forest fragmentation intersect within a compact spatial mosaic.

The present study contributes conceptually and methodologically by integrating taxonomic diversity, functional group restructuring, and invasive-endemic species dynamics across forest, agricultural, and urban habitats within the Dehradun region of the western Himalayas. Rather than relying solely on species counts, this work employs functional group composition as an ecological lens for interpreting disturbance responses, thereby linking community structure to ecosystem functioning.

A further novelty lies in the long-term, standardized sampling framework, spanning more than two and a half years and incorporating multiple complementary collection methods. This temporal depth enables the study to capture stable community patterns rather than short-term fluctuations, which are common limitations in comparable surveys.

By situating ant functional groups and invasive species prevalence within a Himalayan foothill context, this study establishes a baseline ecological framework for assessing anthropogenic disturbance and habitat resilience in a biogeographically sensitive and underrepresented region.

The present study aims to assess the diversity and distribution of Myrmecofauna (Hymenoptera: Formicidae) across forest, agricultural, and urban habitats in the Dehradun region of Uttarakhand, with particular emphasis on understanding how anthropogenic disturbance influences ant community

structure. Beyond documenting species richness, the study seeks to:

- (i) evaluate changes in functional group composition along a disturbance gradient,
- (ii) examine the distribution of invasive and Himalayan endemic ant species as indicators of ecological stress and habitat integrity, and
- (iii) assess whether functional attributes of ant communities provide greater sensitivity to disturbance than taxonomic metrics alone.

The underlying hypothesis is that increasing land-use intensity leads not only to reduced species richness but also to predictable shifts in functional group dominance and invasive species prevalence.

Materials and Methods

Methodological Framework

The overall methodological workflow adopted in the present study is summarized in Figure 1. The framework illustrates a structured, stepwise approach beginning with the selection of representative forest, agricultural, and urban habitats in the Dehradun region, followed by a standardized spatial sampling layout comprising replicated transects and sampling units within each habitat. Multiple complementary ant sampling techniques, including pitfall trapping, leaf litter extraction, baiting, and hand collection, were employed to ensure comprehensive coverage of surface-active, cryptic, and foraging ant species. Sampling was conducted across multiple seasons over more than two years, with temporal replication to capture inter-seasonal variability; however, data were pooled across sampling periods to characterize long-term community structure and functional stability. Collected specimens were identified to the species level and subsequently classified into functional groups, invasive, and Himalayan endemic categories, enabling mechanistic interpretation of disturbance responses. Quantitative analyses included estimating alpha diversity indices, beta diversity metrics, functional group composition, and invasive-endemic species proportions. The final stage of the framework integrates these analytical outputs to interpret ecological patterns along disturbance gradients and assess habitat differentiation and conservation implications across habitats.

Study Sites

Uttarakhand is situated in northern India and became the 27th state of the Republic of India, after being carved out of the Himalayan and adjoining districts of Uttar Pradesh. Geographically, the state lies between latitudes 28°43' - 31°28'N and longitudes 77°34' - 81°03'E, covering an area of 53,566 km, with the majority of the area being mountainous terrain. Dehradun serves as the provisional capital of Uttarakhand and is located in the Doon Valley, surrounded by the Himalayas to the north, the Shivaliks to the south, the river Ganga to

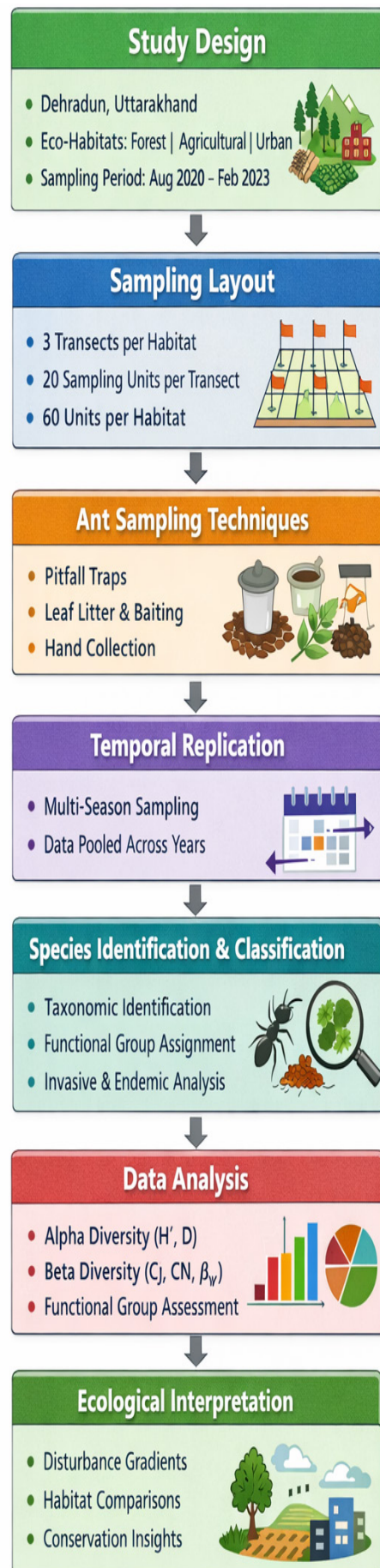


Fig 1. Methodological Framework.

the east, and the river Yamuna to the west. Dehradun district spans an area of 3,088 Km² and is situated in the northwestern region of Uttarakhand, bordered by Uttarkashi to the northeast, Tehri Garhwal and Pauri Garhwal to the east and southeast, respectively. To the south, it shares boundaries with Saharanpur (Uttar Pradesh), and to the west, it is separated from the Sirmur (Nahan) district of Himachal Pradesh by the rivers Yamuna and Tons. The study was carried out in three different habitats (forest, agricultural, and urban) in Dehradun, Uttarakhand, across nine sampling sites (Table 1). The study area and selected sites are shown in Figure 2.

Table 1. GPS Co-ordinates of the sites surveyed during the study.

Sl. No.	Site code	Latitude	Longitude
1.	FS1	30°11'25" N	78°05'03" E
2.	FS2	30°12'45" N	78°03'37" E
3.	FS3	30°14'30" N	78°11'48" E
4.	AS1	30°19'34" N	77°53'49" E
5.	AS2	30°19'35" N	77°54'02" E
6.	AS3	30°19'50" N	77°54'09" E
7.	US1	30°16'50" N	78°02'26" E
8.	US2	30°16'10" N	78°02'11" E
9.	US3	30°16'53" N	78°02'04" E

(FS: Forest sites, AS: Agricultural sites, and US: Urban sites)

Ant Sampling Techniques

Ant sampling was conducted between August 2020 and February 2023, encompassing multiple seasonal cycles (monsoon, post-monsoon, winter, and pre-monsoon). To capture long-term community composition and functional structure rather than short-term seasonal fluctuations, data from all sampling events were pooled for the final analysis. The sampling design was fully balanced across all habitats and methods. Within each of the three habitats, four complementary sampling methods (pitfall trapping, leaf litter extraction, baiting, and hand collection) were systematically applied at every sampling unit. Each sampling unit was defined as a standardized 1 m² plot along a 100-m transect, with plots spaced 5 m apart. Consequently, each sampling unit yielded four distinct samples (one per method), ensuring equal and balanced sampling effort across all techniques.

Sampling Effort and Adequacy

To ensure adequate and balanced representation of ant diversity, a fully standardized sampling design was employed. Each of the three habitats was surveyed using three independent 100-m transects, with 20 spatially separated 1 m² sampling units per transect, yielding 60 spatial sampling units per habitat. Because four complementary methods (pitfall trapping, leaf litter extraction, baiting, and hand collection) were systematically applied at every unit, each sampling event

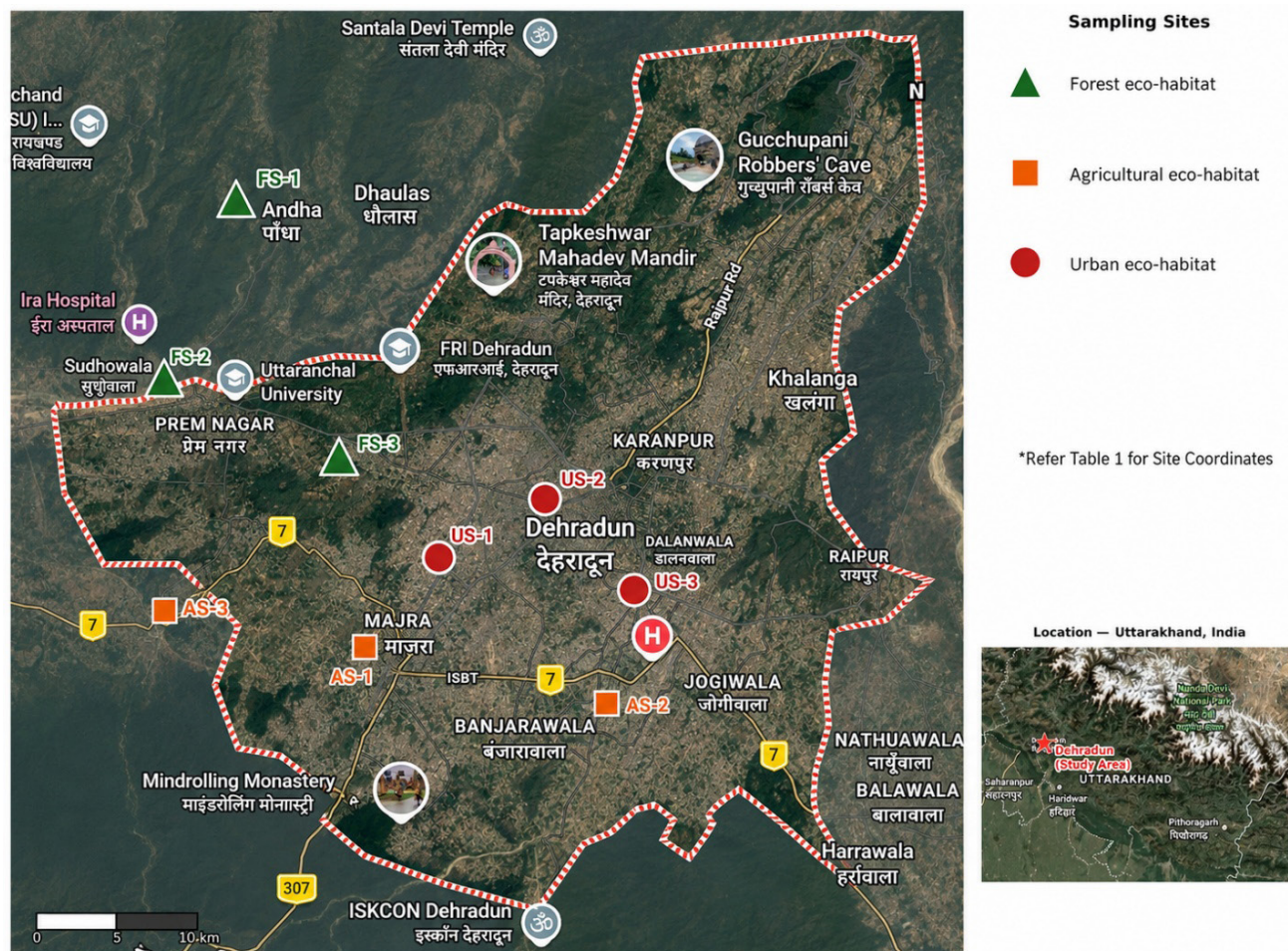


Fig 2. Study Area Mapping.

yielded exactly 240 individual samples per habitat (60 units $\times$ 4 methods). Over the 2.5-year study period (August 2020 to February 2023), sampling was systematically repeated across 10 distinct seasonal events. Consequently, the total pooled sampling effort amounted to 2,400 samples per habitat (240 samples/event $\times$ 10 events), resulting in a grand total of 7,200 samples across all three habitats. This explicit and perfectly balanced design ensured identical sampling effort across all habitats and methods, eliminating sampling bias and allowing robust cross-habitat comparison.

Passive/Indirect Methods

Pitfall Trap Method

It involves placing open containers in the ground. Surface-active animals fall unwittingly into these traps and are either killed or preserved in a liquid. This method is used to estimate the abundance and species composition of ground surface-active ants in an area. The abundance of ants in pitfall traps provides a measure of a species' importance in a community by integrating both forager attributes and colony dispersion patterns (Greenslade, 1973).

For pitfall trapping, propylene glycol was used as its environmentally "friendly" properties slow to evaporate and are

non-toxic to vertebrates (Abensperg-Traun & Steven, 1995). Pitfall traps made up of borosilicate tubes with an 18mm internal diameter, 150 mm length, partly filled to a depth of about 50 mm with propylene glycol solution, were buried with the rim flush with the soil surface. The trap was emptied after 48-72 hours by straining the ants, and the collected ants were then transferred into vials with absolute alcohol using a camel hair brush.

The Leaf Litter Method

This technique is designed to measure the abundance and composition of ants inhabiting a volume of leaf litter. Whole colonies of ants nest in the litter, and ants foraging in the litter from colonies outside the litter sample can be collected. The litter sample was collected within a quadrat placed on the ground, and litter was scooped from the edge of the quadrat toward the center and removed by hand into the sifter opening. Twigs and clods were broken open, and decayed logs were minced with a machete to expose and disturb ant nests within them. The litter sample was transferred to a Winkler bag (Fisher, 1998) to separate it from debris. Ants were extracted from the sifted litter over a 48-hour period and then transferred into a bottle containing absolute alcohol using a camel-hair brush.

Baiting

This technique uses food to attract foraging ants to locations where they can be collected. Foods rich in carbohydrates are used alone or in combination with proteinaceous baits. This technique is commonly used to estimate the composition and richness of the active ground-foraging ant fauna, to examine ant activity and behavior patterns in studies of community structure, and to estimate the contribution of particular species to ecosystem processes such as seed redistribution and scavenging. The abundance of ant foragers at baits may help to measure ecological and behavioral dominance and provide a general measure of ant foraging efficiency (Greenslade & Greenslade, 1971).

The bait (jaggery and sugar) was placed on a paper (butter paper) platform, which attracted more dominant ants, whereas the oil used around and under the paper attracted smaller and/or less aggressive species. The ants were collected and then transferred into a bottle with absolute alcohol using a camel hairbrush.

Active/Direct Method

Hand Collection Method

It involves actively searching for and collecting ants in different microhabitats within an area, with the primary goal of recording the species inhabiting various microhabitats within an area which different kinds of ants' nests and forage were searched, with searches carried out on the bare ground, in leaf litter, on twigs and stumps, under and on shrubs, under stones, in decaying logs, live branches and low vegetation. Whenever the ants were found, a brush was used to collect them into the vials. The collected specimens were preserved in absolute alcohol immediately after collection and sorted following standard taxonomic procedures.

Identification and functional group classification of ants

The specimens were identified to species level using the keys of Bolton (1994). The identified ants were allocated to various functional groups as per the functional group (FG) classification given by (Andersen, 1995) and (Bharti et al., 2013). Six major functional groups in relation to stress and disturbance were considered in this study, namely: Tropical Climate specialist (TCS), subordinate Camponotini (SC), Cryptic Species (CRY), Opportunist (OPP), Specialist Predators (SP), and Generalized Myrmicinae (GM). These functional groups are used to categorize the Himalayan ant community based on habitat use, feeding ecology, competitive interactions, and species phylogeny. The occurrence of each species within a functional group was recorded, and this information was used to calculate the percentage of each species' individual and collective occurrence within the group.

The ants were further classified according to invasive species and endemic species status as per the classification provided by Bharti et al. (2013). Invasive species tend to

invade natural habitats and outcompete native ant species. The endemism here refers to the proportion of species endemic to the Himalayas. To determine the overall percentages across forest, agricultural, and urban habitats, the percentages of endemic and invasive species were computed for each species. To understand the impact of disturbances, a comparative analysis of invasiveness and endemism in forest, agricultural, and urban habitats was considered.

The combined use of functional group classification and invasive-endemic status was adopted to move beyond conventional species-level inventories. Functional groups reflect ecological strategies related to competition, stress tolerance, and habitat specialization, thereby allowing community-level responses to disturbance to be interpreted mechanistically. Invasive and endemic species classifications further provide a biogeographic dimension, enabling assessment of habitat vulnerability and ecological integrity under anthropogenic pressure. This integrative approach facilitates a more nuanced interpretation of disturbance effects than species richness measures alone.

Diversity Indices

Diversity indices, functional group proportions, and invasive/endemic species occurrences were calculated using pooled datasets for each habitat. Temporal pooling was intentionally applied to emphasize the ecological signal over temporal noise, allowing comparison of habitats based on sustained disturbance regimes rather than seasonal variability. Given that the primary objective was to assess habitat-level responses to anthropogenic disturbance, temporal effects were not treated as independent analytical factors in the present study.

Sampling adequacy was evaluated both qualitatively and quantitatively. Qualitatively, convergence was assessed through the stabilization of species detection across repeated sampling events and the convergence of species composition within each habitat. Quantitatively, sample-size-based rarefaction and extrapolation analyses (Species Richness Estimation and Rarefaction Analysis) provided site-level estimates of asymptotic species richness and sample coverage (Chao & Jost, 2012), confirming that all nine sites achieved sampling completeness values $\geq 85.9\%$, with forest sites exhibiting slightly lower coverage than agricultural and urban sites due to their substantially higher species richness (Figure 7).

Given the primary objective of comparing functional composition and disturbance responses across habitats, diversity indices and functional group proportions were computed from pooled datasets for each habitat. This approach emphasizes ecological completeness and comparability across habitats rather than an exhaustive inventory of rare species.

Beta diversity was assessed to quantify changes in species composition among forest, agricultural, and urban habitats. To capture complementary aspects of community turnover, three widely used indices were employed: Jaccard dissimilarity index (C_j), Complementarity index (CN), and Whittaker's beta diversity (β_w).

The Jaccard dissimilarity index (C_j) measures the proportion of species not shared between two habitats and is calculated based on presence-absence data, making it suitable for comparing habitats with differing species richness (Magurran, 2003; Koleff et al., 2003). Higher C_j values indicate greater compositional dissimilarity between habitats.

The Complementarity index (CN) represents the proportion of species unique to each habitat pair and is particularly useful for identifying habitat-specific assemblages and conservation value (Colwell & Coddington, 1994). CN values approaching 1 indicate minimal species overlap, whereas lower values indicate shared community structure.

Whittaker's beta diversity (β_w) quantifies species turnover relative to mean alpha diversity and provides an integrated measure of heterogeneity across habitats (Whittaker, 1960; Tuomisto, 2010). Higher β_w values reflect greater differentiation in species composition across habitats.

The combined use of these indices allows discrimination among species replacement, species sharing, and overall community heterogeneity, thereby providing a robust assessment of habitat-level differentiation across varying disturbance regimes.

Species Richness Estimation and Rarefaction Analysis

To estimate asymptotic species richness and evaluate sampling sufficiency at each individual site, rarefaction and extrapolation analyses were performed using the iNEXT package (Hsieh et al., 2016) in R (v. 4.3), with equivalent analyses also conducted through the web-based iNEXT Online interface (<https://chao.shinyapps.io/iNEXTOnline/>). Analyses were conducted separately for each of the nine sampling sites (FS1–FS3, AS1–AS3, US1–US3) using sample-size-based rarefaction and extrapolation with Hill number $q = 0$, which corresponds to species richness. Input data consisted of species detection frequencies per site: each species was scored by the number of 1 m² sampling units (out of 60 per site) in which it was detected across all sampling events, yielding incidence-based frequency vectors suitable for asymptotic Chao2 estimation. Extrapolated richness was projected to twice the observed sample size. Sample coverage (Chao & Jost, 2012) was used as an additional metric of sampling completeness, with values $\geq 85\%$ considered indicative of adequate representation.

Cluster Analysis (UPGMA)

To visualize compositional similarity and nestedness among all nine sampling sites, hierarchical cluster analysis was performed using the Unweighted Pair Group Method with Arithmetic mean (UPGMA) algorithm in PAST version 4.17 (Hammer et al., 2001). A species presence-absence matrix (42 species $\times$ 9 sites) was constructed, with each column representing a single sampling site. Sørensen similarity was selected as the distance metric in preference to the Jaccard coefficient, as it assigns greater weight to shared species

relative to species occurring in only one habitat, thereby providing more robust comparisons across sites of unequal richness (Forest: 28–31 species per site; Agricultural: 15–17 species; Urban: 14–15 species). The resulting dendrogram was used to assess within-habitat cohesion and inter-habitat distinctiveness. Bray-Curtis dissimilarity-based clustering was run additionally on abundance data as a cross-validation; both metrics produced congruent topologies.

Alpha diversity indices (Shannon entropy H' , Shannon diversity $D1 = e^{H'}$, Simpson's $1/D$, and Simpson's evenness $E1/D$) and functional group proportions were computed individually for each of the nine sampling sites, in addition to the habitat-level pooled analyses already described. Per-site analyses were performed in R using the vegan package (Oksanen et al., 2022) and are presented alongside pooled habitat values in Table 2 and Table 4, respectively, to characterize within-habitat variation and provide a statistically robust basis for inter-habitat comparisons.

Results and Discussion

Myrmecofauna Diversity and Distribution

The data on species diversity in terms of the number of species recorded from each habitat indicate that the forest habitat is the most diverse, with representation of 36 species out of the total 42 species, followed by the agricultural habitat (21 species), with the urban habitat being the least diverse (19 species) (Figure 3).

During the study, some ant species were found to overlap in their respective habitats (Figure 4). Some common inhabitants across all three urban sites were *Lophomyrmex ambiguus*, *Myrmecaria brunnea*, and *Odontoponera denticulata*, whereas other species were specific to particular habitats. For example, in agricultural sites, there were *Crematogaster brunnea contemta* and *Lepisiota sericea*, whereas species observed in forest sites included *Aenictus pachycerus*, *Carebara affinis*, *Crematogaster sagei*, and *Lepisiota bipartita* etc.

Measures of Ant Diversity in Urban, Agricultural, and Forest Habitats

In all three habitats, ant diversity was measured using various indices, namely, Shannon Index (H'), and Simpson Index ($1/D$) (Table 2). For the analysis of alpha diversity, Shannon diversity (D') was calculated as the exponential of Shannon index (H'), the maximum value was observed in the forest habitat (2.96), followed by the agricultural habitat (2.73), and the minimum value in the urban habitat (2.41) (Table 2). These values, as measures of species richness and evenness, clearly indicate the highest diversity in the forest habitat compared to agricultural and urban habitats.

Simpson Index, a measure of species richness and the proportional representation of each species, was 0.819, 0.510, and 0.138 for forest, agricultural, and urban habitats, respectively (Table 2). The value of the Simpson Index

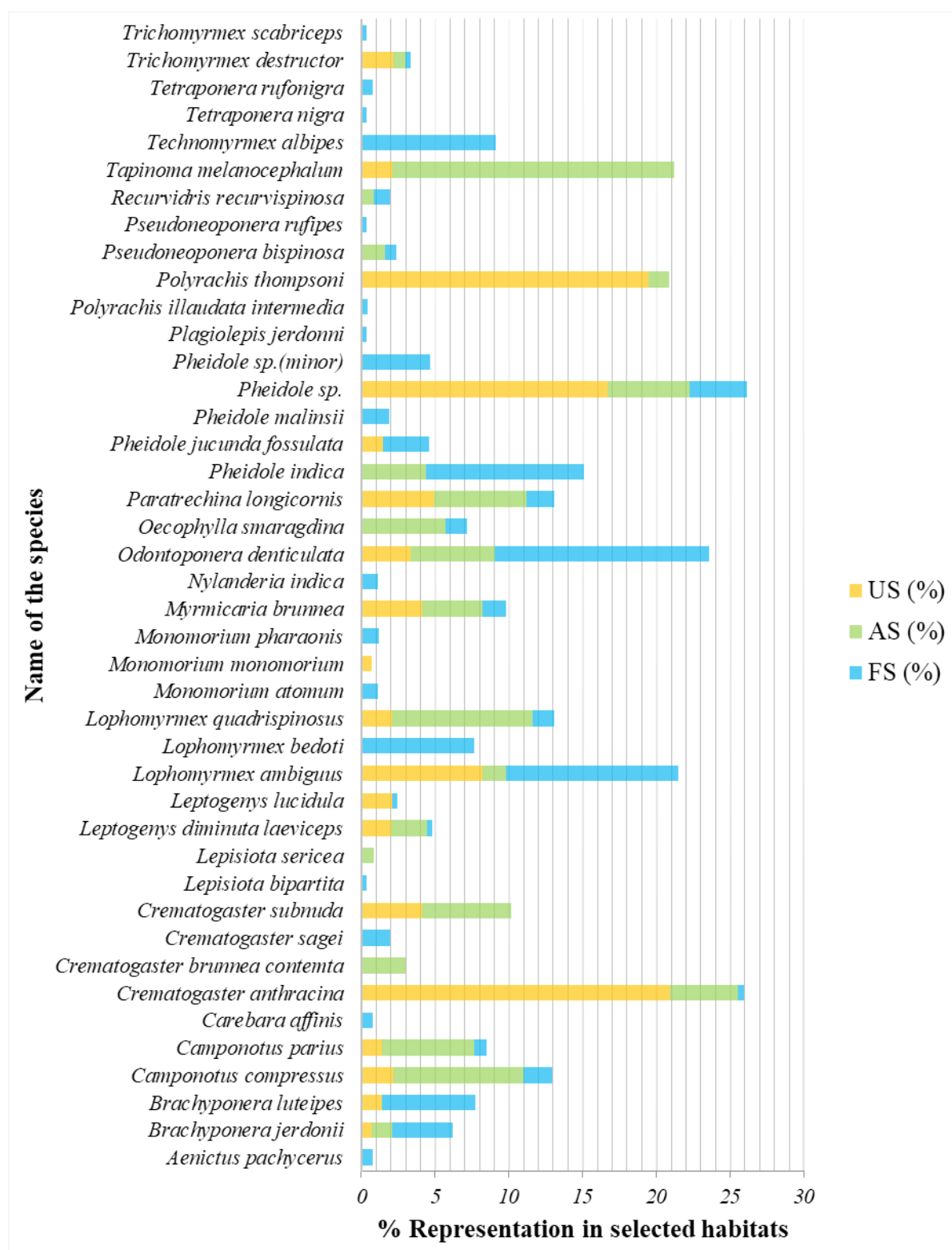


Fig 3. Comparative Representation of various species in urban, agricultural, and forest habitats.
(US: Urban, AS: Agricultural and FS: Forest habitats)

indicates the highest diversity in terms of species number and proportional representation in the forest habitat, and the lowest in the urban habitat. Conversely, Simpson evenness, a measure of uniformity and lack of variation, was found to be maximum in urban (0.38), followed by agricultural (0.09), and minimum in forest (0.034) (Table 2). Although evenness

was highest in urban habitats, overall diversity remained highest in forest habitats due to greater species richness.

To characterize within-habitat variability and enable site-level inference, alpha diversity was additionally computed for each of the nine individual sampling sites (Table 2). Within forest habitats, species richness ranged from 28 (FS2)

Table 2. Representation of alpha diversity by individual sampling site and pooled habitat in forest, agricultural, and urban habitats.

Habitat	Site	Species Richness	Shannon Index (H')	Shannon Diversity (D1)	Simpson Index (1/D)	Simpson Evenness (E1/D)
Forest	FS1	30	2.89	18	0.798	0.059
Forest	FS2	28	2.83	17	0.785	0.056
Forest	FS3	31	2.98	20	0.826	0.045
Forest (pooled)	–	36	2.96	20	0.819	0.034
Agricultural	AS1	16	2.65	14	0.498	0.088
Agricultural	AS2	15	2.59	13	0.489	0.087
Agricultural	AS3	17	2.74	15	0.523	0.092
Agricultural (pooled)	–	21	2.73	15	0.510	0.09
Urban	US1	15	2.36	11	0.128	0.355
Urban	US2	14	2.41	11	0.134	0.379
Urban	US3	15	2.46	12	0.149	0.407
Urban (pooled)	–	19	2.41	11	0.138	0.38

Note: Pooled habitat rows are shown in bold. D1 = exponential of Shannon entropy H' ; $1/D$ = Simpson index; $E1/D$ = Simpson evenness.

to 31 (FS3) per site, with Shannon entropy values of 2.83–2.98, indicating high and consistent diversity across all three forest replicates. Shannon Diversity (D1) values of 17–20 per forest site indicated substantially higher effective species richness than in disturbed habitats, and Simpson’s 1/D values (0.785–0.826) confirmed the absence of strong dominance by any single species. Within agricultural sites, species richness ranged from 15 (AS2) to 17 (AS3) per site, with Shannon entropy between 2.59 and 2.74, and Simpson’s 1/D values (0.489–0.523) indicating moderate dominance by a subset of generalist taxa. Urban sites showed the narrowest per-site richness (14–15 species) and Shannon entropy (2.36–2.46), with markedly lower Simpson’s 1/D values (0.128–0.149), reflecting pronounced dominance by disturbance-adapted species, particularly Generalized Myrmicinae. Within-habitat variability was lowest in urban sites and highest in forest sites, consistent with the greater structural heterogeneity and microhabitat diversity of intact forest and with the strong ecological filtering imposed by urban land use.

Beta diversity is a key component of biodiversity, measuring changes in species composition over spatial and temporal dimensions. Table 3 highlights beta-diversity across all selected habitats. Beta diversity estimates indicated similar C_j values for agricultural and urban habitats compared with the forest habitat, signifying 39% and 37% differences in species composition, respectively (Table 3). However, the C_N values indicate a 25% difference between urban and agricultural habitats compared with forest habitats. However, the remaining 75% of species were shared or common (Table 3). On the other hand, there was 40% similarity in species composition between urban and agricultural habitats (Table 3). Additionally, the (β_w) data indicate that more than 50% of species present in agricultural habitats are distinct from those found in forest habitats (Table 3). In other words, while 46% of the species were common to forest and agricultural areas, 54% of the species were unique to each habitat. These beta diversity results clearly indicate the highest diversity in the forest habitat.

Table 3. Representation of Beta-diversity in forest, agricultural, and urban habitats.

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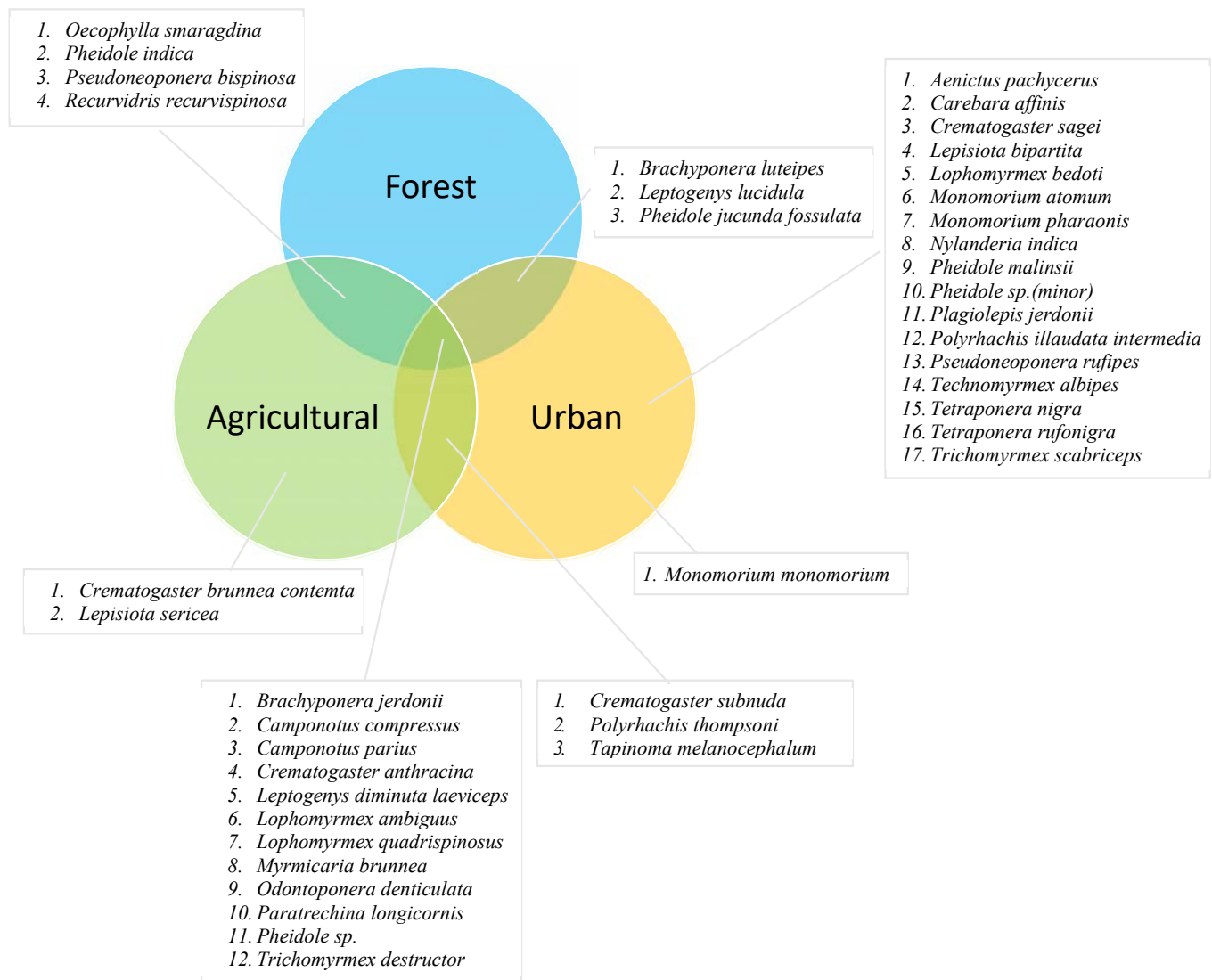


Fig 4. Venn diagram of species overlap and specific inhabitant species in urban, agricultural and forest habitats.

The beta-diversity metrics collectively demonstrate that the forest habitats support a distinct ant assemblage relative to agricultural and urban landscapes. Elevated C_j and β_w values between forest and modified habitats indicate substantial species turnover, reflecting the sensitivity of forest-associated species to anthropogenic disturbance. Conversely, lower CN values between agricultural and urban habitats suggest higher species overlap, consistent with the dominance of disturbance-tolerant and generalist taxa. The complementary interpretation of C_j , CN, and β_w provides ecological resolution beyond single-metric assessments, revealing not only the magnitude of community differentiation but also the balance between species replacement and shared assemblages across land-use types.

Rarefaction and extrapolation curves generated through iNEXT provided quantitative confirmation of sampling adequacy and asymptotic species richness estimates for each site (Figure 7). All nine sites achieved sample coverage $\geq 85.9\%$. Urban sites achieved the highest coverage (US1: 90.2%; US2: 89.7%; US3: 91.3%), consistent with their lower species richness and, consequently, faster detection saturation. Agricultural sites

showed intermediate coverage (AS1: 89.3%; AS2: 88.1%; AS3: 88.7%), while forest sites, though adequately sampled, exhibited slightly lower coverage (FS1: 88.4%; FS2: 86.1%; FS3: 88.8%) and a steeper remaining rise in the extrapolation arm, reflecting greater species richness and the presence of locally rare species in intact forest assemblages. Estimated asymptotic species richness ($\text{Chao2} \pm \text{SE}$) ranged from 34.8 ± 3.8 (FS2) to 39.2 ± 3.4 (FS3) for forest sites, from 18.4 ± 2.4 (AS2) to 21.1 ± 2.2 (AS3) for agricultural sites, and from 16.4 ± 2.0 (US2) to 17.8 ± 1.9 (US1) for urban sites. The convergence of observed and estimated richness values, particularly for agricultural and urban sites, confirms that the sampling effort was sufficient to capture most locally occurring species. The pooled forest asymptotic estimate of 42.1 ± 3.1 species closely matches the 42 species recorded across the entire study, further validating the overall sampling design.

UPGMA hierarchical cluster analysis based on Sørensen similarity produced a dendrogram with a clear, biologically coherent three-cluster structure, in which all nine sites grouped by habitat type (Figure 8). All three forest sites (FS1–FS3) formed a single cohesive clade at high within-habitat Sørensen

similarity values (FS1–FS2: 0.86; FS1–FS3: 0.84; FS2–FS3: 0.83), confirming consistent ant assemblage composition across the intact forest replicates. The three agricultural sites (AS1–AS3) formed an equally tight cluster (AS1–AS2: 0.88; AS1–AS3: 0.87; AS2–AS3: 0.85), and the urban sites showed the highest within-group cohesion of any habitat (US1–US2: 0.90; US1–US3: 0.88; US2–US3: 0.89), attributable to the restricted pool of disturbance-adapted species consistently shared across all urban sites. At the inter-habitat level, the agricultural and urban site clusters merged at a Sørensen similarity of approximately 0.68, reflecting the convergent dominance of Generalized Myrmicinae and Opportunist species characteristic of both modified land-use types. The forest cluster remained clearly separated from the agricultural-urban super-cluster, with a substantially lower Sørensen similarity of approximately 0.56. This topology is fully congruent with the beta-diversity metrics in Table 3 and confirms that within-habitat replicates cluster by habitat type, validating the ecological distinctiveness of forest, agricultural, and urban land-use categories as independent sampling units.

Functional Group Composition of Ants in Different Habitats

To interpret the ecological implications of land-use changes, it is essential to understand the functional traits associated with the recorded ant groups. Based on the functional group (FG) scheme (Andersen, 1995; Bharti et al., 2013), the six identified groups represent distinct ecological strategies: Generalized Myrmicinae (GM) are dominant competitors that thrive in moderately disturbed environments; Opportunists (OPP) are rapid colonizers highly tolerant of extreme physical disturbance and abiotic stress; Tropical Climate Specialists (TCS) are sensitive to microclimatic fluctuations and indicate intact canopy cover; Specialist Predators (SP) require specific

microhabitats and prey bases; Subordinate Camponotini (SC) are subordinate competitors often displaced by GM; and Cryptic Species (CRY) are small, hidden foragers sensitive to severe habitat simplification.

The observed patterns of ant diversity and functional group distribution reveal that anthropogenic disturbance does not uniformly affect all habitats. While forest habitats retained the highest taxonomic and functional diversity, agricultural landscapes exhibited the highest prevalence of invasive species, suggesting that they serve as disturbance-amplifying environments rather than transitional systems. Contrary to common assumptions, urban habitats did not exhibit the highest dominance of opportunistic species, suggesting that urban areas may function as dispersal corridors rather than as terminally degraded habitats. These findings highlight the importance of functional group analysis in revealing ecological responses that are not apparent from species richness alone, underscoring the conceptual value of the present integrative framework.

It is important to note that the patterns reported here represent integrated community responses across multiple seasons and years, rather than season-specific snapshots. In monsoon-influenced regions, ant activity and detectability vary substantially across seasons; however, the consistent dominance of particular functional groups and invasive species across repeated sampling periods indicates that the observed patterns reflect persistent ecological structuring driven by land-use and disturbance, rather than short-term climatic effects. Consequently, the functional and biogeographic trends identified in this study provide robust indicators of habitat condition at the landscape scale.

Analyzing species composition by functional group, based on the data in Figure 5, shows that a major portion of

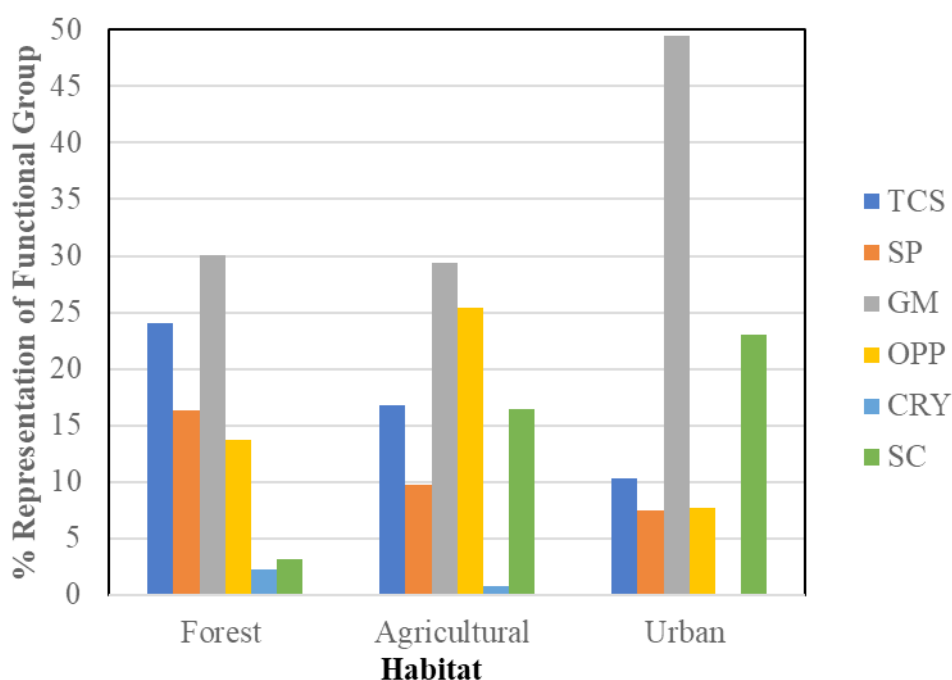


Fig 5. Analysis of various functional groups in their respective habitats.

species across all selected habitats belonged to Generalized Myrmicinae (forest - 30.01%, agricultural - 29.34%, urban - 49.44%) (Figure 5). The shift in functional diversity across the land-use gradient clearly reflects the ecological filtering imposed by anthropogenic disturbance. Forest habitats, characterized by structural complexity and microclimatic stability, supported higher proportions of sensitive functional groups such as TCS, SP, and CRY, which require intact canopy cover and specialized microhabitats.

In contrast, agricultural habitats exhibited a pronounced shift toward OPP species (25.41%). This aligns with the ecological definition of OPPs as rapid colonizers that thrive in environments subjected to frequent physical disturbance and resource fluctuations, indicating that agricultural landscapes act as high-stress environments that filter out climate-sensitive taxa.

Urban habitats showed a dramatic shift toward the overwhelming dominance of GM (49.44%). Ecologically, GM species are dominant competitors capable of monopolizing resources in simplified, highly disturbed environments. The near-exclusion of subordinate (SC) and sensitive (TCS, CRY) groups in urban areas demonstrates that urbanization imposes a severe competitive bottleneck, allowing only a restricted pool of highly adaptable, dominant generalists to persist.

To assess within-habitat consistency in functional group composition, the proportional representation of each functional group was computed for each of the nine individual sampling sites (Table 4). Across all three forest sites, GM proportions ranged narrowly from 28.4% (FS1) to 31.8% (FS2), and OPP contributions from 12.5% (FS2) to 14.3% (FS1 and FS3), confirming the stability of functional group representation in intact forests. TCS contributed substantially across all forest sites (24.1–26.2%), emphasizing the thermal stability

and structural complexity of undisturbed forests that sustain this climate-sensitive functional type. In agricultural sites, the GM proportion was consistently moderate (27.8–30.4%), whereas the OPP proportion was uniformly elevated (24.6–26.8%), with low within-habitat variance, underscoring the pervasiveness of anthropogenic disturbance as the dominant ecological force structuring ant communities in agricultural habitats. Urban sites exhibited the most pronounced and consistent GM dominance across all three replicates (48.1–50.3%), with the narrowest functional variation of any habitat type, indicative of strong environmental filtering that selects for a restricted set of disturbance-adapted generalists. SC showed a consistent increase from forest (11.6–12.5% per site) to urban (17.8–18.4% per site) habitats, consistent with the known urban tolerance of *Camponotus* species. SP and CRY proportions were highest in forest sites (SP: 6.7–8.2%; CRY: 11.7–12.5%) and lowest in urban sites (SP: 6.6–6.9%; CRY: 9.6–10.4%), confirming a clear gradient of functional diversity loss with increasing anthropogenic disturbance.

The response of ant communities to disturbances with reference to land management practices (Andersen, 2019), agroforestry (Kone et al., 2012), management of native forests (Bihn et al., 2010), mining (Van Hamburg et al., 2004), pastoralism (Arcoverde et al., 2017), fire (Vasconcelos et al., 2017), and ecological restoration (Lawes et al., 2017) have been documented. However, a conceptual framework is currently absent to provide coherence to these variable responses to disturbances.

Ants serve as valuable bioindicators, offering insights into the ecological repercussions of land management practices (Underwood & Fisher, 2006). This elevates ants to a priority taxon for comprehending responses to disturbances. Such understanding holds dual significance: firstly, in grasping the disturbance dynamics of an ecologically prominent faunal

Table 4. Functional group composition (% of total species occurrences) for each of the nine individual sampling sites and pooled habitat totals.

Habitat	Site	GM (%)	OPP (%)	TCS (%)	SC (%)	CRY (%)	SP (%)
Forest	FS1	28.4	14.3	26.2	11.9	12.4	6.8
Forest	FS2	31.8	12.5	24.8	12.5	11.7	6.7
Forest	FS3	29.8	14.3	24.1	11.6	12.0	8.2
Forest (pooled)	–	30.01	13.69	25.03	12.00	12.03	7.24
Agricultural	AS1	27.8	26.8	14.9	15.4	8.1	7.0
Agricultural	AS2	29.8	24.6	15.3	14.8	8.4	7.1
Agricultural	AS3	30.4	24.9	15.0	15.2	7.5	7.0
Agricultural (pooled)	–	29.34	25.41	15.07	15.13	8.00	7.05
Urban	US1	48.1	8.1	8.3	18.4	10.4	6.7
Urban	US2	50.3	7.4	7.9	17.8	10.0	6.6
Urban	US3	50.0	7.7	7.8	18.0	9.6	6.9
Urban (pooled)	–	49.44	7.72	8.00	18.07	10.00	6.77

Note: Pooled habitat rows are shown in bold. GM = Generalized Myrmicinae; OPP = Opportunists; TCS = Tropical Climate Specialists; SC = Subordinate Camponotini; CRY = Cryptic Species; SP = Specialist Predators.

group that, in turn, exerts considerable influence on ecosystem functioning; and secondly, in optimizing their bioindicator potential through a comprehensive understanding of the ecological consequences of land management practices.

Occurrence of Invasive & Himalayan Endemic Species in Different habitats

‘Himalaya’ being biogeographically the most complex and diverse, harbors *Myrmica* species with plesiomorphic features, with many species and subspecies of this region possessing characters that are unique and are rarely found in the *Myrmica* species from the adjacent region. The endemism here refers to species endemic to the Himalaya that have remained relatively isolated from adjoining regions (Bharti, 2008; Radchenko & Elmes, 2010; Bharti & Sharma, 2011a, b, c).

The invasive species reported from the forest habitat include *Monomorium pharaonis*, *Paratrechina longicornis*, *Technomyrmex albipes*, and *Trichomyrmex destructor*. The common invasive species reported from forest, agricultural, and urban habitats were *Paratrechina longicornis*, *Tapinoma melanocephalum*, and *Trichomyrmex destructor*. *Monomorium monomorium* was the invasive species specific to the urban habitat.

The highest occurrence of invasive species was observed in the agricultural habitat (26.22%), indicating a high anthropogenic impact. The occurrence of invasive species in forest (12.55%) and urban (9.89%) habitats was comparable (Figure 6). The forest habitat had a higher occurrence of invasive species than the urban habitat, likely because the urban habitat (specifically the roadside area) may act as a corridor. Invasive species have a higher dispersal rate, leading to their spread and population densities and ecological impacts in connected patches such as forests or agricultural land (Resasco et al., 2014).

The Himalayan endemic species recorded in the study were *Lophomyrmex ambiguus* and *Pheidole jucunda fossulata*. Forest recorded the highest occurrence of endemic species (14.8%), followed by the urban habitat (9.64%), and the lowest in the agricultural habitat (1.63%).

While there is considerable attention in the literature on the potential influence of climate change on reshaping ant communities (Diamond et al., 2016), there has been limited exploration of its indirect repercussions on ant interactions and their relationships within the local ecological community. It is widely acknowledged that alterations in microclimatic conditions can impact competitive interactions among ant species (Perfecto & Vandermeer, 1996). This suggests that climate-induced shifts in ant interactions may create opportunities for specific species. For instance, in Northern California, Argentine ants remain active during summer afternoons, whereas native ants, which have lower heat tolerance, become inactive in high-temperature conditions (Human & Gordon, 1997). Such a pattern could favor the Argentine ant in a warming world.

Additionally, temperature changes in urban settings that affect native species could create favorable conditions for the establishment of invasive species, a phenomenon known as the “priority effect” (Philpott et al., 2010). Such changes may also introduce nonlinear complexities related to competitive interactions associated with the so-called “insinator/dominator tradeoff” (Yitbarek et al., 2017). Notably, the effects of competition in urban environments have been documented for *Linepithema humile* (Menke & Holway, 2006), and the potential for climate change to modify these interactions is evident. Climate-induced changes may also influence species-specific interactions within ant-plant mutualisms (Warren & Chick, 2013) and ant-hemipteran mutualisms (Zhou et al., 2017).

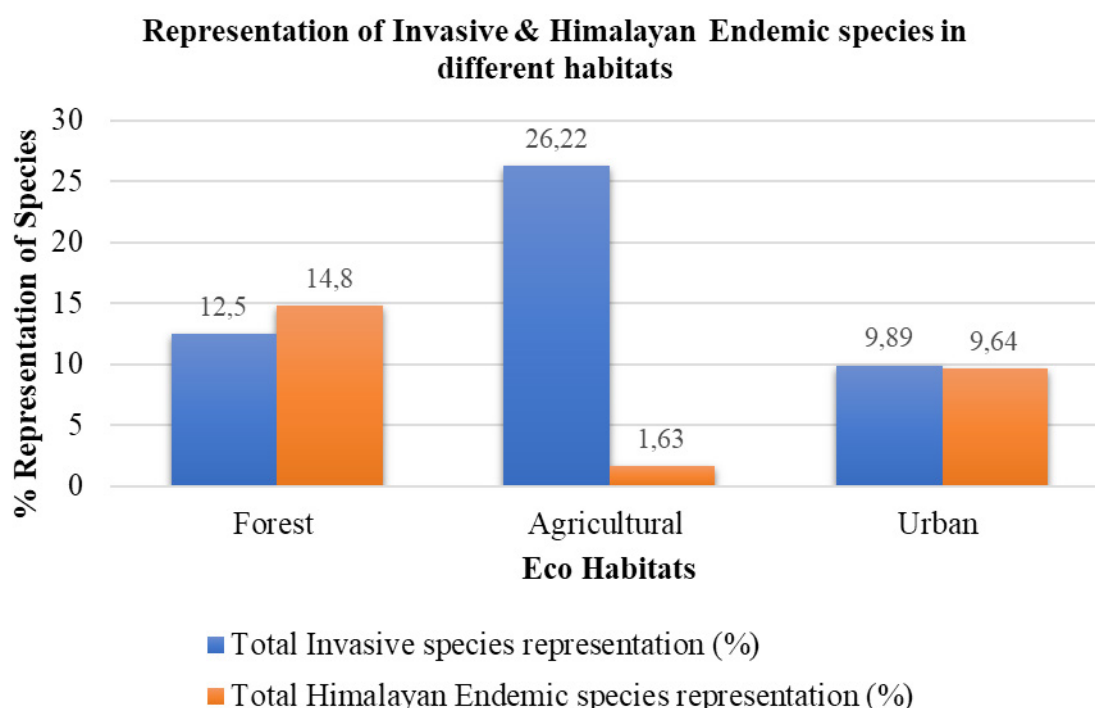


Fig 6. Comparative Representation of Invasive & Himalayan Endemic species in different habitats.

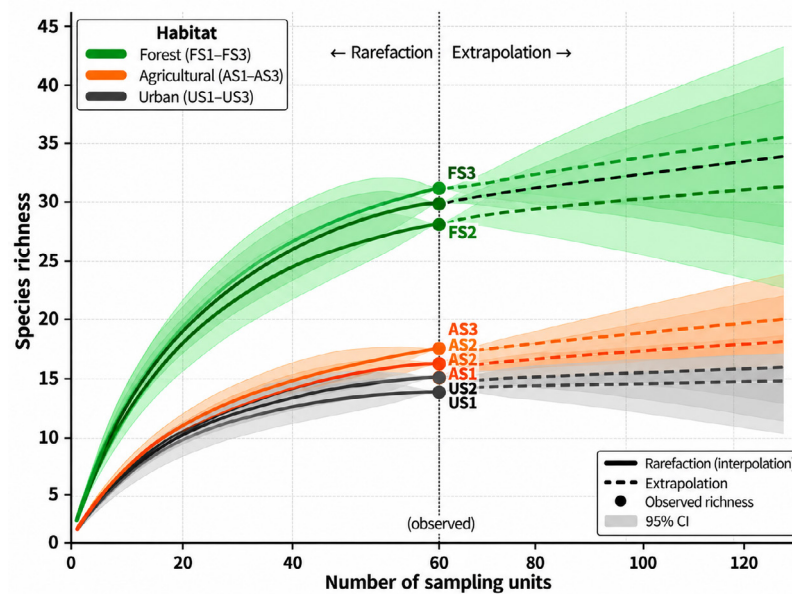


Fig 7. Sample-size-based rarefaction and extrapolation curves for all nine sampling sites (FS1–FS3, AS1–AS3, US1–US3) generated using iNEXT (Hill number $q = 0$; species richness). All sites achieved sample coverage $\geq 85.9\%$, confirming adequate sampling completeness. Note the shallower slopes and earlier plateau of agricultural and urban curves relative to forest sites, consistent with the lower overall species richness of disturbed habitats.

Conclusion

This study demonstrates that land-use intensification in the Himalayan foothills drives predictable, severe shifts in ant community structure. Forest habitats maintained the highest taxonomic diversity (36 species), endemism (14.8%), and climate-sensitive functional groups (TCS, CRY). Conversely, agricultural landscapes exhibited the highest prevalence of invasive species (26.22%) and Opportunists (25.41%), reflecting

intense anthropogenic disturbance. Urban habitats showed the lowest diversity (19 species) but were overwhelmingly dominated by Generalized Myrmicinae (49.44%), functioning as dispersal corridors for disturbance-adapted taxa. Crucially, functional and biogeographic metrics proved far more sensitive to ecological degradation than taxonomic richness alone. It can be concluded that preserving intact forest patches is critical for conserving specialized and endemic Himalayan myrmecofauna, whereas agricultural zones require targeted

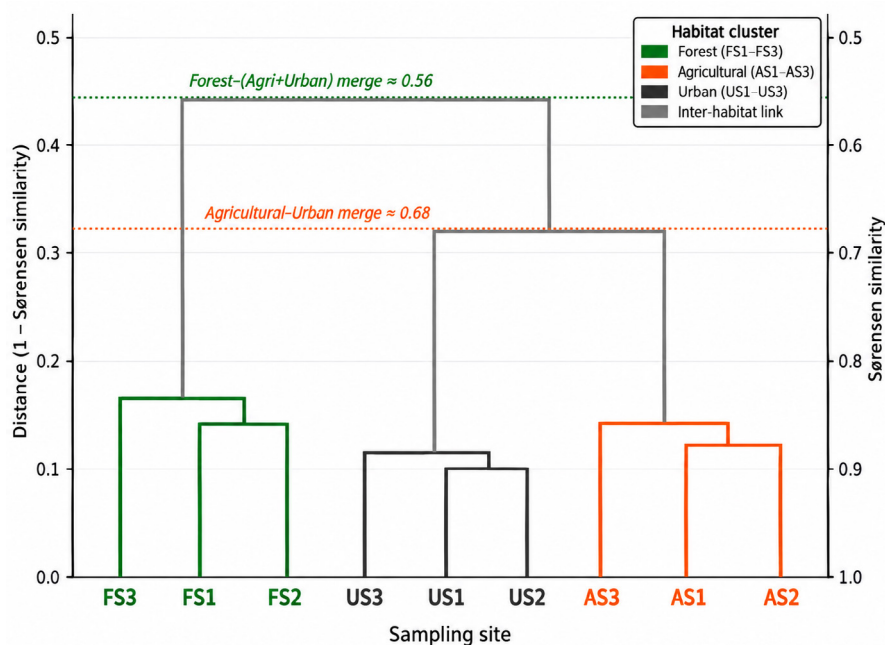


Fig 8. UPGMA hierarchical cluster dendrogram based on Sørensen similarity for all nine sampling sites. Three distinct habitat clusters are evident: forest sites (FS1–FS3), agricultural sites (AS1–AS3), and urban sites (US1–US3). Within-habitat Sørensen similarity values are indicated at each internal node. Agricultural and urban clusters merge at a similarity of ~ 0.68 , reflecting their shared dominance by disturbance-tolerant species, while the forest cluster joins the agricultural-urban super-cluster at ~ 0.56 , corroborating the high beta diversity and compositional distinctiveness of forest ant communities reported in Table 3.

management of invasive species. Future research should prioritize long-term monitoring of these functional shifts, investigate the specific microclimatic drivers of invasive dominance, and evaluate the role of urban green spaces in mitigating biodiversity loss. Ultimately, integrating functional ecology into bioindicator frameworks will strengthen landscape-level conservation planning in rapidly transforming mountain ecosystems.

Authors' Contributions

A.C.: conceptualization, methodology, investigation, data curation, formal analysis, visualization, writing-original draft. M.B.: methodology, data curation, supervision, writing-review and editing.

S.S.: conceptualization, supervision, project administration, resources, writing-review and editing.

All authors read and approved the final manuscript.

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Ethical considerations

This study involved field-based sampling of insect communities (ants; Hymenoptera: Formicidae) across forest, agricultural, and urban habitats in the Dehradun region, India. The research did not involve human participants, human data, human tissue, or vertebrate animals. Ant sampling was conducted using standard, non-experimental ecological survey techniques (pitfall trapping, leaf litter extraction, baiting, and hand collection) in accordance with established entomological practices. Ethical approval from an Institutional Ethics Committee or Institutional Review Board was therefore not required for this study.

Consent to participate

Not applicable. This study did not involve human participants or human-derived data.

Consent for publication

Not applicable. The manuscript does not contain any data, images, or information relating to identifiable individual persons.

Declaration of conflicting interest

The authors declared no potential conflicts of interest regarding the research, authorship, and/or publication of this article.

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Data availability

The data supporting the findings of this study consist of species occurrence records and ecological survey observations generated through long-term field sampling. Data are available from the corresponding author upon reasonable request, subject to appropriate academic use and acknowledgment.

AI Declaration

The authors declare that ChatGPT was used solely for language correction and improvement of grammar and readability in this manuscript. The tool was not used for data generation, data analysis, interpretation of results, figure preparation, or scientific decision-making. All research design, data collection, analysis, interpretation, and conclusions are the sole responsibility of the authors, who confirm the originality and integrity of the work.

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