

5-20-2026

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How to Cite this Article

Nazir, Takhmina and Hussain, Mubashar (2026) "Distributional Dynamics and Patterns of Co-Existence in Dung Beetles (Tribe: Onitini) Across Agricultural Landscapes of Punjab, Pakistan," *Baghdad Science Journal*: Vol. 23: Iss. 5, Article 7.

DOI: <https://doi.org/10.21123/2411-7986.5291>

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RESEARCH ARTICLE

Distributional Dynamics and Patterns of Co-Existence in Dung Beetles (Tribe: Onitini) Across Agricultural Landscapes of Punjab, Pakistan

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ABSTRACT

Dung beetles (Scarabaeidae: Scarabaeinae) play a crucial role in dung removal and nutrient cycling. We assessed the distributional patterns of diversity of the tribe Onitini across 12 subdivisions in Gujranwala, Gujrat, and Sialkot districts of Punjab, Pakistan. Surveys were conducted twice a month with an inter-visit interval of ~2 weeks by placing three pitfall traps along each 1000 m transect, each spaced ~330 m apart. Data were collected from nine traps placed along three transects at each location within the subdivisions. Gujrat district demonstrated the highest species richness, recording all 11 species, followed by Sialkot and Gujranwala. *Onitis castaneus* was the dominant species in all districts in winter. *Onitis excavatus* was most abundant in spring and summer seasons, both in the Gujranwala and Sialkot districts. In summer, *O. subopacus* was dominant in Sialkot. PERMANOVA indicated no significant differences in species composition among districts ($p = 0.278$, $R^2 = 0.084$), while NMDS revealed strong overlap among divisions. SIMPER analysis showed variations in the relative abundance among districts, resulting in high Bray–Curtis dissimilarities. The spatial dissimilarity observed was mainly contributed by *O. castaneus*, *O. excavatus*, and *O. subopacus*. *Onitis singhalensis* and *O. crassus* were recorded exclusively from Gujrat, indicating local habitat association. Dung beetle assemblages were also significantly influenced by seasons ($R^2 = 0.165$). The land use types also influenced abundance patterns, specifically in districts. This study provides the first region-wide ecological comparison of Onitini assemblages in Punjab and establishes a baseline for future assessments of dung beetle diversity and ecosystem functioning under agricultural intensification.

Keywords: Checklist, Dung beetles, Gujrat, Paracoprids, Tunnelers

Introduction

Arthropods play a central role in terrestrial ecosystems by regulating key ecological processes and contributing disproportionately to biodiversity and ecosystem functioning¹ and sustainability.² Among insects, dung beetles are particularly important ecosystem service providers,³ such as bioturbation,⁴ dung decomposition,⁵ and nutrient cycling.⁶ These coprophagous beetles are highly sensitive to changes in habitat structure, land use,

and resource availability.⁷ Dung beetles belonging to the tribe Onitini (subfamily: Scarabaeinae) are functionally important insect species in the terrestrial ecosystems.⁸ These beetles demonstrate varied behavioral and trophic strategies which enable them to occupy diverse dung-based microhabitats. Additionally, the nesting behavior of these beetles helps them in resource partitioning and coexistence.⁹ In the context of global distribution, this tribe comprises 18 genera with 210 species, which are mostly obligate coprophages.¹⁰

Received 31 August 2025; revised 26 December 2025; accepted 7 January 2026.
Available online 20 May 2026

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<https://doi.org/10.21123/2411-7986.5291>

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Agroecosystems show variations in the landscape at a local scale, such as croplands, pastures, agroforestry, and infrastructure.¹¹ These local landscape variations result in different environmental conditions and resources, which influence community structure during different seasons.¹² Agroecosystems are characterized by anthropogenic activities in land-use intensity and habitat modifications, which affect distributional patterns of community assemblages, their ecological interactions and seasonal dynamics.¹³ Major threats to the dung beetle communities in agricultural landscapes include agricultural intensification, changes in livestock management, use of pesticides, and habitat fragmentation. These factors have resulted in a decline in abundance¹⁴ of many species, lower diversity¹⁵ at the local level, and a reduction in functional roles¹⁶ as a whole. Identifying the patterns of local distribution and dominance of dung beetle species is key to understanding community reorganization in landscapes with anthropogenic disturbances. Investigating community structure in human-influenced landscapes is becoming an increasingly important area of research in contemporary insect ecology.¹⁷

The study area, which is also referred to as the industrial triangle, comprises three districts (Gujranwala, Sialkot and Gujrat) in the province of Punjab, Pakistan.¹⁸ This area provides diverse local environmental conditions suitable for the evaluation of the biodiversity and ecology of dung beetles. The presence of industrial areas, extensive agricultural lands and diverse agro-climatic conditions provides heterogeneity, which supports higher livestock densities and continuous dung availability. These conditions promote community stability, diversity and higher abundance.^{19,20} Such heterogeneity provides a natural gradient of resource availability and environmental conditions, which shape dung beetle assemblages.²¹

The coexistence and exploitation of ephemeral resources by dung beetles is of particular interest in landscape ecology, mainly due to the role of dung beetles in the provision of ecosystem services. The coexistence is maintained through resource partitioning and spatial, temporal, or functional differentiation that reduces competitive exclusion.²² Dung beetles show temporal niche partitioning through seasonal and phenological segregation. The differences in dung burial behavior (nesting strategies) are key determinants of distributional patterns in agricultural systems where dung availability fluctuates spatiotemporally.²³ For instance, in intensive land use scenarios, a few generalist species dominate with reduced species richness, a key pattern observed in agroecosystems.²⁴

Recent surveys indicate variations in the species richness and abundance of different species belonging to the tribe Onitini, particularly from various ecological regions of Punjab. For example, the Onitini of Gilgit Baltistan of northern Pakistan⁸ has been reported, and a checklist of dung beetles from the repository of Pakistan Museum of Natural History (PMNH), Islamabad, was recently published.²⁵ Therefore, more detailed surveys need to be conducted across habitats and seasons to better capture the local diversity of dung beetles. However, available studies are almost exclusively taxonomic, lacking analyses of population dynamics, habitat relationships, and the ecological mechanisms underlying coexistence in Onitini communities. In Punjab, including Sialkot, Jhelum, and Gujrat, the research on dung beetles has largely focused on overall Scarabaeinae assemblages, providing species inventories and broad habitat-level diversity patterns, but treating *Onitis* and other Onitini species only as components of the wider fauna. Consequently, how Onitini assemblages respond to land-use variation and seasonality and how coexistence is maintained under resource-limited agricultural conditions remains poorly understood. In this study, we address these gaps by examining the distribution, abundance, and community structure of Onitini dung beetles across major agricultural districts of Punjab, with a particular focus on spatial heterogeneity, seasonal dynamics, and coexistence mechanisms. We hypothesize that species richness peaks in heterogeneous landscapes due to increased resource availability. This study thus provides a new regional baseline and a contribution towards insights into the ways in which coexistence in such an ecologically significant tribe is being preserved under anthropogenically altered conditions.

Material and methods

Study areas

Gujrat (32.5731°N, 74.1005°E; 156–401 m above sea level) lies in the northern semi-arid zone of Punjab, Pakistan, covering approximately 3.79 million acres between the Chenab and Jhelum rivers. The landscape comprises a mosaic of rainfed and irrigated plains dominated by croplands, pastures, and agroforestry patches. Agro-climatically, Gujrat falls within Arid Irrigated Zone II, with mean annual temperatures ranging from 16.8°C to 29.8°C and annual rainfall between 714 and 1,107 mm. Soils vary from loam to medium loam, supporting diverse agricultural practices.²⁶ Major crops include wheat, rice, maize, millets, pulses, oilseeds, and seasonal vegetables. The production of livestock is also very common,

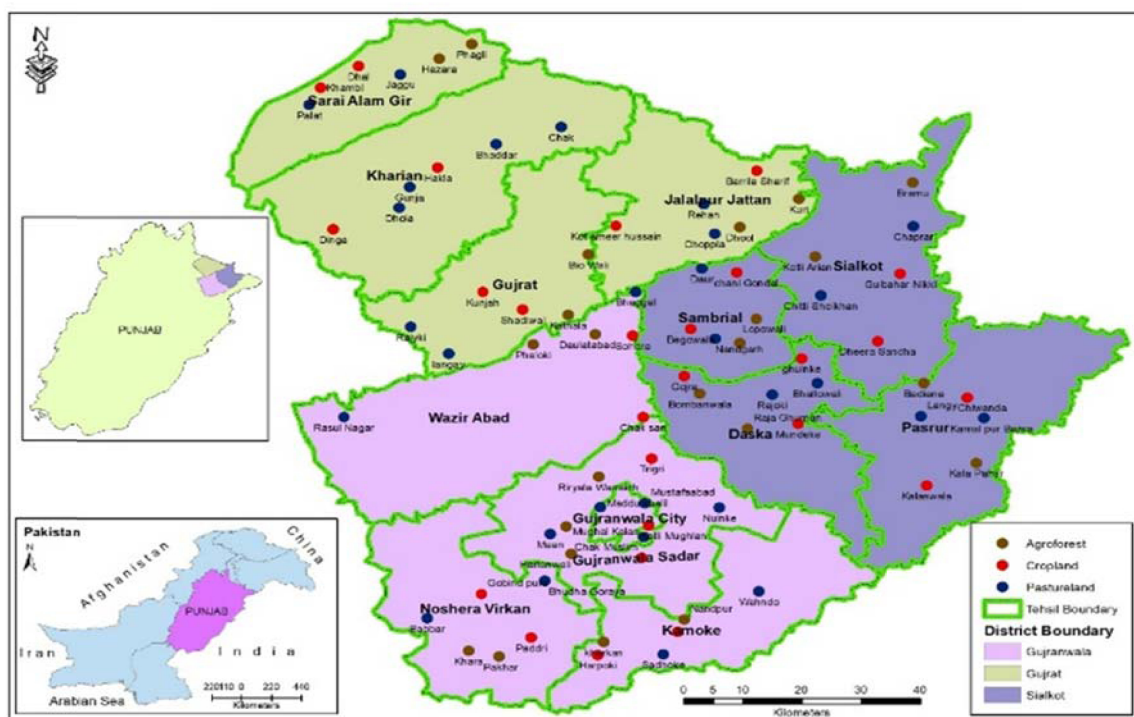


Fig. 1. Study area showing sampling sites for Onitini dung beetles within the subdivisions of Gujrat, Gujranwala, and Sialkot districts of Punjab, Pakistan.

and cattle, buffalo, goats, sheep, horses, mules, and donkeys are an essential part of the farming system.²⁷

Gujranwala (32.1566°N, 74.1945°E; 226 m above sea level) is located at the heart of Punjab, and covers an area of approximately 2.9 million acres.²⁸ It belongs to the semi-arid subtropical region and has alluvial plains, which are highly cultivated. Its climate is hot and humid (up to 40 °C) in summer, mild in winter, and the yearly rain is 600-1,000 mm, the majority of which falls during the monsoon.²⁹ The soils are mainly alluvial loam and clay loam, which are very fertile and suitable for intensive farming.³⁰ The district is also one of the top producers of wheat, rice, sugarcane, maize, and fodder crops, in addition to vegetables and fruits. Small-scale subsistence farming and larger commercial systems are based on a dense livestock population, which consists of cattle, buffalo, sheep, goats, and equines.³¹

Sialkot District (32.4945°N, 74.5229°E; 250-300 m above sea level) is an area of almost 1.9 million acres, located between the Chenab and the Ravi rivers, in northeastern Punjab.³² Its climate is humid subtropical, which implies hot summers, cool winters, and abundant rainfall (1,000-1,500 mm/year), which makes the region one of the wettest regions of Punjab.³³ It has soils primarily of loam-sandy loam type, which are favorable for various types of cropping.

Rice-wheat rotations, maize, sugarcane, fodder and vegetables dominate agriculture and citrus and guava orchards are the major fruit crops.³⁴

Dung beetle sampling

The study was conducted across three districts, encompassing 12 administrative subdivisions (locally called tehsils) in the province of Punjab, Pakistan. Within this spatial framework, a total of 78 sampling sites were identified to represent variations in land-use types and habitat conditions within each tehsil. The geographic distribution of districts, subdivisions, and sampling sites is illustrated in Fig. 1. The site selection was based on the preliminary surveys to ensure spatial independence and to capture local-scale heterogeneity in dung beetle assemblages. The sampling was performed from December 2023 to November 2024 by visiting the sites twice a month with an inter-visit interval of ~2 weeks. Environmental variation was accounted for by incorporating land-use type (pasture, agroforestry, and croplands) as a categorical covariate in the analyses. We installed traps once and reinstalled them if disturbed or damaged. All traps were otherwise standardized in dung type, design, and sampling duration. Weather

Table 1. Accession numbers of specimens deposited in the Pakistan Museum of Natural History (PMNH), Islamabad.

Species Name	Repository	Accession Number
<i>Onitis belial</i> (Fabricius, 1798)	PMNH, Islamabad, Pakistan	PMNH-ENT-2025-71885
<i>Onitis caffer</i> (Boheman, 1857)	PMNH, Islamabad, Pakistan	PMNH-ENT-2025-71886
<i>Onitis castaneus</i> (Redtenbacher, 1848)	PMNH, Islamabad, Pakistan	PMNH-ENT-2025-71887
<i>Onitis crassus</i> (Sharp, 1875)	PMNH, Islamabad, Pakistan	Damaged
<i>Onitis excavatus</i> (Arrow, 1931)	PMNH, Islamabad, Pakistan	PMNH-ENT-2025-71888
<i>Onitis falcatus</i> (Wulfen, 1786)	PMNH, Islamabad, Pakistan	PMNH-ENT-2025-71889
<i>Onitis philemon</i> (Fabricius, 1801)	PMNH, Islamabad, Pakistan	PMNH-ENT-2025-71890
<i>Onitis singhalensis</i> (Lansberge, 1875)	PMNH, Islamabad, Pakistan	PMNH-ENT-2025-71891
<i>Onitis subopacus</i> (Arrow, 1931)	PMNH, Islamabad, Pakistan	PMNH-ENT-2025-71892
<i>Onitis virens</i> (Lansberge, 1875)	PMNH, Islamabad, Pakistan	PMNH-ENT-2025-71893

conditions and agricultural activities occasionally disrupted trapping, meaning that not all traps remained functional during every sampling event, which resulted in variation in effective trap effort among months. Therefore, we pooled trap data at the location levels and then at the subdivisions.

At each sampling site, three 1,000-m transects were established, spaced approximately 250 m apart. Along each transect, three pitfall traps were deployed at ~330-m intervals, yielding a total of nine traps per site. Sampling procedures were applied consistently across all transects to ensure comparable effort. A considerable variation in the type and size of pitfall traps used to assess dung beetle diversity and distribution, highlighting limitations in methodological standardization and the need for trap modification to obtain complete local inventories.³⁵ Given this variability, flat pitfall traps were used, as previous studies have shown that they are particularly effective for sampling paracoprid and telecoprid dung beetles.³⁶ Cattle dung has been used extensively in the quantification of dung beetle assemblages.³⁷

Cattle, buffalo, goats, sheep, and equids were found in the study area. Cattle dung has been reported as the most abundant resource utilized by dung beetles.³⁸ Therefore, cattle dung, the most abundant and consistently available resource in the study area, was used to standardize sampling of local dung beetle assemblages.

Trap type and size choice were determined through a review of the literature, which indicates that pitfall traps are the most commonly used method for sampling dung beetles, which vary in size and design.³⁹ We used small-sized plastic containers (600 mL with a 10cm diameter at the top) to construct pitfall traps for surveys; these traps were buried in the soil and covered with lids with different-sized holes. Approximately 400g of cattle dung was placed on the lid of each trap. The traps were left for 48h and then emptied for data collection.²⁰ This design, where bait was placed on a perforated lid rather than directly

inside the trap, provides a natural environment for the beetles to be attracted to pats.⁴⁰ Sampling consisted of handpicking from the pitfall traps and the floatation method.^{35,41}

Preservation and identification

Collected specimens were preserved in 70% ethanol before examination and identification, which was carried out using relevant published literature and identification keys. Collected specimens were sorted and identified based on the available published literature, and identification keys.^{42,43} Because sample sizes varied among districts, we employed coverage-based rarefaction and extrapolation (Chao 1) with 95% confidence intervals to enable fair comparisons of species richness.

The identified specimens were deposited in the Pakistan Museum of Natural History (PMNH), Islamabad, Pakistan, and the corresponding accession numbers issued by the PMNH are summarized Table 1 & Fig. 2. (A, B, C, D, E, F, G, H and I).

Data analysis

Data analyses included quantification of species richness, relative abundance, patterns of community composition, spatial turnover, and seasonal variation in Onitini assemblages. Data collected from individual traps were pooled at the site level before statistical analyses. Relative abundance (%) of each species was calculated at the subdivision and district levels. To understand patterns of distribution at the subdivision and district level, we computed α -diversity metrics Shannon–Wiener (H'), Simpson's diversity ($1-D$), Berger–Parker dominance, Pielou's evenness (J'), and Fisher's α . Menhinick and Margalef indices were used as richness-sensitive indicators to account for differences in sampling effort. These analyses were performed using PAST (v.5.3). We applied

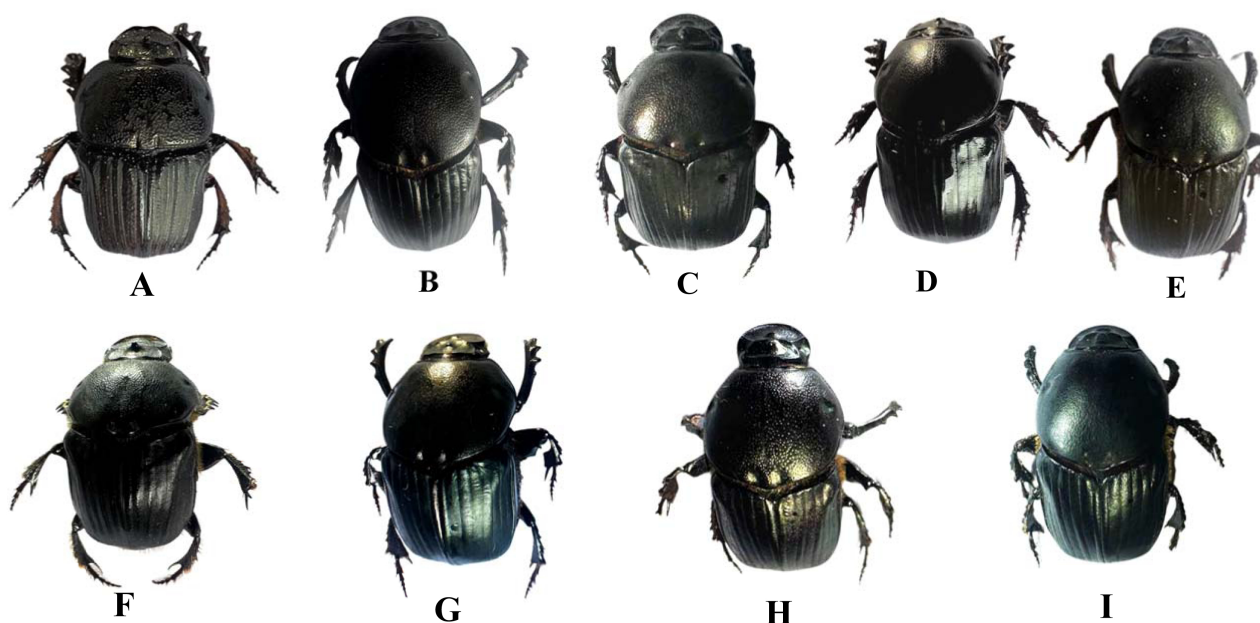


Fig. 2. (A, B, C, D, E, F, G, H and I). Habitus of the species (Dorsal view) of A. *Cheironitis indicus* (Lansberge, 1875), B. *Onitis falcatus* (Wulfen, 1786), C. *Onitis philemon* (Fabricius, 1798), D. *Onitis subopacus* (Arrow, 1931), E. *Onitis virens* (Lansberge, 1875), F. *Onitis belial* (Fabricius, 1798), G. *Onitis excavatus* (Arrow, 1931), H. *Onitis castaneus* (Redtenbacher, 1848), and I. *Onitis singhalensis* (Lansberge, 1875).

SIMPER analysis to quantify the contribution of each species to Bray–Curtis dissimilarities among district pairs on square-root-transformed data. Species were ranked by their individual contributions, and those whose cumulative contribution accounted for roughly 70–80% of the total dissimilarity were classified as ecologically important, as they collectively captured the main structure of compositional turnover among districts. Because sampling effort varied across localities, richness comparisons were standardized through coverage-based rarefaction and extrapolation using the iNEXT package. We computed Hill numbers of order $q = 0$ (richness), $q = 1$ (Shannon diversity), and $q = 2$ (Simpson diversity), each with 95% confidence intervals. Rank–abundance curves were drawn to visualize patterns of dominance and evenness across districts. Bray–Curtis dissimilarities were calculated from square-root-transformed abundance data to assess community composition and to reduce the influence of highly dominant species. NMDS was carried out using the vegan package in R (v.4.5.2) based on Bray–Curtis dissimilarities, and stress values were used to evaluate ordination fit. To test whether assemblage composition differed among districts and among seasons, we performed PERMANOVA using the adonis2 function (vegan) with 9,999 permutations, and we report pseudo- F , R^2 , and permutation p -values for each factor. We assessed

the homogeneity of multivariate dispersion for the same grouping factors (district and season) using betadisper, with significance evaluated by a permutation test (permutest; 999 permutations), before interpreting PERMANOVA results. Where the overall PERMANOVA revealed significant differences, we conducted pairwise comparisons to identify the groups that differed from each other.

Results

Relative abundance

Among the eleven recorded species, *Onitis excavatus* (24.65%), *O. castaneus* (25.02%), and *O. subopacus* (23.03%) dominated overall abundance. District-wise, *O. excavatus* was most abundant in Gujranwala (41.83%) and Gujrat (26.73%), and *O. subopacus* in Sialkot (40.86%). Rare species ($<1\%$) included *Cheironitis indicus*, *O. belial*, and *O. caffer*, each confined to specific districts. The highest number of unique or rare species (*C. indicus*, *O. singhalensis*, *O. caffer*, *O. crassus*) were supported by Gujrat. The richness of the species was six in Gujranwala, eleven in Gujrat, and eight species in Sialkot [Table 2](#).

The distribution and relative abundance of Onitini species varied across the twelve localities in

Table 2. Overall relative abundance (%) of dung beetle species of tribe Onitini across three districts of Punjab, Pakistan.

Species	Gujranwala	Gujrat	Sialkot	Overall
<i>C. indicus</i> (Lansberge, 1875)	–	1.76	2.86	1.77
<i>O. belial</i> (Fabricius, 1798)	–	0.38	0.86	0.44
<i>O. caffer</i> (Boheman, 1857)	–	0.38	1.43	0.59
<i>O. castaneus</i> (Redtenbacher, 1848)	18.75	25.09	28.57	25.02
<i>O. crassus</i> (Sharp, 1875)	–	2.51	–	1.48
<i>O. excavatus</i> (Arrow, 1931)	41.83	26.73	9.71	24.65
<i>O. falcatus</i> (Wulfen, 1786)	14.42	6.02	–	5.76
<i>O. philemon</i> (Fabricius, 1801)	13.94	2.76	7.43	5.68
<i>O. singhalensis</i> (Lansberge, 1875)	–	9.16	–	5.39
<i>O. subopacus</i> (Arrow, 1931)	9.13	18.82	40.86	23.03
<i>O. virens</i> (Lansberge, 1875)	1.92	6.40	8.29	6.20

Table 3. Relative abundance (%) of dung beetle species (Tribe Onitini) across twelve subdivisions of the three districts, i.e., Gujranwala, Gujrat, and Sialkot.

Species	Gujranwala					Gujrat			Sialkot			
	Gujranwala City	Gujranwala Saddar	Kamoki	Nowshera Virkan	Wazirabad	Gujrat	Kharian	Sarai Alamgir	Daska	Pasrur	Sambrial	Sialkot
<i>C. indicus</i>	–	–	–	–	–	0.50	1.03	4.93	3.08	6.36	2.22	–
<i>O. belial</i>	–	–	–	–	–	0.25	1.03	–	1.54	–	4.44	–
<i>O. caffer</i>	–	–	–	–	–	0.75	–	–	–	2.73	–	1.54
<i>O. castaneus</i>	11.11	19.15	10.00	40.00	14.29	17.54	30.26	34.98	50.77	18.18	40.00	22.31
<i>O. crassus</i>	–	–	–	–	–	5.01	–	–	–	–	–	–
<i>O. excavatus</i>	39.68	65.96	43.33	17.50	39.29	26.82	23.08	30.05	–	10.91	2.22	16.15
<i>O. falcatus</i>	9.52	–	26.67	32.50	10.71	7.02	2.56	7.39	–	–	–	–
<i>O. philemon</i>	23.81	10.64	13.33	5.00	10.71	2.26	2.05	4.43	–	12.73	–	9.23
<i>O. singhalensis</i>	–	–	–	–	–	13.03	3.08	7.39	–	–	–	–
<i>O. subopacus</i>	11.11	4.26	6.67	2.50	25.00	19.55	28.21	8.37	38.46	40.91	51.11	38.46
<i>O. virens</i>	4.76	–	–	2.50	–	7.27	8.72	2.46	6.15	8.18	–	12.31

Gujranwala, Gujrat, and Sialkot. *Onitis castaneus* was the most abundant species, with the highest relative abundance observed in Daska (50.77%) and consistent presence across all districts. *Onitis excavatus* showed strong presence in Gujranwala (39.68%) and Gujrat (26.82%), with notable peaks in Gujranwala Saddar (65.96%) and Kamoki (43.33%). *Onitis subopacus* was also widespread, peaking in Sambrial (51.11%) and found in high numbers in Daska (38.46%) and Pasrur (40.91%). Other species like *Onitis philemon* and *Onitis virens* were more localized, with *O. philemon* reaching 23.81% in Gujranwala City and 12.73% in Pasrur, while *O. virens* had a notable presence in Sialkot (12.31%). *Cheironitis indicus*, *O. belial*, *O. singhalensis*, *O. crassus* and *Onitis caffer* were not observed in Gujranwala. *O. singhalensis*, *O. crassus* and *O. falcatus* were not found in Sialkot district Table 3. The significant variations were demonstrated in the seasonal abundance of species of the tribe Onitini across three districts, i.e., Gujranwala, Gujrat, and Sialkot. In winter, *Onitis castaneus* was the most dominant species, showing relative abundances of 84.78% in Gujranwala, 76.82% in Gujrat, and 85.47% in Sialkot. While in autumn, *O. subopacus* demonstrated maximum relative abundance in Gujranwala (83.33%), followed by Sialkot. Surprisingly,

O. subopacus and *O. virens* were the only two species recorded from Gujranwala. In Gujrat, *O. belial*, *O. castaneus* and *O. singhalensis* were also observed during the autumn season, whereas two species were observed: *O. castaneus* and *O. philemon*. In Sialkot, *O. philemon* and *O. belial* were noted during the autumn season. While *O. caffer*, *O. castaneus* and *O. philemon* were recovered from the winter season. While *Onitis castaneus* dominated overall in all districts, other species, such as *Onitis philemon* and *Onitis subopacus*, exhibited moderate seasonal activity across multiple seasons. Some species, like *Onitis belial* and *Cheironitis indicus*, had very restricted seasonal windows. Gujranwala showed pronounced seasonal specialization, with most species active in only one or two seasons. Gujrat exhibited a more evenly distributed seasonal activity pattern, while Sialkot had strong seasonal peaks, with *Onitis subopacus* dominating spring and *Onitis castaneus* remaining the primary species in winter Table 4.

Temporal completeness and abundance–richness relationships

The survey showed that the coverage-based completeness remained high during the sampling period.

Table 4. Species (tribe Onitini) relative abundance (%) during different seasons. The seasonal abundance was calculated for each district separately.

Districts	Species	Autumn	Spring	Summer	Winter
Gujranwala	<i>O. castaneus</i>	–	–	–	84.78
	<i>O. excavatus</i>	–	76.47	45.71	–
	<i>O. falcatus</i>	–	09.8	23.81	–
	<i>O. philemon</i>	–	11.76	15.24	15.22
	<i>O. subopacus</i>	83.33	1.96	12.38	–
	<i>O. virens</i>	16.67	–	2.86	–
Gujrat	<i>C. indicus</i>	–	–	3.99	–
	<i>O. belial</i>	5.45	–	–	–
	<i>O. caffer</i>	–	–	–	1.36
	<i>O. castaneus</i>	27.27	9.36	–	76.82
	<i>O. crassus</i>	–	–	–	9.09
	<i>O. excavatus</i>	–	42.11	40.17	–
	<i>O. falcatus</i>	–	7.02	10.26	–
	<i>O. philemon</i>	–	5.85	1.14	3.64
	<i>O. singhalensis</i>	21.82	5.26	14.53	0.45
	<i>O. subopacus</i>	38.18	14.62	29.63	–
	<i>O. virens</i>	7.27	15.79	0.28	8.64
	<i>C. indicus</i>	–	–	4.88	–
	<i>O. belial</i>	17.65	–	–	–
	<i>O. caffer</i>	–	–	–	4.27
Sialkot	<i>O. castaneus</i>	–	–	–	85.47
	<i>O. excavatus</i>	–	–	16.59	–
	<i>O. philemon</i>	82.35	–	–	10.26
	<i>O. subopacus</i>	–	100	64.39	–
	<i>O. virens</i>	–	–	14.15	–

Monthly Good's coverage ranged from 0.972 to 1.000. The lower values were recorded in September (0.972) and February (0.988) due to the presence of rare species. For seasonal Good's coverage, which ranged from 0.997 to 1.000, the lowest value was observed in Winter (0.997) with one rare species. This sample coverage suggests nearly complete representation of the species during sampling months. The seasonal patterns remained similar even after excluding months with lower species numbers (July, October, and September). A Poisson generalized linear model (GLM) was used to examine how season and total abundance affected species richness. A dispersion check using Pearson residuals showed no overdispersion ($\varphi = 0.64$), indicating that the Poisson model was appropriate for the data. The model explained that the species richness also increased by about 0.78% for each unit increase in abundance ($\beta = 0.0077 \pm 0.0020$ SE, $z = 3.82$, $p = 0.00013$). Seasonal effects, however, were not significant compared to the reference season (Spring: $\beta = 0.275$, $p = 0.48$; Summer: $\beta = -0.189$, $p = 0.64$; Winter: $\beta = -0.403$, $p = 0.29$).

Spatial variation in species diversity and community structure

Variations in species diversity across three districts were observed, with Gujrat district exhibiting the

Table 5. Comparison of diversity indices of dung beetle communities (tribe Onitini) across Gujranwala, Gujrat and Sialkot in the province of Punjab, Pakistan.

Metric	Gujranwala	Gujrat	Sialkot
Taxa_S	6	11	8
Individuals	208	797	350
Dominance_D	0.256	0.1877	0.269
Simpson_1-D	0.745	0.813	0.731
Shannon_H	1.54	1.889	1.563
Evenness_e^H/S	0.777	0.601	0.597
Brillouin	1.471	1.851	1.507
Menhinick	0.416	0.390	0.428
Margalef	0.937	1.497	1.195
Equitability_J	0.852	0.785	0.747
Fisher_alpha	1.154	1.806	1.459
Berger-Parker	0.418	0.267	0.409
Chao-1	6	11	8
iChao-1	6	11	8
ACE	6	11	8
Squares	6	11	8

highest species richness and abundance. In the Gujrat district, higher Shannon, low dominance (Berger-Parker), and moderate evenness values showed a uniform community structure without a single dominant species Table 5. In contrast, Gujranwala and Sialkot showed lower richness and abundance values, while higher dominance values were observed, which reflects the presence of a few dominant species. Gujranwala exhibited relatively high evenness despite low richness. This explains a more evenly distributed abundance among fewer species of dung beetle in the communities. Interestingly, Gujranwala showed relatively high evenness but fewer species. The estimators (Chao-1, iChao-1, ACE, and Squares) all predict similar trends in species richness across the three districts. At subdivision levels, Gujrat, Kharian and Sarai Alamgir demonstrated maximum species richness in Gujrat. Pasrur and Sialkot subdivisions in Sialkot districts showed greater richness, while in Gujranwala, higher richness of species was observed in Gujranwala City and Nowshera Virkan Table 6.

Multivariate structuring of Onitini assemblages

The NMDS ordination based on Bray-Curtis dissimilarities showed minimal overlap in Onitini assemblages among Gujranwala, Gujrat, and Sialkot (stress = 0.061; Fig. 3). This shows a clear, two-dimensional view of community relationships. The low stress value (< 0.1) means that the distances in the ordination space match the observed dissimilarities, confirming the reliability of community similarity. Community assemblages from the study districts clustered with only slight separation. This aligns with the weak spatial structuring identified by PERMANOVA with no significant differences

Table 6. Comparison of diversity indices of dung beetle communities (tribe Onitini) across subdivisions of Gujranwala, Gujrat and Sialkot in the province of Punjab, Pakistan.

Metric	Gujranwala					Gujrat			Sialkot			
	Gujranwala City	Gujranwala Saddar	Kamoki	Nowshera Virkan	Wazirabad	Gujrat	Kharian	Sarai Alamgir	Daska	Pasrur	Sambrial	Sialkot
Taxa_S	7	5	6	7	6	12	10	9	6	8	6	7
Individuals	126	94	60	80	56	798	390	406	130	220	90	260
Dominance_D	0.307	0.364	0.311	0.317	0.303	0.292	0.307	0.307	0.348	0.307	0.349	0.309
Simpson_1-D	0.693	0.636	0.689	0.684	0.697	0.708	0.693	0.693	0.652	0.693	0.651	0.691
Shannon_H	1.500	1.196	1.432	1.416	1.473	1.667	1.527	1.553	1.240	1.538	1.229	1.474
Evenness_e ^H /S	0.640	0.662	0.698	0.589	0.727	0.441	0.460	0.525	0.576	0.582	0.570	0.624
Brillouin	1.384	1.097	1.253	1.261	1.280	1.628	1.468	1.497	1.153	1.455	1.115	1.411
Menhinick	0.624	0.516	0.775	0.783	0.802	0.425	0.506	0.447	0.526	0.539	0.633	0.434
Margalef	1.241	0.880	1.221	1.369	1.242	1.646	1.509	1.332	1.027	1.298	1.111	1.079
Equitability_J	0.759	0.730	0.776	0.709	0.797	0.668	0.658	0.702	0.681	0.732	0.671	0.752
Fisher_alpha	1.598	1.127	1.660	1.846	1.703	2.003	1.871	1.630	1.300	1.628	1.447	1.325
Berger-Parker	0.500	0.500	0.500	0.500	0.500	0.500	0.500	0.500	0.500	0.500	0.500	0.500
Chao-1	7	5	6	7.494	6	12.5	10	9	6.496	8	6.494	7
iChao-1	7	5	6	8.975	6	12.62	10	9	6.496	8	7.978	7
ACE	7	5	6	10.22	6	12.96	10	9	6.694	8	9	7
Squares	7	5	6	8.303	6	12.29	10	9	6.353	8	7.426	7

in assemblage composition across districts, with a small effect size ($F = 1.34$, $p = 0.278$; $R^2 = 0.084$). The effect size indicates that less than 9% of the total variation in community composition was attributable to district-level differences. However, significant differences in the community structure were observed ($F = 31.88$, $p = 0.001$). Where season explained a moderate proportion of community variation ($R^2 = 0.165$). This highlighted that season was a stronger driver of community structure than spatial variations. However, multivariate dispersion varied significantly between seasons (PERMDISP: $F = 34.32$, $p = 0.001$). Thus, reflecting differences in beta diversity within each season. This pattern was also observed in the NMDS ordination, where the differences were reflected in the spread of the groups, rather than just a clear separation of centroids.

SIMPER analysis

SIMPER analysis of species abundances showed that a few Onitis species were responsible for most of the differences between districts. For example, in the Gujranwala–Gujrat comparison, we observed an average dissimilarity of 79.50, where the top five species explained about 76% of the dissimilarity. *O. castaneus* (23.69%) and *O. excavatus* (20.48%) were the main contributors. A similar pattern was found in the Sialkot–Gujrat comparison (average dissimilarity = 81.63), where *O. castaneus*, *O. subopacus*, and *O. excavatus* together made up more than 56% of the dissimilarity. These species were more abundant in Gujrat than in Sialkot Table 7. However, Sialkot and Gujranwala (average dissimilarity = 85.21) showed the greatest differences in the community composi-

tion. Here, the five leading taxa (*O. castaneus*, *O. subopacus*, *O. excavatus*, *O. philemon* and *O. falcatus*) accounted for nearly 84% of the dissimilarity. *O. castaneus*, *O. subopacus* and *O. philemon* were more abundant in Sialkot, whereas *O. excavatus* was more abundant in Gujranwala. *O. castaneus*, *O. subopacus* and *O. excavatus* were the most dominant species. Among districts, the spatial variation in their abundances was the main contributor to these detectable differences in dung beetle communities.

The results of the SIMPER Analysis indicated that variations were observed in the contribution of dung beetles to the dissimilarity. The highest diversity was noted in Wazirabad, Gujrat and Gujranwala City subdivisions, which was reflected in the rarefaction–extrapolation curves ($q = 0$ –2) rising above those of other subdivisions. Kamoki and Kharian showed intermediate diversity with curves approaching plateaus more rapidly. However, Pasrur, Nowshera Virkan and Sarai Alamgir demonstrated the lowest diversity. The curves flattened early with narrow confidence intervals, suggesting species-poor and well-sampled assemblages Fig. 4. Coverage-based rarefaction and extrapolation revealed clear differences in taxonomic diversity across all Hill-number orders ($q = 0, 1, 2$) among sites.

The results also highlighted that diversity increased with sample coverage. The extrapolated curves showed that some communities, like $q = 0$, had not reached full richness yet. For species richness ($q = 0$), Wazirabad, Sialkot, Gujranwala City, and Gujranwala Saddar had the highest values (> 10 species). While Pasrur, Sambrial, and Sarai Alamgir had lower richness.

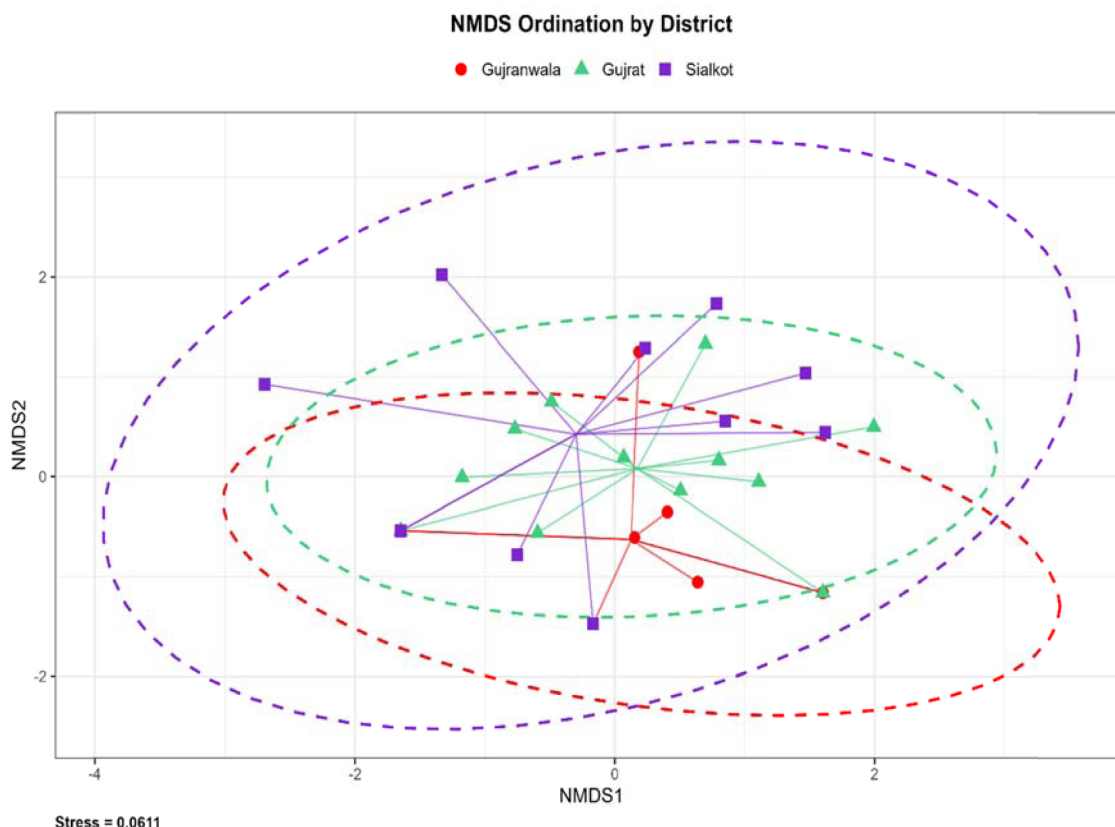


Fig. 3. The NMDS ordination (Bray–Curtis distance) of Onitini dung beetle assemblages from Gujranwala, Gujrat, and Sialkot (Stress = 0.061; 95% CI). Spider lines indicate group dispersion and centroids.

We also observed smaller differences in Shannon diversity ($q = 1$) values in Wazirabad and Gujranwala Saddar, which were the most diverse subdivisions. These findings suggested that rare species played a bigger role. However, Simpson diversity ($q = 2$) exhibited similar patterns across many communities, and Wazirabad, Sialkot, and Gujranwala Saddar were the most dominant subdivisions [Fig. 5](#).

Rank–abundance curves indicate clear differences in the abundance of species among subdivisions. Gujrat reflected the highest overall abundance and species richness. Several dominant species were present, and a long tail also suggested the presence of low-abundance taxa. Sialkot exhibited intermediate abundance with a moderate decline in ranks, indicating lower evenness than Gujrat. Gujranwala had the lowest abundance and richness, with a steep decline and few high-ranking species. Overall, Gujrat supported the greatest diversity, followed by Sialkot and Gujranwala [Fig. 6](#).

Land use type

Negative binomial models fit the data much better than the Poisson model ($\Delta AIC = 3845.32$). Adding

a district $\times$ land-use interaction slightly improved fit over the additive negative binomial model ($\Delta AIC = 1.98$), so we retained the interaction model for inference [Table 8](#).

Pairwise land-use contrasts within districts revealed limited but district-specific differences in mean abundance. In Gujranwala, none of the land-use contrasts differed significantly after Tukey adjustment (all $p > 0.19$). In Gujrat, agroforestry supported significantly higher abundance than cropland (IRR = 1.88, $p = 0.027$), while cropland had significantly lower abundance than pasture (IRR = 0.56, $p = 0.046$). No significant difference was detected between agroforestry and pasture in Gujrat. In Sialkot, none of the pairwise contrasts were statistically significant, although abundance tended to be higher in agroforestry and cropland relative to pasture. Overall, significant land-use effects were detected only in Gujrat, indicating context-dependent responses across districts. Land-use differences were significant only in Gujrat, where agroforestry had higher abundance than cropland (IRR = 1.88, $p = 0.0267$) and cropland had lower abundance than pasture (IRR = 0.56, $p = 0.0463$), while no contrasts were significant in Gujranwala or Sialkot (all $p \geq 0.145$) [Table 9](#).

Table 7. Top five contributing beetle species based on square-root-transformed abundance data (SIMPER: Bray–Curtis dissimilarity).

			Mean	
Taxon	Average dissimilarity	% Contribution	Gujranwala	Gujrat
Gujranwala vs Gujrat (Average dissimilarity = 79.50)				
<i>O. castaneus</i>	18.84	23.69	0.95	2.73
<i>O. excavatus</i>	16.29	20.48	1.93	2.61
<i>O. subopacus</i>	10.39	13.07	0.76	2.17
<i>O. singhalensis</i>	7.75	9.75	–	1.64
<i>O. philemon</i>	7.28	9.16	1.12	0.87
% contribution top five species		76.15		
Sialkot vs Gujrat (Average dissimilarity = 81.63)				
			Sialkot	Gujrat
<i>O. castaneus</i>	19.26	23.6	1.53	2.73
<i>O. subopacus</i>	13.78	16.88	2.07	2.17
<i>O. excavatus</i>	13.2	16.17	0.68	2.61
<i>O. singhalensis</i>	7.58	9.29	–	1.64
<i>O. virens</i>	6.71	8.22	0.57	1.31
% contribution top five species		74.16		
Sialkot vs Gujranwala (Average dissimilarity = 85.21)				
			Sialkot	Gujranwala
<i>O. castaneus</i>	19.4	22.77	0.95	1.53
<i>O. subopacus</i>	17.51	20.55	0.76	2.07
<i>O. excavatus</i>	17.01	19.96	1.93	0.68
<i>O. philemon</i>	12.59	14.78	1.12	0.66
<i>O. falcatus</i>	4.81	5.64	0.8	–
% contribution top five species		83.7		

Table 8. Model comparison using Akaike's Information Criterion (AIC). Degrees of freedom (df), AIC, and Δ AIC (difference from the best-supported model; Δ AIC = 0) are shown for the candidate models. The negative binomial model, including the district $\times$ land-use interaction, had the lowest AIC and was therefore the top-ranked model.

Model	df	AIC	Δ AIC
NB with district $\times$ landuse	20	2509.63	0
NB additive (m_nb)	16	2511.6	1.98
Poisson (m1)	15	6354.95	3845.32

Estimated mean responses differed across districts and land-use types. In Gujranwala, mean values were lowest in cropland (1.63; 95% CI: 0.87–3.06) and agroforestry (1.85; 0.99–3.47) and highest in pasture (3.38; 1.83–6.23). In Gujrat, agroforestry showed the highest mean (3.71; 2.59–5.33), followed by pasture (3.53; 2.46–5.07), while cropland had the lowest mean (1.97; 1.36–2.87). In Sialkot, agroforestry (5.52; 3.18–9.59) and cropland (5.42; 3.12–9.42) exhibited the highest mean values among all district–land-use combinations, whereas pasture had comparatively lower values (2.67; 1.50–4.74). Overall, the results indicate substantial spatial variation, with consistently higher mean responses in Sialkot and greater variability among land-use types within districts [Table 10](#).

Discussion

Tribe Onitini (Scarabaeinae: family Scarabaeidae) includes coprophagous tunnelling species having a worldwide distribution. This study focused on surveying dung beetle assemblages of the tribe Onitini across three districts, i.e., Gujrat, Gujranwala and Sialkot of Punjab, Pakistan. Spatiotemporal heterogeneity and seasonal changes in environmental conditions, dung availability, and anthropogenic activities in the habitat are key determinants of community structures. In our study, overall, 11 species were identified from three districts in year-round surveys. These results reflect that local conditions influence the diversity of dung beetle assemblages. Gujrat district showed relatively higher species richness and abundance as compared to Gujranwala and Sialkot districts. Some species, however, were more dominant in other districts, particularly *O. subopacus*. Studies have reported that species richness, abundance, and dominance are greatly influenced by anthropogenic activities in the habitat, which may impair resource availability and utilization by dung beetles.⁴⁴ Our study sites have a gradient of change in the cropping intensity, livestock density, and microclimatic conditions. Earlier studies recorded that community structure

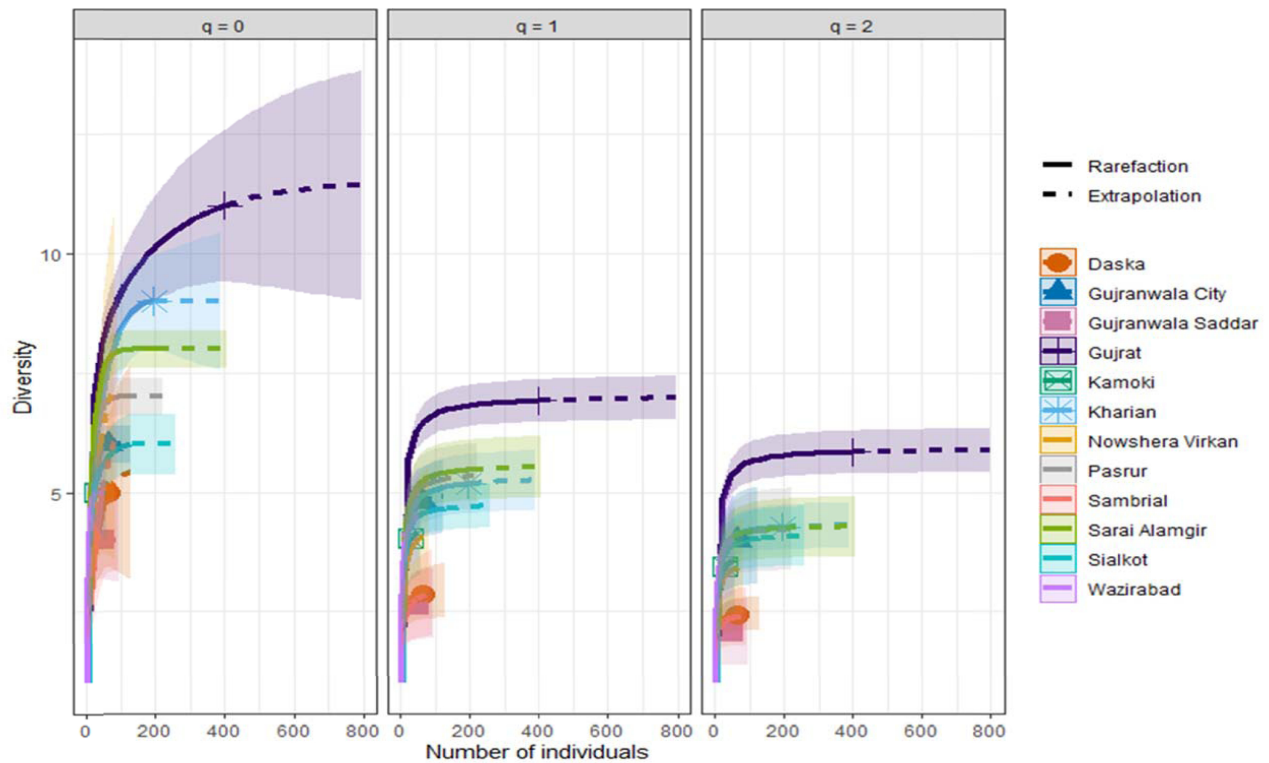


Fig. 4. Rarefaction and extrapolation curves of dung beetle assemblages across 12 subdivisions of Gujrat, Sialkot and Gujranwala Districts, Punjab, Pakistan.

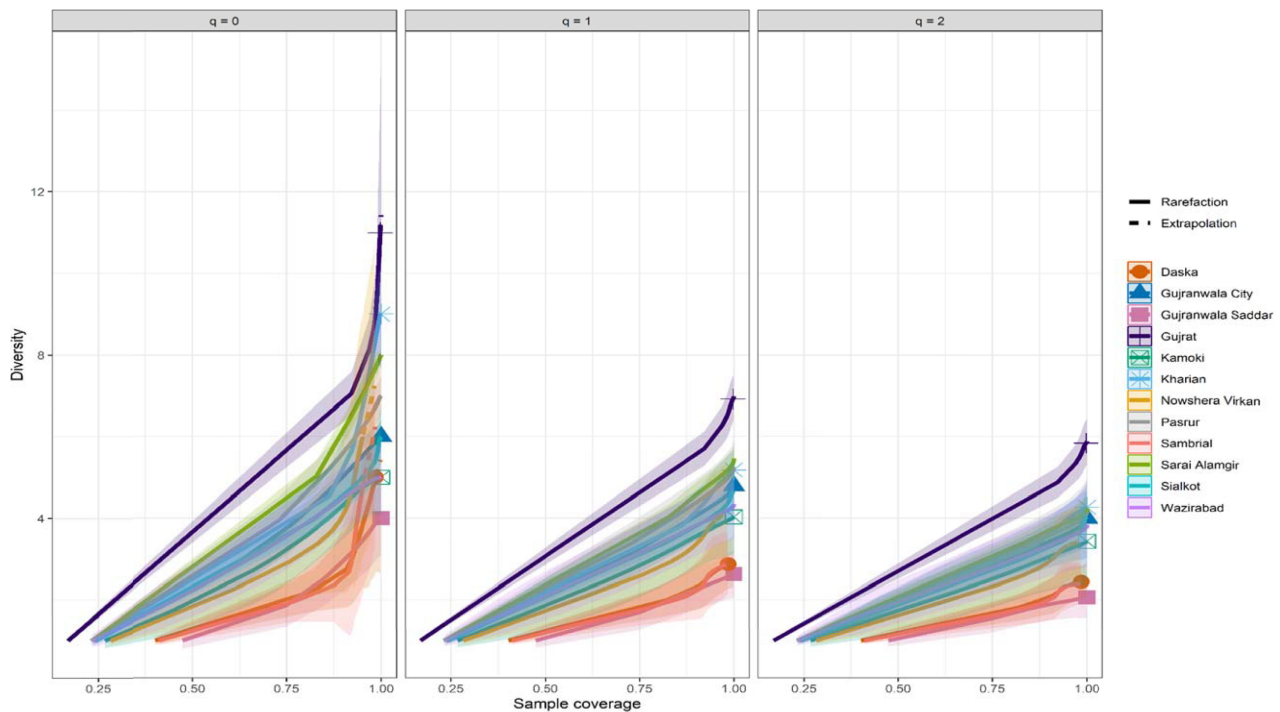


Fig. 5. Sample-coverage-based rarefaction and extrapolation curves for Hill numbers of order $q = 0$ (species richness), $q = 1$ (Shannon diversity), and $q = 2$ (Simpson diversity) across all sampling locations.

Table 9. Pairwise land-use contrasts within each district from the negative binomial interaction model, expressed as incidence rate ratios (IRR).

District	Contrast	IRR	SE	z	p (Tukey)	Sig.
Gujranwala	agroforestry / cropland	1.138	0.488	0.302	0.951	
	agroforestry / pasture	0.549	0.231	-1.428	0.326	
	cropland / pasture	0.482	0.204	-1.729	0.194	
Gujrat	agroforestry / cropland	1.879	0.459	2.581	0.0267	*
	agroforestry / pasture	1.051	0.253	0.208	0.977	
	cropland / pasture	0.559	0.137	-2.374	0.0463	*
Sialkot	agroforestry / cropland	1.018	0.386	0.046	0.999	
	agroforestry / pasture	2.069	0.800	1.878	0.145	
	cropland / pasture	2.033	0.787	1.832	0.159	

IRR > 1 indicates higher mean abundance in the numerator land-use; IRR < 1 indicates lower mean abundance. Significance: * $p < 0.05$. P-values Tukey-adjusted within each district; contrasts averaged over species.

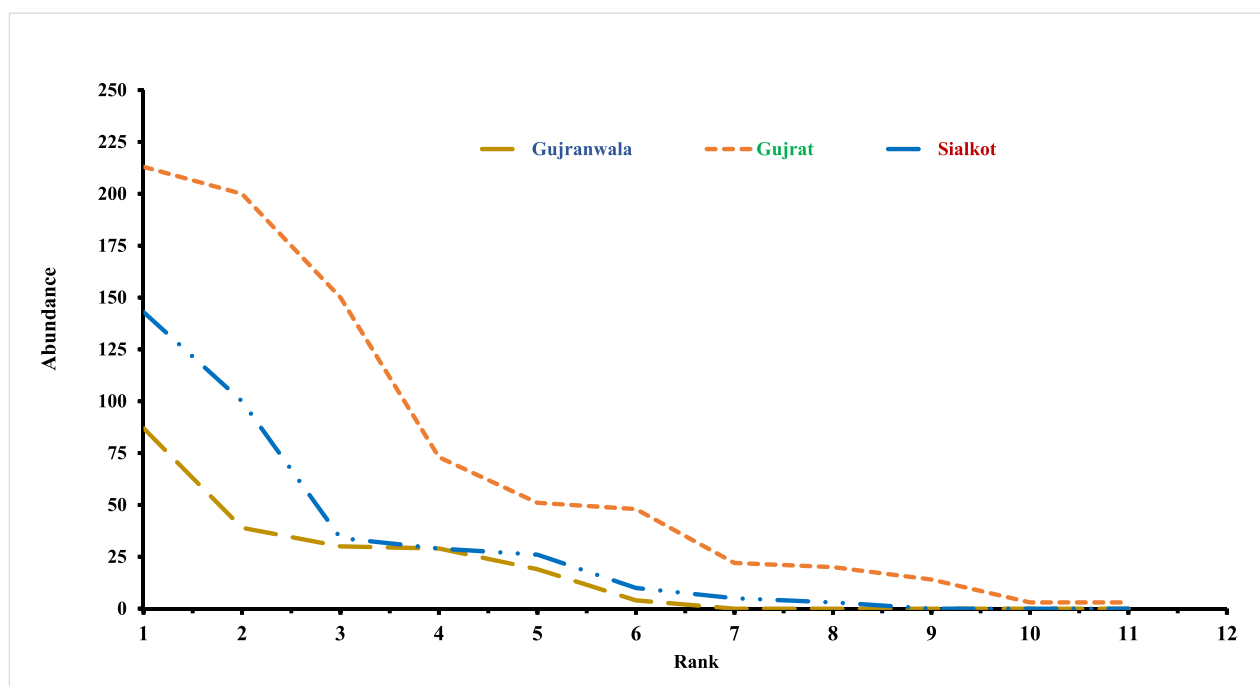


Fig. 6. Rank–abundance curves for insect communities recorded from three districts of Punjab, Pakistan. Each curve represents the relationship between species rank and their corresponding abundances in Gujranwala, Gujrat, and Sialkot.

greatly depends on microclimatic conditions, such as livestock density.⁴⁵ Similarly, land-use type and soil heterogeneity in the spatial context shape dung beetle community composition as these factors are associated with dung availability. The relatively higher diversity and lower dominance in Gujrat can be explained by the presence of rainfed and canal irrigated areas with ample opportunities for animal grazing in pastures and agroforestry patches. These sites serve as permanent sites for these dung beetle species. Thus, more stable and resilient assemblages of dung beetles can be expected in areas with consistent resource availability.⁴ We observed seasonal variations in the species richness and abundance among districts and subdivisions. Seasons

play a significant role in the species richness and relative abundance of species. For example, dominant species remain active throughout the year, while rare taxa appear only during brief and specific periods.⁴⁶

Compositional similarity among the three districts was observed with a low NMDS stress value, confirming overlap, which reflected true ecological similarity, and not ordination artefacts. This spatial structure was determined by a few dominant species with noticeable differences in abundance patterns. These dung beetle communities reflect intensive land use and comparatively lower dung availability in the study area. In these conditions, niche availability is limited, but it helps maintain a more even competition among the remaining species.³ Sialkot had

Table 10. Estimated mean response values (with 95% confidence intervals) across districts and land-use types derived from the best-supported negative binomial model.

District	Land use	Mean (95% CI)
Gujranwala	Agroforestry	1.853 (0.989–3.470)
	Cropland	1.628 (0.865–3.063)
	Pasture	3.377 (1.832–6.226)
Gujrat	Agroforestry	3.710 (2.585–5.326)
	Cropland	1.974 (1.358–2.870)
	Pasture	3.530 (2.457–5.071)
Sialkot	Agroforestry	5.517 (3.176–9.585)
	Cropland	5.421 (3.120–9.422)
	Pasture	2.667 (1.502–4.735)

intermediate richness but showed strong dominance of *O. subopacus*. This suggests climatic filtering in which local conditions favor one species, ultimately creating steep rank-abundance curves and lower evenness.¹⁴ However, PERMANOVA and NMDS revealed uniform composition of species across districts. SIMPER analysis identified *O. castaneus*, *O. excavatus*, and *O. subopacus* as key contributors to spatial dissimilarity.

We detected seasonal variations in abundance, but only a moderate effect on community structure was observed. For example, *O. castaneus* demonstrated the greatest abundance during the winter season. While the dominant species in our study maintained relatively high abundance across different seasons. This was due to their wide physiological tolerance, adaptable activity patterns, and ability to make use of varying dung resources. These traits are characteristic of successful paracoprid generalists in agricultural environments.^{9,10} Although interaction networks or null co-occurrence models were not explicitly tested, observed temporal segregation and dominance patterns are consistent with established coexistence mechanisms in dung beetle communities. Rarefaction analyses indicated high sampling completeness; however, fortnightly sampling may have missed short-lived activity peaks, and seasonal patterns should therefore be interpreted as smoothed trends rather than precise phenological maxima. Multivariate analyses reinforced this interpretation: PERMANOVA detected significant seasonal differences, whereas district-level differences were weak or non-significant, consistent with the strong overlap observed in NMDS ordination. However, dispersion also differed among seasons (PERMDISP), indicating that seasonal effects reflect both shifts in mean community composition and changes in within-season heterogeneity. Accordingly, effect sizes (R^2) and ordination patterns provide more ecologically meaningful interpretations than p-values alone. Although statistically significant, the seasonal effect was moderate in magnitude ($R^2 = 0.165$), with most

compositional variation ($> 80\%$) attributable to other unmeasured environmental or stochastic factors.

The low frequency of the rare taxa like *C. indicus*, *O. belial* and *O. crassus* may indicate reliance on short climatic periods or availability of dung resources. This observation is consistent with the trends reported in other studies that reveal that specialist dung beetles tend to take advantage of transient resources in response to rainfall, temperature conditions, or local habitat features.⁴⁷ Surprisingly, seasonal structure differed among districts. Gujranwala exhibited strong seasonal specialization, whereas Gujrat supported more evenly distributed activity across seasons. This supports the buffering role of habitat heterogeneity against phenological constraints. *O. castaneus*, *O. excavatus*, and *O. subopacus* showed persistency across habitats, which suggests that these species have adaptability to a wide range of dung resources. The numerical superiority of these dung beetle species across landscapes may be attributed to their ecological traits, which help them in rapid pat detection, strong burrowing potential, and the ability to tolerate fluctuating microclimates.¹⁰ For example, in Sialkot, *O. subopacus* showed dominance ($> 40\%$ abundance). This explains how a single species can affect community structure when conditions strongly favor its life-history strategy.

In Gujrat, a flatter rank-abundance curve showed more resource partitioning and less competitive asymmetry, which is in line with high species richness and environmental heterogeneity. Hill-number analyses showed that $q = 0$ (richness) was dominated by the effect of rare species, but that $q = 1$ and $q = 2$ diversity across districts converged. One of the weaknesses of this study is that dung availability and vegetation structure were not directly measured, and a separation between the independent effects of these two variables could not be made with the land-use categories. Also, dung-baited pitfalls, traps and handpicking could be under-representative of deeply tunneling species or weakly attracted to dung species, which can bias richness and composition estimates. Despite these limitations, Onitini collections in the agricultural landscapes of Punjab were organized more firmly around seasonal than across-district spatial change. Weak spatial differentiation but moderate seasonal structuring in a common pool of species was identified through multivariate analyses that were dominated by a few generalist taxa that were complemented by occasional specialists. The findings highlight the significance of phenology, heterogeneity of the habitat and sustained dung supply in sustaining dung beetle diversity and ecosystem processes in agroecosystems under intense management.

Conclusion

Distributional patterns of dung beetles of Tribe Onitini indicated that habitat heterogeneity and seasonal variations are key determinants of species richness and overall community structure. Gujrat, being the most diverse district, supported both unique and rare taxa. Whereas Gujranwala and Sialkot showed lower diversity and greater dominance by a few species. *O. castaneus*, *O. excavatus*, and *O. subopacus* were major species in the study area, which contributed most strongly to the dissimilarity of the districts. *O. castaneus* was the single dominant species in the winter season.

Authors' declaration

- Conflicts of Interest: None.
- We hereby confirm that all the Figures and Tables in the manuscript are ours. Furthermore, any Figures and images that are not ours have been included with the necessary permission for republication, which is attached to the manuscript.
- No human studies are present in the manuscript.
- The author has signed an animal welfare statement.
- Ethical Clearance: The project was approved by the local ethical committee at University of Gujrat.

Author's contribution statement

T. N. and M.H. conceptualised the study and performed data curations. T. N. identified the specimens and prepared manuscript. M. H. supervised the research work, performed formal analysis, reviewed & edited the manuscript during the revisions.

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ديناميكيات التوزيع وأنماط التعايش في خنافس الروث قبيلة (Onitini) عبر المناظر الزراعية في البنجاب، باكستان

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الخلاصة

تلعب خنافس الروث (Scarabaeidae: Scarabaeinae) دورًا مهمًا في إزالة الروث ودورة المغذيات. قمنا بتقييم أنماط التوزيع والتنوع لقبيلة Onitini عبر 12 تقسيمًا إداريًا في مناطق غوجرانوالا، وغوجرات، وسيلالكوت في إقليم البنجاب، باكستان. أجريت المسوحات مرتين شهريًا بفواصل زمني يقارب أسبوعين بين الزيارات، وذلك من خلال وضع ثلاث مصائد حفريّة على طول كل خط مسح بطول 1000 متر، مع ترك مسافة تقارب 330 مترًا بين كل مصيدة وأخرى. جُمعت البيانات من تسع مصائد موزعة على ثلاثة خطوط مسح في كل موقع ضمن التقسيمات الإدارية. أظهرت منطقة غوجرات أعلى غنى نوعي، حيث سُجلت جميع الأنواع الأحد عشر، تلتها سيلالكوت ثم غوجرانوالا. وكان النوع *Onitis castaneus* هو النوع السائد في جميع المناطق خلال فصل الشتاء. أما *Onitis excavatus* فقد كان الأكثر وفرة خلال فصلي الربيع والصيف في كلٍّ من غوجرانوالا وسيلالكوت. وفي فصل الصيف، كان *O. subopacus* هو النوع السائد في سيلالكوت. أظهر تحليل PERMANOVA عدم وجود فروق معنوية في تركيب الأنواع بين المناطق ($R^2 = 0.084$, $p = 0.278$)، في حين كشف تحليل NMDS عن تداخل كبير بين التقسيمات. كما أظهر تحليل SIMPER اختلافات في الوفرة النسبية بين المناطق، مما أدى إلى ارتفاع قيم عدم التشابه وفق مؤشر Bray–Curtis. وكان الاختلاف المكاني الملحوظ ناتجًا بصورة رئيسية عن الأنواع *O. excavatus* و *O. subopacus* و *Onitis singhalensis* و *O. crassus* حصرًا في غوجرات، مما يشير إلى ارتباطهما بموائل محلية محددة. كما تأثرت تجمعات خنافس الروث بشكل ملحوظ بالفصول ($R^2 = 0.165$). كذلك أثرت أنماط استخدام الأراضي في أنماط الوفرة، خاصة على مستوى المناطق. توفر هذه الدراسة أول مقارنة بيئية واسعة النطاق لتجمعات Onitini في البنجاب، كما تضع خط أساس للتقييمات المستقبلية لتنوع خنافس الروث ووظائف النظم البيئية تحت ظروف التكثيف الزراعي.

الكلمات المفتاحية: قائمة الأنواع، خنافس الروث، غوجرات، خنافس الحفر (Paracoprids)، الأنواع النفقية.