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Original article

Elevation-Driven Turnover of Ant Assemblages (Hymenoptera: Formicidae) in a Mediterranean Mountain System: Diversity, Seasonality, and Thermal Drivers in Al-Jabal Al-Akhdar, Libya

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Abstract
Elevational gradients act as natural laboratories for isolating the climatic constraints on insect diversity, yet Mediterranean North Africa remains one of the least-documented regions for such analyses despite hosting internationally recognised biodiversity hotspots. We present the first systematic, multi-seasonal survey of epigaeic ant (Hymenoptera: Formicidae) assemblages along a 30–625 m elevational transect in Al-Jabal Al-Akhdar, north-eastern Libya, and use it to test how altitude and local microclimate jointly structure community composition, dominance and phenology in an understudied Mediterranean-type ecosystem. Standardised time-unit hand collection was carried out at three sites spanning the gradient (coastal Ras Al-Helal, ~30 m; intermediate Al-Wasita, ~220 m; highland Sidi Al-Hamri, ~625 m) across four seasons between June 2025 and March 2026. A total of 1,505 individuals representing seven species were recorded. Overall community diversity was moderate-to-high (Shannon–Wiener H' = 1.88; Simpson's index of diversity, 1–D = 0.84) and increased with elevation (H' = 1.54 at the coast to 1.92 in the highlands), a pattern that diverges from the monotonic richness declines typical of temperate mountains but parallels several recent Mediterranean and arid-zone elevational studies. Thermophilic, open-habitat taxa (*Cataglyphis cf. albicans, Solenopsis fugax*) dominated the coastal lowlands, mesic forest specialists (*Camponotus barbaricus*) prevailed in the highlands, and the granivorous *Messor ebeninus* displayed marked ecological plasticity across the gradient. Ant abundance was strongly and positively correlated with air temperature (r = 0.52–0.88) and negatively correlated with relative humidity (r = –0.42 to –0.75), corroborating thermal-constraint models of ant foraging activity. These results establish Al-Jabal Al-Akhdar myrmecofauna as a sensitive bioindicator system for Mediterranean climatic gradients and provide a quantitative baseline for detecting future climate-driven range shifts in a chronically under-surveyed part of the Mediterranean Basin.
Keywords. Formicidae, Elevational Gradient, Mediterranean Biodiversity, Bioindicators, Thermal Ecology.

Introduction

Ants (Hymenoptera: Formicidae) are among the most ecologically dominant terrestrial arthropods, contributing an estimated 12 megatons of dry carbon to global biomass, more than the combined mass of wild birds and mammals, and mediating nutrient cycling, soil turnover, seed dispersal, and pest regulation across virtually every terrestrial biome [1]. Their sedentary colony structure, high sensitivity to microclimate, and taxonomic tractability make them one of the most widely validated invertebrate bioindicator taxa for tracking habitat quality and climate-driven biodiversity change [2]. Elevational gradients compress steep climatic and vegetational transitions into short geographic distances, offering a powerful, space-for-time proxy for anticipating biotic responses to warming. However, the shape of the ant richness–elevation relationship is far from universal: temperate mountain systems typically show monotonic declines in richness with elevation, whereas arid and Mediterranean systems frequently show mid-elevation peaks or even increasing diversity toward cooler, more mesic highlands, reflecting a trade-off between thermal stress at altitude and desiccation stress at low elevation [3,4].

Recent Mediterranean-mountain evidence reinforces this non-monotonic, moisture-mediated pattern and shows that community turnover, rather than simple richness loss, is the dominant signature of elevational change in these systems, with clear implications for the vulnerability of high-elevation specialist assemblages under continued warming [4]. Despite this growing global evidence base, the North African, and specifically Libyan, myrmecofauna remains critically understudied. Early regional surveys were largely faunistic and non-systematic [5,6], and no prior study has quantitatively resolved how ant diversity, dominance structure, and seasonal activity respond to the elevational and bioclimatic gradient of Al-Jabal Al-Akhdar, a Mediterranean karstic massif recognised as a regional centre of endemism. This represents a substantive knowledge gap: without baseline quantitative data, it is not possible to assess whether this myrmecofauna is likely to track projected warming through upslope range contraction, a risk explicitly identified for thermally restricted highland ant lineages in comparable Mediterranean and Irano-Turanian systems [7,8]. The present study addresses this gap by providing a standardised, four-season inventory of ant assemblages across three sites spanning the full elevational range of Al-Jabal Al-Akhdar (30–625 m a.s.l.).

Building on the original thesis dataset, we reframe the analysis around three interlinked aims that define the novelty and contribution of this work: (i) to quantify how species richness, diversity indices and dominance structure change along the elevational gradient, testing whether Al-Jabal Al-Akhdar conforms to the temperate (monotonic decline) or Mediterranean/arid (mesic-highland enrichment) pattern reported elsewhere; (ii) to identify the microclimatic (temperature, humidity) correlates of seasonal ant activity, situating the results within the broader thermal-ecology literature on ant foraging constraints [9,10,11]; and (iii) to identify candidate indicator species for each bioclimatic zone that could underpin future long-term monitoring of climate-change impacts in this biodiversity hotspot. In doing so, this study

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provides the first quantitative myrmecological baseline for Al-Jabal Al-Akhdar and contributes a rare North African data point to the global synthesis of elevational ant ecology.

Methods

Study area

Fieldwork was conducted at three sites distributed along the elevational gradient of Al-Jabal Al-Akhdar, north-eastern Libya: Ras Al-Helal (coastal, ~30 m a.s.l.; humid Mediterranean scrub), Al-Wasita (intermediate, ~220 m a.s.l.; mixed cultivated and natural vegetation), and Sidi Al-Hamri (highland, ~625 m a.s.l.; structurally complex maquis with fruit trees, grasses and agricultural plots). Mean July air temperature and relative humidity ranged from 27–29 °C and 55–70%, respectively, across the three sites.

Sampling design

Ant assemblages were sampled over four consecutive seasons (June 2025–March 2026) using a standardised Time-Unit Sampling (TUS) protocol: 40-minute active hand-collection searches per site per session, targeting epigaeic and cryptic microhabitats (beneath stones, within leaf litter and decaying wood, on low vegetation and tree trunks, and along foraging trails). This active-search approach was selected specifically because it recovers cryptic, refuge-nesting taxa that passive pitfall or bait methods routinely under-sample [12,13]. Specimens were preserved in 70% ethanol and identified to species or morphospecies using regional taxonomic keys [14,15,6].

Microclimate and biodiversity metrics

Air temperature and relative humidity were recorded in situ with a portable digital thermo-hygrometer concurrently with each collection event. Community structure was characterised using species richness, the Shannon–Wiener index (H') and Simpson's index of diversity (1–D).

Statistical analysis

Data were analysed in Minitab v.17. One-way ANOVA (with Tukey's post-hoc pairwise comparisons) was used to test for differences in abundance and diversity among sites, and Pearson correlation coefficients (r) quantified the association between abiotic variables (temperature, humidity, elevation) and ant abundance/richness. Significance was set at $P < 0.05$.

Results

Overall composition and seasonal abundance

A total of 1,505 individuals representing seven Formicidae species were recorded across the three sites over the ten-month study. Abundance peaked in summer (562 individuals) and declined progressively through autumn (320) to a winter minimum (135), before a spring resurgence (488), reflecting the classic thermally-modulated activity cycle of Mediterranean ant communities (Table 1). *Messor barbarus* (20.7%) and *Cataglyphis cf. albicans* (20.2%) were co-dominant, while *Trichomyrmex simrothi* was the rarest taxon (5.9%).

Table 1. Seasonal abundance and relative proportion of ant species collected across the three study sites (June 2025–March 2026)

Species	Summer	Autumn	Winter	Spring	Total (N)	%
Cataglyphis cf. albicans	165	42	12	85	304	20.2
Lepisiota frauenfeldi	78	55	10	92	235	15.6
Solenopsis fugax	120	38	8	64	230	15.3
Messor barbarus	82	75	45	110	312	20.7
Messor ebeninus	45	58	35	62	200	13.3
Camponotus barbaricus	32	40	18	45	135	9.0
Trichomyrmex simrothi	40	12	7	30	89	5.9
Total	562	320	135	488	1505	100

Elevational structuring of species abundance

Site elevation significantly structured the abundance of five of the seven species (Table 2). Thermophilic, open-habitat species *Cataglyphis cf. albicans* and *Solenopsis fugax* were significantly more abundant at the coastal site (5.50 ± 1.85 and 4.15 ± 1.20, respectively) than in the highlands (1.20 ± 0.75 and 1.05 ± 0.60; both $P < 0.05$). The reverse pattern held for the mesic, wood-nesting *Camponotus barbaricus* (3.85 ± 1.60 in the highlands vs 1.15 ± 0.95 at the coast; $P = 0.012$). *Messor barbarus* and *Messor ebeninus* showed no significant elevational preference ($P > 0.4$), indicating broad ecological plasticity, while *Lepisiota frauenfeldi* was similarly distributed across all three sites ($P = 0.520$).

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Table 2. Mean abundance (± SD) of each species across the elevational gradient, with one-way ANOVA results.

Species	Ras Al-Helal (Low)	Al-Wasita (Mid)	Sidi Al-Hamri (High)	P-value	Significance
Cataglyphis cf. albicans	5.50 ± 1.85	3.10 ± 1.20	1.20 ± 0.75	0.001	Significant
Solenopsis fugax	4.15 ± 1.20	2.30 ± 1.10	1.05 ± 0.60	0.008	Significant
Trichomyrmex simrothi	3.20 ± 1.10	1.80 ± 0.90	1.05 ± 0.45	0.035	Significant
Camponotus barbaricus	1.15 ± 0.95	2.45 ± 1.10	3.85 ± 1.60	0.012	Significant
Messor barbarous	2.80 ± 1.35	3.50 ± 1.60	3.20 ± 1.40	0.440	Non-significant
Messor ebeninus	2.10 ± 1.05	2.95 ± 1.30	3.25 ± 1.45	0.640	Non-significant
Lepisiota frauenfeldi	2.40 ± 1.15	3.10 ± 1.40	2.85 ± 1.25	0.520	Non-significant

(Figure 1) visualises this elevational structuring as a species × site abundance matrix, ordered from the most coastal-thermophilic taxa (top) to the most highland-mesic taxa (bottom). The clear diagonal colour gradient illustrates that species turnover, rather than uniform decline, underlies the community-level response to elevation: *Cataglyphis. albicans* and *Solenopsis fugax* are concentrated in the warm coastal cell, *Camponotus barbaricus* in the cool highland cell, while the two *Messor species* form a comparatively flat, elevation-independent colour band across all three columns, a visual signature of the ecological plasticity discussed further in Section 4.3.

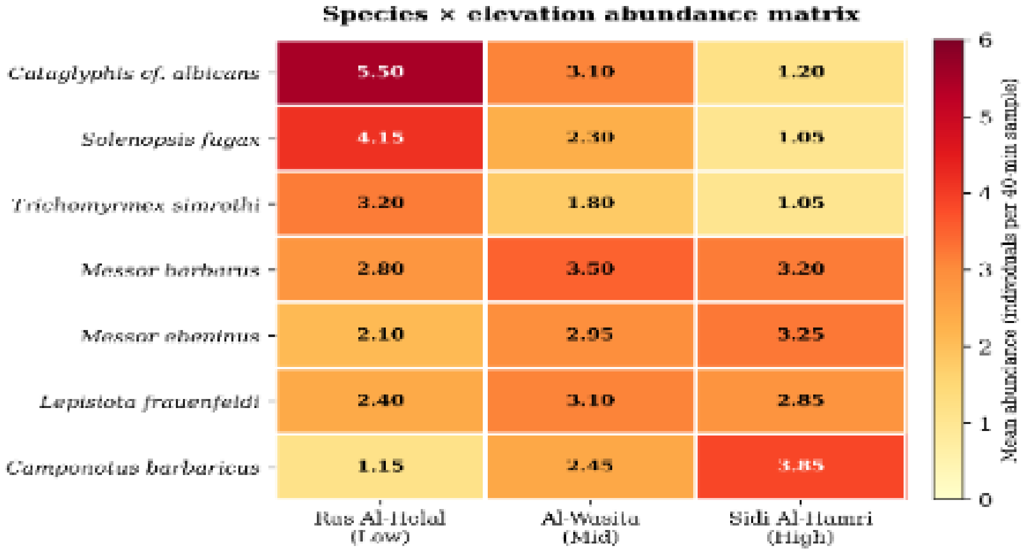

Figure 1. Heatmap of mean abundance (individuals per 40-minute sample) for each species across the three elevational sites. Warmer colours indicate higher abundance. Species are ordered from the most coastal/thermophilic (top) to the most highland/mesic (bottom), highlighting the diagonal pattern of elevational turnover and the flat, elevation-independent band formed by the two Messor species.

Diversity indices along the gradient

Pooled community diversity was moderate-to-high (H' = 1.878; Simpson's 1–D = 0.839). Diversity increased with elevation: Sidi Al-Hamri (highland) recorded the highest Shannon index (H' = 1.92), followed by Al-Wasita (H' = 1.72), while the coastal Ras Al-Helal site recorded the lowest diversity (H' = 1.54), consistent with the structurally more complex, multi-niche vegetation of the highland maquis relative to the coastal scrub. Notably, this rise in diversity occurred even as the overall (summed) abundance of individuals declined slightly from coast to highland (Figure 1), indicating that the highland community is more evenly composed of several moderately abundant species, whereas the coastal community is more strongly dominated by a small number of thermophilic taxa.

This divergence between the abundance and diversity trends is the clearest quantitative signature of the study: it shows that elevation in Al-Jabal Al-Akhdar does not simply suppress ant activity at altitude, as reported for many temperate mountains, but instead reorganises the community into a more balanced assemblage, a pattern interpreted further in Section 4.1.

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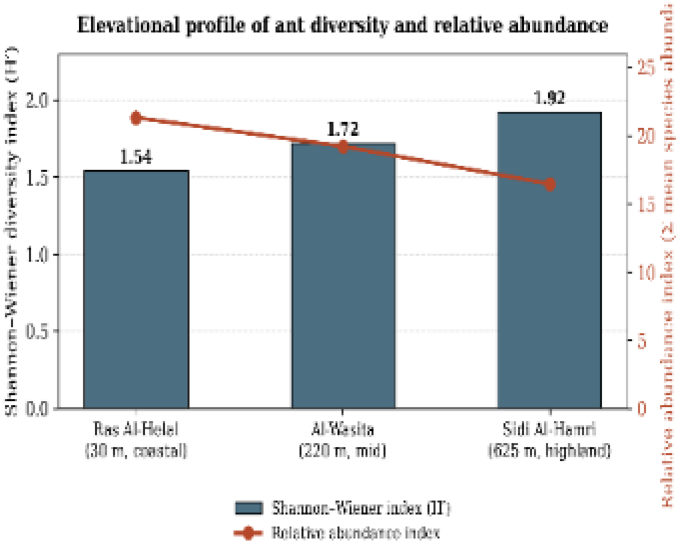

Figure 2. Elevational profile of ant diversity (Shannon–Wiener index H', columns, left axis) and relative abundance (sum of mean species abundances, line, right axis) across the three study sites. Diversity rises with elevation while relative abundance falls slightly, showing that highland assemblages are more even rather than more numerous

Climatic correlates of abundance

Pearson correlation analysis confirmed a strong, consistent thermal signal across the community: ant abundance correlated positively with air temperature for all seven species (r = 0.52–0.88, all P < 0.05), most strongly in *Cataglyphis cf. albicans* (r = 0.88, P = 0.001) and Solenopsis fugax (r = 0.82, P = 0.001). Conversely, relative humidity was negatively correlated with abundance across all species (r = –0.42 to –0.75), again strongest in the two thermophilic taxa (C. cf. albicans: r = –0.75; S. fugax: r = –0.68; both P = 0.001). These relationships confirm that thermal and hydric constraints, rather than elevation per se, are the proximate drivers of the observed spatial and seasonal patterns (Figure 3).

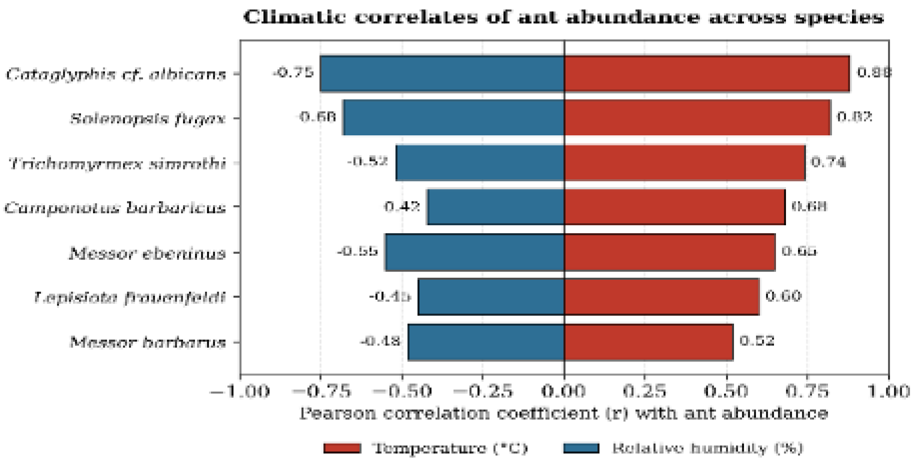

Figure 3. Pearson correlation coefficients (r) between ant abundance and air temperature (red bars, positive) versus relative humidity (blue bars, negative) for each species, ranked by the strength of the temperature response. Thermophilic coastal specialists (Cataglyphis cf. albicans, Solenopsis fugax) show the strongest bidirectional response, while the elevation-plastic Messor barbarus shows the weakest.

The near-perfect mirroring of the temperature and humidity bars for every species in (Figure 3) (i.e., species with the strongest positive temperature correlation also show the strongest negative humidity correlation) indicates that these two variables are not acting as independent drivers but as two faces of the same underlying thermal-activity constraint, since low humidity and high temperature co-occur seasonally at all three sites.

Discussion

This study provides the first quantitative, multi-seasonal characterisation of ant community structure along an elevational gradient in Libya, and situates the Al-Jabal Al-Akhdar myrmecofauna within the broader global debate on how ant diversity responds to elevation under a Mediterranean climatic regime. Diversity increased, rather than declined, with elevation in our system (H': 1.54 → 1.72 → 1.92 from coast to highland; Figure 1). This contrasts with temperate mountains, where richness typically falls monotonically with altitude [4], but is fully consistent with several recent Mediterranean and semi-arid elevational studies, which report that low-elevation drought stress, rather than cold stress at altitude, is often the

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primary constraint on ant diversity in these systems, so that structurally complex, moisture-buffered highland vegetation supports richer, more even assemblages than exposed, thermally extreme coastal habitats [3,4]. Our finding that the highland site combined the greatest vegetational heterogeneity (fruit trees, grasses, agricultural mosaics) with the highest diversity index reinforces the now well-supported view that microhabitat complexity, more than elevation itself, is the proximate driver of ant niche partitioning in Mediterranean mountains [4].
Critically, (Figure 1) shows that this diversity gain is decoupled from raw abundance, which instead declines slightly toward the highlands, demonstrating that the highland gain in H' reflects greater evenness among co-occurring species rather than a simple numerical increase in ant activity. The sharp elevational segregation between *Cataglyphis cf. albicans/Solenopsis fugax* (coastal, thermophilic) and Camponotus barbaricus (highland, mesic), clearly visible as the diagonal colour gradient in (Figure 2), mirrors a well-documented physiological trade-off in ant thermal ecology: Cataglyphis species are classically among the most heat-tolerant terrestrial animals, foraging at near-lethal surface temperatures to exploit thermal refugia from predation (a strategy extensively documented in Palaearctic desert Cataglyphis taxa [16]), while wood- and litter-nesting genera depend on the buffered, humid microclimates of shaded, structurally complex habitats. The strong positive temperature–abundance and negative humidity–abundance correlations we observed for all seven species (r up to 0.88 and down to –0.75; Figure 3) are quantitatively consistent with recent experimental and observational work showing that ant foraging activity is tightly coupled to ambient thermal and hydric conditions, whether in Mediterranean urban ant assemblages [9], temperate forest ants during heatwave conditions [11], or cavity-nesting ants exposed to urban heat-island effects [10]. The consistent ranking of species in (Figure 3), with the same two thermophilic taxa showing both the strongest positive temperature response and the strongest negative humidity response — indicates a shared physiological sensitivity threshold rather than species-specific idiosyncrasy. Taken together, these convergent lines of evidence suggest that the seasonal collapse in abundance we observed in winter (135 individuals) is best explained as a direct thermal-activity constraint rather than a true demographic decline, and that colonies persist below ground during the coldest months rather than experiencing mass mortality.
Messor barbarus and *Messor ebeninus* showed no significant elevational preference, in contrast to the sharply zoned Cataglyphis/Camponotus pair visible in (Figure 2) as the comparatively flat, muted colour band running across all three columns for both Messor rows, in contrast to the strong diagonal gradient formed by the other five species. Comparable ecological flexibility across gradients has recently been documented in other Palaearctic Messor lineages, including detailed taxonomic and distributional work on the genus in the eastern Mediterranean [17], and is consistent with the taxon's dependence on seed availability, a resource that, unlike temperature, is not tightly elevation-structured across the mosaic of cultivated and natural vegetation typical of Al-Jabal Al-Akhdar. This plasticity is ecologically significant because Messor spp. contribute disproportionately to seed dispersal and soil turnover; their persistence across the full elevational range suggests that this ecosystem service is likely to be more climate-resilient than the ranges of the more thermally specialised taxa. Our results identify Cataglyphis cf. albicans and Solenopsis fugax as strong candidate indicators of coastal thermal stress, and Camponotus barbaricus as an indicator of highland mesic-forest integrity, providing a practical, low-cost monitoring toolkit for tracking future climate impacts in this UNESCO-recognised biosphere reserve landscape. This mirrors the logic of recent species distribution modelling work in comparable Irano-Turanian mountain systems, which shows that vegetation-buffered, NDVI-rich habitats act as critical climatic refugia for moisture-sensitive ant taxa under warming scenarios, while thermally specialised lowland species are projected to face the greatest range instability [7]. If similar dynamics apply in Al-Jabal Al-Akhdar, continued warming and aridification could be expected to compress the ranges of highland mesic specialists such as C. barbaricus while further favouring the expansion of thermophilic coastal taxa upslope, a testable prediction for future long-term monitoring.
Our pattern of increasing diversity with elevation departs from the classical mid-domain or monotonic-decline models most often reported from higher, colder mountain ranges such as the Alps [4] or the high-elevation gradients of central Spain, where richness instead peaks at intermediate elevations before declining toward cold, resource-poor summits. The comparatively modest elevational range of Al-Jabal Al-Akhdar (30–625 m) means that our highland site likely falls well within the ascending, moisture-driven limb of the broader Mediterranean elevational diversity curve, rather than approaching any cold-limited descending limb a distinction that should be tested with additional, higher-elevation sampling in future work. We also note that our seven-species inventory, while adequate to resolve clear elevational and thermal structuring, is modest relative to the richness recorded in more extensively sampled Mediterranean and Irano-Turanian gradients (e.g., [3]), and likely reflects both the genuinely lower regional species pool of North African Formicidae and the restriction of our method to epigaeic hand-collection; complementary pitfall and bait sampling would likely reveal additional cryptic or arboreal taxa in future surveys.

Conclusion

This study delivers the first quantitative, seasonally resolved baseline for ant biodiversity along an elevational gradient in Libya, demonstrating that microclimatic conditions, not elevation per se, are the proximate drivers of community composition, dominance and seasonal activity in the Al-Jabal Al-Akhdar myrmecofauna. The coexistence of sharply zoned thermal specialists (*Cataglyphis cf. albicans, Camponotus barbaricus*) alongside elevation-plastic granivores (Messor spp.) illustrates the diverse strategies by which Mediterranean ants partition a compressed climatic gradient. These findings contribute a much-needed North African data point to the global synthesis of elevational insect ecology and establish a

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practical, indicator-species framework for long-term biodiversity monitoring in this regionally important biosphere reserve as Mediterranean climates continue to warm and dry.

Conflict of interest. Nil

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