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Urbanisation homogenises the functional trait space and reduces body size of an arboreal ant species (Hymenoptera: Formicidae)

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Abstract

Urban environments are known to significantly influence the ecological dynamics of ant communities, since some ant groups are strongly associated with cities. Although there is an increasing interest in identifying "urban phenotypes" in insects, the impact of urbanisation on morphological functional traits of ants remains poorly studied. This study investigates intraspecific variation in the morphology of the generalist arboreal ant *Crematogaster scutellaris* (Olivier, 1792) along a local urbanisation gradient within a metropolitan city in northern Italy. More than 500 workers were sampled, photographed, and functionally relevant morphological traits related to body size (pronotal and head width), defensive function (propodeal spines), and sensory abilities (antennae and eyes) were measured. The work aimed to show whether a shift in intraspecific functional traits is underway according to the urban functional trait space homogenisation hypothesis and / or the urban ecological filter hypothesis. The overall multi-dimensional trait space of ants from highly urbanised areas was reduced compared with those from less urbanised areas, indicating that morphological homogenisation is associated with increasing urbanisation. In addition, highly urbanised areas hosted smaller ants, with a higher density of ommatidia in the compound eyes, and with shorter antennae, suggesting that an ecological filter may be acting on the species. Possible urban environmental factors linked to these differences include increased temperatures (reduced body size), proportion of trees (positively correlated with antenna length), and proportion of cemented areas (positively correlated with ommatidia density). These findings highlight urbanisation as a significant driver of morphological variation in *C. scutellaris*.

Key words: *Crematogaster scutellaris*, environmental filtering, phenotypic plasticity, urban green spaces, homogenisation hypothesis

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Introduction

Urbanisation is one of the main drivers of land-use changes, threatening the health of ecosystems (Nuissl & Siedentop 2021). Cities are typically characterised by higher mean temperatures compared with surrounding rural areas, a phenomenon known as the Urban Heat Island effect (Deilami & al. 2018). This can significantly impact local populations of ectotherm organisms such as arthropods (Piano & al. 2017, Cabon & al. 2024b). In addition, urban green spaces often suffer from intensive management (e.g., mowing or pruning) which reduces the quantity and quality of available vegetation and suitable microhabitats (Chollet & al. 2018, Peng & al. 2020, Trigos-Peral & al. 2020). The urban matrix can also present a patchwork of isolated parks due to infrastructures, which can compromise habitat connectivity (Angel & al. 2012).

Despite these challenges, cities have been shown to support a remarkable diversity of insects (Adams & al. 2020, Theodorou & al. 2020), which provide crucial ecosystem services (Castelli & al. 2020, Korányi & al. 2022). In addition, urban environments have been identified as relevant spots for the establishment and dispersal of invasive insect species (Polidori & al. 2021, López-Collar & al. 2024). However, urbanisation can also be a threat to insect communities leading to possible declines in functional diversity and / or species composition, as seen in several insects (Geppert & al. 2023, Pernat & al. 2024) including ants (Hymenoptera: Formicidae) (Holway & Suarez 2006, Buczkowski & Richmond 2012, Perfecto & Philpott 2023), as well as in multi-taxa approaches (Knop 2016). Recently, attention has been paid to shifts in the composition of urban insect communities (e.g., Geppert & al. 2023), but intraspecific shifts in functional traits of target species have been partly overlooked (Tommasi & al. 2022, Gonçalves-Souza & al. 2023, Ferrari & al. 2024a, b). For example, it was shown that urbanisation reduces ant diversity especially in the tropics and that urban areas were more strongly dominated by one or a few species, compared with natural habitats (Perez & al. 2022). In addition, urban landscape simplification, acting as an environmental filter, was also shown to reduce the number of species and to favour smaller ants with smaller heads (Nooten & al. 2019). However, less is known whether certain ant species vary in their functional traits across urbanisation gradients.

Functional traits include morphological, biochemical, physiological, or behavioural traits that influence an organism's fitness, health, and ability to exploit environmental resources (Wainwright 1994, Moczek 2010, Vandewalle & al. 2010, Renault & al. 2018). In this regard, several hypotheses have been proposed in the field of urban ecology (Hahs & al. 2023), including (i) the urban homogenisation of functional traits hypothesis and (ii) the urban ecological filter hypothesis.

According to the homogenisation hypothesis, anthropogenic disturbance may lead to a decrease in both the taxonomic and the functional diversity (i.e., the diversity in functional traits) of communities (Ferrari & Polidori 2022), possibly reducing the resilience of these communities and threatening the ecosystem services they provide (Theodorou 2022, Vaz & al. 2023). While this process has been extensively documented at the community level (Wagner & al. 2021), its implications at the intraspecific level remain comparatively underexplored (Ibarra-Isassi & al. 2023). In particular, more homogeneous functional traits may make target species more vulnerable to environmental change. Ultimately, this homogenisation may limit the functions provided by the species, leading to a degradation of ecosystem services (Hung & al. 2019). This hypothesis is often based on the fact that urbanisation alters climatic conditions and / or resource availability, leading to possible phenotypic responses or genetic adaptations, homogenising the functional traits of the most plastic urban species (Pernat & al. 2024).

Slightly different is the ecological filter hypothesis, which is based on the fact that only certain species (if the focus is on the community; e.g., Ferrari & Polidori 2022) or individuals with certain characteristics (if the focus is species-level; e.g., Merckx & al. 2018) can successfully occupy urban habitats. In the latter case, only some individuals of a species can colonise the most urbanised areas because they have some characteristics that increase their chances of effectively exploiting urban conditions (Lokatis & al. 2023). Indeed, according to this hypothesis, urbanisation constitutes a hierarchically imposed filter through which species / individuals must have the appropriate traits to pass in order to colonise or persist in an urban environment (Aronson & al. 2016). Both the homogenisation and the filter hypotheses predict a general simplification of the functional diversity of urban-dwelling insects and are often difficult to disentangle or may act synergistically.

These two hypotheses have already been confirmed by observing general changes in the functional traits of ants across naturally occurring environmental gradients, but essentially at the community level. For example, the homogenisation hypothesis was confirmed by the simpler ant communities in *Eucalyptus* plantations (managed and unmanaged) than the richer communities of a native Atlantic rainforest (Martello & al. 2018). In contrast, the ecological filter hypothesis has been shown to be true for ant assemblages in an American ecological reserve, where ground cover, surface temperature, vapour pressure deficit, and plant diversity were strongly correlated with community composition (Wiescher & al. 2012).

In the light of these possible urban ecology scenarios and the evidence from other environmental gradients, ants can be considered as effective bioindicators due to their cosmopolitan distribution (Schultheiss & al. 2022), often inhabiting anthropogenic landscapes (Uno & al. 2010, Santos 2016). Ants provide several urban ecosystem services such as nutrient recycling, predation, decomposition, and seed dispersal (Sanford & al. 2009, Del Toro & al. 2012). In addition, ant morphology offers a well-established framework for understanding the impacts of anthropogenic disturbances on these insects (Arnan & al. 2014, Parr & Bishop 2022). In ants, commonly studied morphological functional traits include head size (Parr & al. 2003), antennal scape length (Almeida & al. 2023), and compound eye area (Parr & al. 2017). Environmental changes due to anthropogenic activities have already been shown to affect some of these traits in insects. For example, hotter urban environments are often associated with smaller ants (Nooten & al. 2019), bees, and wasps (e.g., Ferrari & al. 2024b) possibly due to increased developmental temperatures and better thermoregulatory abilities of smaller insects. Moreover, green habitat fragmentation may filter for ants (Liu & al. 2019), bees, and wasps (Ferrari & al. 2024b) with improved dispersal abilities to better navigate fragmented areas. In addition, fragmented areas may also filter for better sensory abilities as shown in ants (Liu & al. 2019), bees (Ferrari & al. 2024a), or

butterflies (Turlure & al. 2016). Even non-morphological phenotypic traits, such as behaviour, were found to shift across urbanisation gradients (Gaber & al. 2024, Ferrari & Polidori 2025). For example, diet, trophic position, and colony structure were found to be variably altered in ants living in urban areas (Peng & al. 2023, Trigos-Peral & al. 2024, Ferrari & Polidori 2025). Furthermore, bolder and more risk-taking individuals seem to be favoured in cities. Importantly, not all traits necessarily change across all taxa, as has been shown in ants and other arthropods (Johnson & Stahlschmidt 2020, Tommasi & al. 2022, Cabon & al. 2024a, Ferrari & al. 2024b).

Alongside the analysis of single trait means or shifts, recent studies have emphasised the importance of trait covariation in adequately describing the functional trait space occupied by species (Laughlin & Messier 2015). This multivariate approach highlights the coordinated expression of multiple traits, which collectively respond to environmental conditions (i.e., how several traits co-vary in response to some environmental pressure, Pigliucci 2003). This approach has already been applied to ants (Wiescher & al. 2012, da Silva Utta & al. 2024), offering valuable insights into the complex interplay between morphology and environmental pressures. Overall, these studies elucidate how species respond to habitat change and provide a deeper understanding of patterns observed at the community level, linking species performance to the ecological filters or homogenisation effect provided by urban areas (Violle & al. 2012, Montes de Oca-Aguilar & al. 2022).

The present study investigates the effects of urbanisation on morphological functional traits in workers of the ant *Crematogaster scutellaris* (Olivier, 1792), focusing on traits related to body size, sensory systems, and defensive structures, using an Italian metropolitan city as a model system. Building on the cited studies, this work aims to show whether an intraspecific shift in functional traits is underway, according to the urban functional trait space homogenisation hypothesis and / or the urban ecological filter hypothesis. According to the homogenisation hypothesis, urban ant populations would show a reduced functional trait space compared with the populations from the less urbanised areas (multivariate approach). According to the filter hypothesis, urbanised areas would favour smaller body sizes (as a result of resource depletion or increased developmental temperatures), enhanced visual systems (to better navigate fragmented habitats), reduced antennal length (due to increased chemical stimuli in vegetated areas and possible increased developmental temperature), and enlarged defensive structures (to cope with increased competition and aggression) (univariate approach).

Material and methods

Studied species and sampling activity

Crematogaster scutellaris is a widespread species in Western Palearctic countries (Seifert 2018) that primarily nests under bark and dead wood, in old cynipid galls, and in man-made structures such as wall cracks (Giannetti & al. 2024, 2025a). This species is a predator of invertebrates but can also feed on dead insects (Castracani & al. 2017) and is also often found associated with colonies of aphids, whose honeydew is a source of sugars (Giannetti & al. 2021) (Fig. 1A).

Sampling was conducted in the metropolitan area of Milan (northern Italy), a large city characterised by parks of different sizes, making it an ideal setting to study urbanisation gradients. Sampling was carried out by inspecting the undergrowth of trees or under bark in the specific search for *Crematogaster scutellaris*, during August and September 2023, in a 25-day window. Each of the georeferenced nine sampling sites (Fig. 1B, Data S1) was visited on a single sunny day.

The identification of a nest as a single colony was based on several indicators, including the presence of brood (i.e., larvae and pupae) and a high concentration of individuals congregating at tree bases, within hollows, or beneath tree bark. To ensure consistency in colony size and maturity, only nests exhibiting a high density of individuals in their immediate vicinity were selected, after an inspection of the surroundings within a distance radius of 5 to 10 metres, suggesting an extended period of adaptation to the local environment. Colony individuality was verified by confirming the absence of foraging ants between the three selected nests (along an imaginary straight line) from a safe distance of 30 - 40 m from each nest. In 96.3% of cases, nests were separated by distances exceeding 40 m, and 92.6% were separated by more than 80 m. The mean distance between nests was 158.7 m (± 2 m standard error), with a minimum recorded distance of 38.8 m (observed in a single instance) and a maximum of 374.2 m (Data S1).

A total of 540 ants (20 ants per three colonies at each of the nine sampling sites) were collected using an entomological aspirator, stored in 25 ml test tubes in the field, and then frozen dry in the laboratory at -20 °C. Subsequently, specimens were identified under the microscope following Seifert (2018).

Landscape characterization

First, an a priori categorisation in 1 km² urbanisation grids of the Milan metropolitan area was carried out to identify suitable candidate sites for fieldwork. According to a standardised method developed in the framework of a larger project on Italian urban biodiversity (Dondina & al. 2024), sampling sites were identified along a green area size-fragmentation gradient using Land Cover and Land Use layers of the ISPRA 2021 National Maps (SINAnet Ispra 2021). This categorisation considered the extent of vegetated areas (A - D in ascending order) and their fragmentation (1 - 4 in descending order) (Fig. S1, as digital supplementary material to this article, at the journal's web pages) (Dondina & al. 2024).

Once the sampling sites were identified, a finer scale habitat characterisation was undertaken. The central geographic coordinates of the three colonies sampled for each site were used to create a 250-meter buffer of land-use.

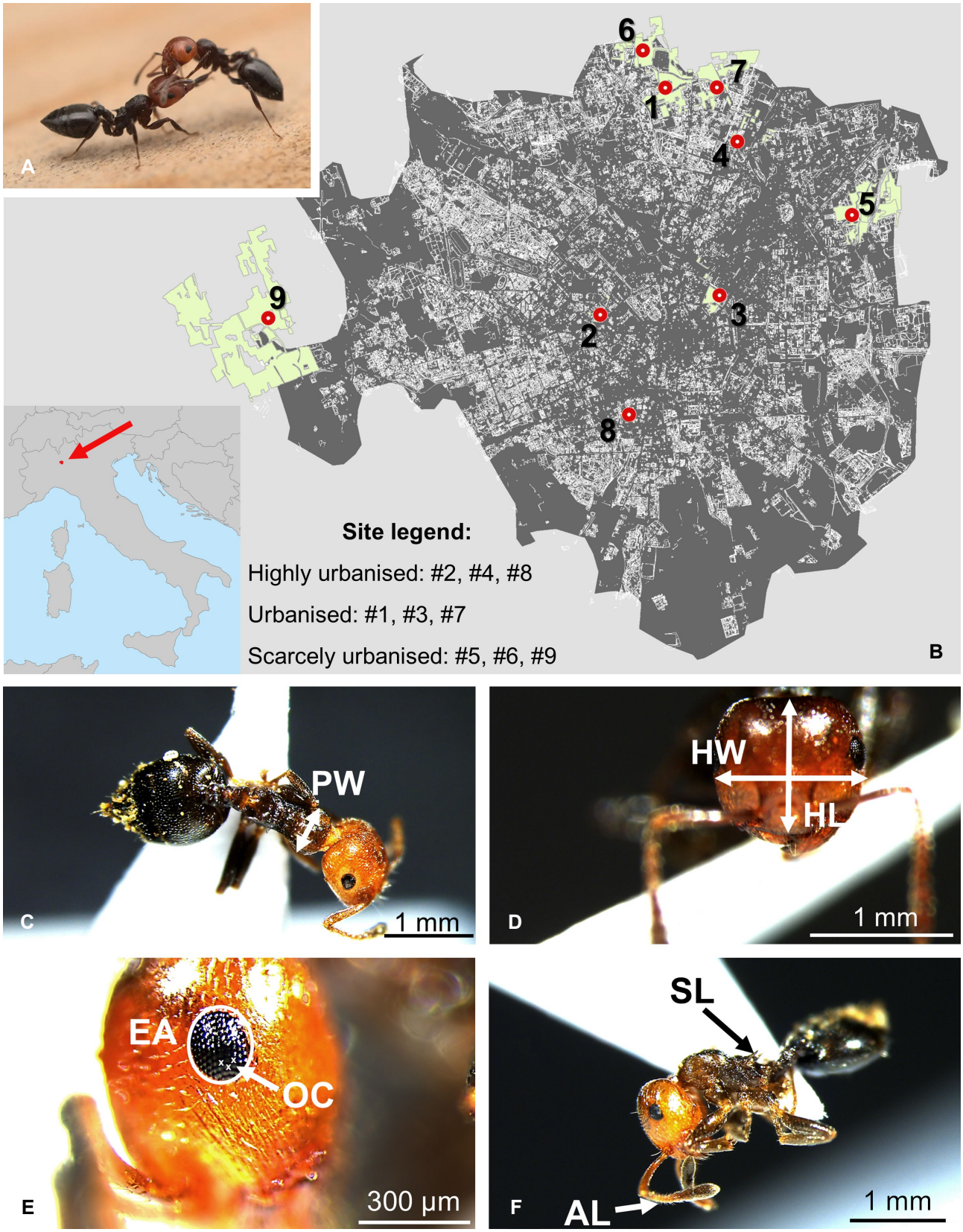

Fig. 1: (A) Picture of *Crematogaster scutellaris* workers in nature (property of author EN). (B) Map showing the location of the Metropolitan City of Milan (red dot in the Italian peninsula) and the exact location of the sampling sites (site numbers are reported in the supplementary Dataset, sheet = "Analysis"). (C) - (F) examples of the functional traits considered in this study. PW: pronotal width in top view, HW and HL: head width and length in frontal view, EA: eye area, OC: ommatidia count, SL: spine length, AL: antenna length.

Tab. 1: Morphological functional traits analysed in workers of *Crematogaster scutellaris*. Abbreviations refer to Figure 1.

Suggested functional significance	Biological meaning	Functional trait	Abbreviation	Reference	Description	Expected outcome in urban areas
Worker body size proxies	Body size, dispersal ability	Pronotal Width	PW	Sarty & al. (2006)	Length from side to side of the pronotum in top view	Reduced (Ferrari & al. 2024a)
	Body size	Head Width	HW	Sarty & al. (2006)	Distance between the centre of the compound eyes in frontal view	Smaller (Chen & Neoh 2023)
	Body size	Head Length	HL	Drager & al. (2023)	Distance between vertex and clypeus in frontal view	Smaller (Chen & Neoh 2023)
	Shape of the head	Head Aspect Ratio	Head AR	calculated here	HW / HL	-
Defensive function	Defensive ability	Spine Length	SL	Adapted from Blanchard & al. (2020)	Length of the propodeal spine	Shorter (following hypothesis from Theodorou 2022)
Sensory traits affecting habitat utilisation	Image resolution, visual acuity	Eye Area	EA	adapted from Gibbs & Parr (2013)	Area of the compound eye	Larger (Ferrari & al. 2024b)
	Image resolution, visual acuity	Ommatidia Count	OC	counted here	Number of ommatidia	Higher (Ferrari & al. 2024b)
	Image resolution, visual acuity	Ommatidia Density	OD	calculated here	OC / EA	Higher (Jelley & Barden 2021; Ferrari & al. 2024b)
	Chemo-tactile perception	Antenna Length	AL	adapted from Sommer & Wehner (2012)	Length of the pedicel, scape, and flagellum	Shorter (Braun & Lortie 2024; Ferrari & al. 2024b; Yates & al. 2014)

This buffer was chosen to describe the environment and calculate all the landscape metrics in which the ants of the three colonies were likely to have lived and foraged according to the territory defended by this species (Frizzi & al. 2014). Land-use metrics were retrieved from ESA WorldCover 2021 v200, which is provided at 10 m resolution and is freely available (ESA WorldCover 2021). The raster of the Milan metropolitan area was downloaded and imported into QGIS v.3.34.5, and landscape metrics were extracted using the Landscape Ecology Statistics (LecoS) plugin (Jung 2016). LecoS relies on FRAGSTATS, a spatial pattern analysis program for categorical maps (McGarigal 1995).

In the subsequent analysis, only cemented, grassland, and tree cover were considered as these were almost the only land-use classes represented in the buffers. Six metrics were considered for each class: landscape proportion, edge density (a proxy for geometric fragmentation of patches, calculated as the proportion between perimeter and area of the patches), patch density within buffer (number of patches of the same class divided by the buffer area), largest patch area within buffer, Euclidean nearest neighbour distance (the shorter distance between patches of the same class), and patch cohesion index (a measure of connectedness between patches of the same type) (Tab. S1 and Data S1; https://fragstats.org/index.php/fragstats-metrics/patch-based-metrics).

In addition, the building height in the same buffers was added as a further urbanisation variable of 10 m spatial resolution using the raster layer Urban Atlas Building Height 2012, from the Copernicus Land Monitoring System portfolio (Copernicus 2024). Building height provides an indication of the isolation of a green patch within the urban impervious matrix, particularly for species whose dispersal or colonization relies on aerial movement. Finally, the mean land surface temperature between June and September – to cover the period of activity of the sampled colonies – was extracted for each site using the product MOD11A2 (Modis 2008).

Morphological functional traits

Frozen ants were glued to entomological cards and pinned in groups of three individuals. From the initial 540 specimens, a total of 536 ants were prepared and analysed

for this study, since four specimens were accidentally ruined during sampling, transport, or pinning process. All these specimens were then photographed under a Leica (Wetzlar, Germany) M205 FCA stereomicroscope mounted with a Leica DFC7000 T camera. The following traits were measured: from the dorsal photo (Fig. 1C), pronotal width (PW, from side to side); from the frontal head photo (Fig. 1D), head width across eyes and length (HW and HL respectively, Seifert 2018). The head aspect ratio (HW / HL) was then calculated. PW and HW were taken as proxies for the body size of the ants (Okrutniak & al. 2020, Pie & Tschá 2013). From the lateral head photograph (Fig. 1E), the area of the eye was measured and the number of ommatidia was counted. Even though the eye possesses a three-dimensional structure, the standardisation of the method across all samples provides a reasonable method to compare its size across individuals. The density of ommatidia (number per mm²) was then calculated. From the lateral photo (Fig. 1F), the length of the propodeal spine was measured. Finally, the antennae were detached with a forceps, glued to A4 white paper, scanned at 600 dpi and subsequently measured. All measurements were made from scaled photographs using ImageJ (Schneider & al. 2012). A summary description of the morphological functional traits is given in Table 1.

Functional space metrics

The R package "funspace" (Carmona & al. 2024) was used to calculate functional space metrics regarding the populations of ants. The following metrics were calculated. The functional richness quantifies the area in a two-dimensional context of the functional trait space occupied by each urbanisation category. The functional divergence is the degree to which units (individuals in this case) in a group (urbanisation category) have different trait combinations, and it quantifies how much the trait probability density function is distributed towards the edges of the functional trait space occupied by a category. Both the functional richness and functional divergence are the larger the more the units of a group are different between them.

Finally, the theoretical area generated using a multivariate normal distribution (null distribution) was tested against the observed functional trait area (null test). Null models were run 999 times and built with a multivariate normal distribution, creating a dataset of normally distributed variables with the same mean and covariance as the observations used to construct the functional space (Carmona & al. 2021). This null model corresponds to the expectation that some trait combinations, particularly those towards the centre of the space, are more likely than others, and the resulting space has the approximate shape of an ellipse.

Statistical analysis

All the statistical analyses were performed in R v.4.4.2 (R Core Team 2024). First, a correlation matrix (using Pearson's r) was created to visualise how the morphological functional traits covary between themselves. The same was done to visualise how the environmental variables (at 250 m scale) covaried and clustered between them.

Next, a Principal Component Analysis (PCA) using centred and scaled (mean = 0, standard deviation = 1) environmental variables at 250 m scale was run. Although no single landscape metric can be identified as the best descriptor of urbanisation (Fig. S2), overall, the nine sampling sites well described a local urbanisation gradient, as cemented surfaces varied from 0% to 43%. Three groups were identified: scarcely urban (SU, sites number 5, 6, and 9 in Fig. 1), urban (U, sites number 1, 3, and 7 in Fig. 1), and highly urban (HU, sites number 2, 4, and 8 in Fig. 1). The three groups had the following characteristics: SU: cemented area < 10%, T_{mean} = 33.43 °C; U: cemented 10 - 20%, T_{mean} = 34.09 °C; HU: cemented > 20%, T_{mean} = 34.9 °C. The clustering was consistent both when plotting PC1 (38.57% of variance explained) versus PC2 (29.08%) and PC1 versus PC3 (15.49%). PC1 identifies a gradient of cementation and therefore a degree of urbanisation. Lower

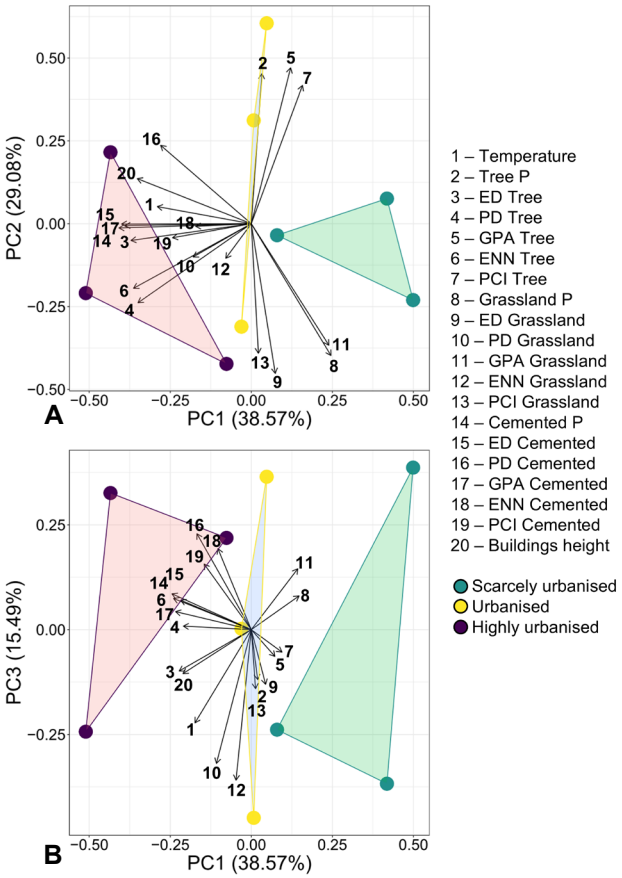

Fig. 2: Principal component analysis (PCA) plots used to categorise the sampling sites. (A) PC1 and PC2, (B) PC1 and PC3. Points are the nine sampling sites; arrows are the loadings of the PCA. The percentage of variance explained is reported in brackets. Environmental metrics are abbreviated as follows. P: proportion; ED: edge density; PD: patch density; GPA: greatest patch area; ENN: Euclidean nearest neighbour distance; PCI: physical connection index (see Appendix, Tab. S1 further details).

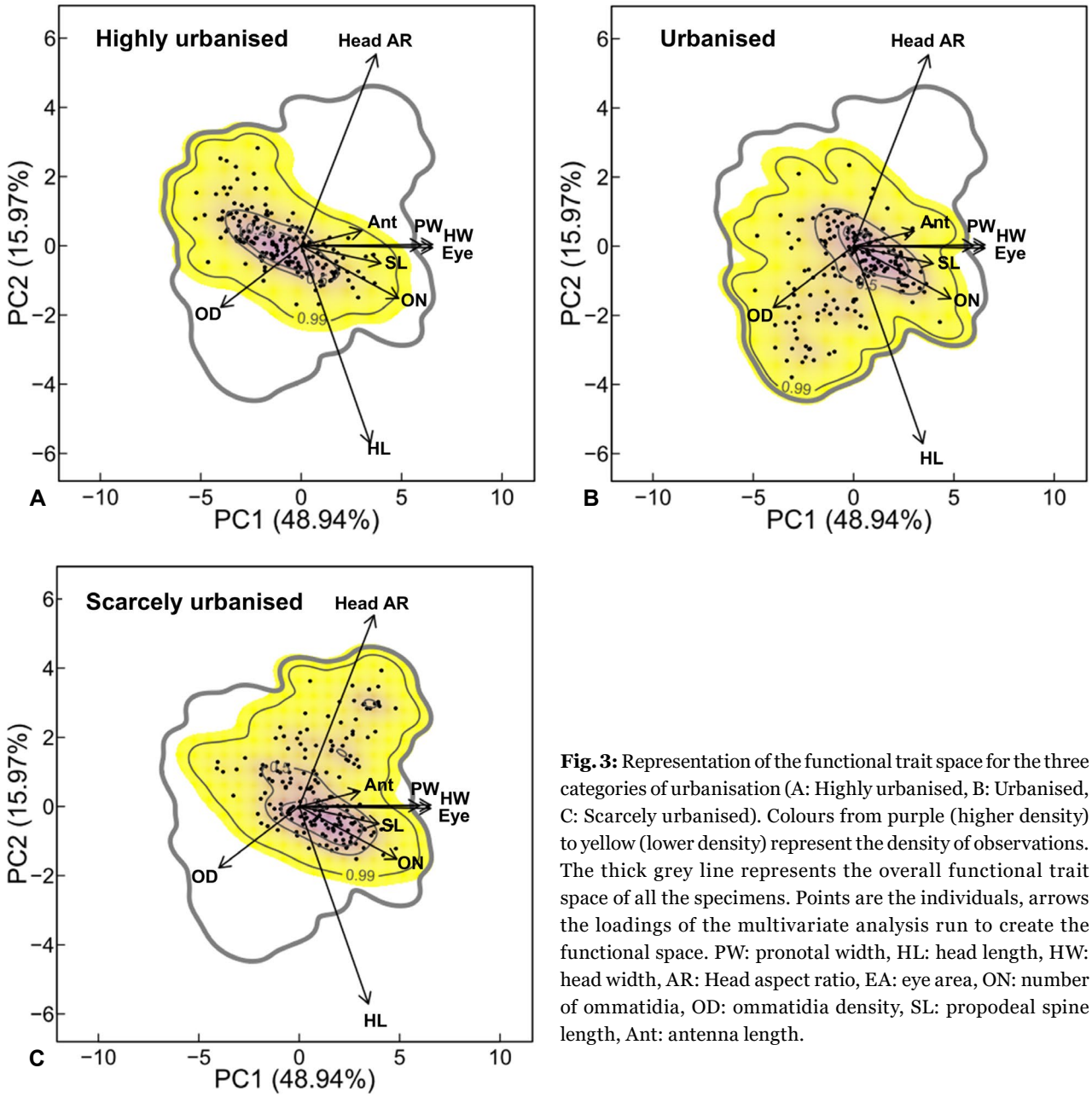

Fig. 3: Representation of the functional trait space for the three categories of urbanisation (A: Highly urbanised, B: Urbanised, C: Scarcely urbanised). Colours from purple (higher density) to yellow (lower density) represent the density of observations. The thick grey line represents the overall functional trait space of all the specimens. Points are the individuals, arrows the loadings of the multivariate analysis run to create the functional space. PW: pronotal width, HL: head length, HW: head width, AR: Head aspect ratio, EA: eye area, ON: number of ommatidia, OD: ommatidia density, SL: propodeal spine length, Ant: antenna length.

values of PC1 are associated with sites with the highest proportions of cemented areas (Fig. 2A), irrespective of the type of vegetation (tree or grassland). PC2 describes the type of vegetation (Fig. 2A). Higher values of PC2 are associated with sites characterised by trees, while lower values are associated with sites characterised by grassland. PC3 (Fig. 2B), even if it does not explain that much variance, highlights again a degree of urbanisation, with lower values associated with more cemented and less vegetated areas. Next, a Redundancy Analysis (RDA) was performed to test whether the three urbanisation categories (HU, U, and SU) significantly explained ant global morphology.

Finally, two separate generalised linear mixed models (with site and colony as random effects) were built using the package "glmmTMB" (Brooks & al. 2017) using the single functional traits as response variables. Models also included PW (except for the model of PW itself and head metrics as these are also body size proxies) to take into account size-dependent relationships. The first model included the urbanisation categories (HU, U, and SU) as the sole fixed effect, the second model included the extrapolated PC1 and PC2 from the PCA. For the first model (categories) a post hoc Tukey test was run for pairwise comparisons. The variance inflation factors were always checked to be less than 2. The normality of the distribution of random effects and residuals was visually checked using the package "performance" (Lüdecke & al. 2021). For all the analyses, an alpha level of 0.05 was assumed as a threshold for discriminating statistically significant results.

Plots were made in "ggplot2" (Wickham 2011) with a colour-blind friendly palette from the "viridis" package (Garnier & al. 2024). All the data are available in Data S1 (following the principles of Keller & al. 2023).

Results

Morphology of *Crematogaster scutellaris* workers

Functional trait measures are reported as mean ± standard error (max. - min.). Considerable variation was found in the morphological functional traits analysed. Mean PW was 1.10 mm ± 0.01 (1.35 - 0.81), HW was 1.05 mm ± 0.01 (1.28 - 0.82), HL was 0.99 mm ± 0.01 (1.19 - 0.78), head AR was 1.07 ± 0.01 (1.46 - 0.76), propodeal SL was 0.19 mm ± 0.01 (0.30 - 0.19), EA was 0.03 mm² ± 0.01 (0.04 - 0.02), the ON was 116.69 ± 0.82 (167 - 87), OD was 3847.80 ommatidia / mm² ± 21.22 (4807.69 - 2852.94), and AL was 2.32 mm ± 0.02 (3.46 - 1.27).

All functional traits, except AL, appeared to be strongly correlated with PW, the best proxy for the body size (Fig. S3). This means that larger ants have larger heads, larger eyes and more ommatidia (with reduced density), and longer propodeal spines.

Tab. 2: Summary statistics of the generalised linear mixed models used to test the effects of the urbanisation categories on the morphological functional traits considered. S.E.: standard error, PW: pronotal width, *t* = test statistic, *P* = P-value. Categories are abbreviated as SU: scarcely urbanised, U: urbanised, HU: highly urbanised. Statistically significant results (P < 0.05) are boldfaced.

Functional trait	Comparisons	Estimate	S.E.	*t*	*P*
Pronotal width	**HU – SU**	**-0.085**	**0.035**	**-2.419**	**0.042**
	HU – U	-0.035	0.035	-1.003	0.575
	U – SU	0.050	0.035	1.416	0.333
Head width	HU – SU	-0.074	0.041	-1.805	0.169
	HU – U	-0.031	0.041	-0.761	0.727
	U – SU	0.043	0.041	1.044	0.549
Head length	HU – SU	-0.023	0.033	-0.688	0.771
	HU – U	-0.069	0.033	2.060	0.099
	U – SU	-0.046	0.033	-1.372	0.356
Head aspect ratio	HU – SU	-0.054	0.045	-1.209	0.448
	HU – U	0.038	0.045	0.852	0.671
	U – SU	0.093	0.045	2.061	0.099
Propodeal spine length	HU – SU	-0.017	0.007	-2.295	0.057
	HU – U	-0.013	0.007	-1.708	0.203
	U – SU	0.004	0.007	0.587	0.827
	PW	**0.083**	**0.012**	**6.711**	**<0.001**
Eye area	HU – SU	0.002	0.001	-2.062	0.099
	HU – U	-0.001	0.001	-0.613	0.813
	U – SU	0.001	0.001	1.460	0.311
	PW^²	**0.011**	**0.001**	**17.429**	**<0.001**
Ommatidia count	HU – SU	1.478	3.750	0.394	0.918
	HU – U	2.477	3.730	0.665	0.784
	U – SU	0.999	3.730	0.268	0.961
	PW	**61.091**	**5.119**	**11.935**	**<0.001**
Ommatidia density	**HU – SU**	**280.000**	**82.100**	**3.414**	**0.002**
	HU – U	153.000	81.400	1.877	0.146
	U – SU	-128.000	81.600	-1.564	0.262
	PW	**-936.525**	**141.060**	**-6.639**	**<0.001**
Antenna length	HU – SU	-0.270	0.187	-1.448	0.317
	HU – U	-0.274	0.186	-1.470	0.306
	U – SU	-0.004	0.186	-0.021	0.999
	PW	**0.780**	**0.099**	**7.902**	**<0.001**

Tab. 3: Summary statistics of the generalised linear mixed models used to test the effects of urbanisation principal components on the morphological functional traits considered. S.E.: standard error, PW: pronotal width, *t* = test statistic, *P* = P-value. Principal Component (PC) 1 represents the cemented area, PC2 represents the type of vegetation (from mostly herbaceous to mostly trees). Statistically significant results (P < 0.05) are boldfaced.

Functional trait	Predictors	Estimate	S.E.	*t*	*P*
Pronotal width	PC1	0.007	0.007	1.056	0.291
	PC2	0.001	0.007	0.012	0.991
Head width	PC1	0.007	0.007	0.994	0.320
	PC2	-0.001	0.008	-0.182	0.856
Head length	PC1	-0.001	0.005	-0.057	0.954
	PC2	0.011	0.006	1.725	0.084
Head aspect ratio	PC1	0.008	0.007	1.142	0.254
	PC2	-0.012	0.008	-1.414	0.157
Propodeal spine length	PC1	0.001	0.001	1.067	0.286
	PC2	0.001	0.001	0.644	0.519
	PW	**0.084**	**0.012**	**6.864**	**< 0.001**
Eye area	PC1	0.001	0.001	1.737	0.082
	PC2	-0.001	0.001	-0.374	0.709
	PW^2	**0.011**	**0.001**	**17.470**	**< 0.001**
Ommatidia count	PC1	-0.215	0.577	-0.372	0.710
	PC2	-0.439	0.664	-0.661	0.509
	PW	**61.017**	**5.090**	**11.988**	**< 0.001**
Ommatidia density	**PC1**	**-38.206**	**14.297**	**-2.672**	**0.008**
	PC2	-6.510	16.430	-0.396	0.692
	PW	**-960.660**	**142.132**	**-6.759**	**< 0.001**
Antenna length	PC1	0.042	0.022	1.919	0.055
	PC2	**0.073**	**0.025**	**2.928**	**0.003**
	PW	**0.785**	**0.098**	**7.976**	**< 0.001**

Functional trait space across urbanisation categories

Categorisation in scarcely urban (SU), urban (U) and highly urban (HU) areas significantly explained the variation in the overall ant morphology: RDA, d.f. = 2, 533, F = 40.036, P < 0.001 (functional trait space Fig. 3).

In particular, the SU area had a functional richness of 60.65, a functional divergence of 0.55, and its functional traits space area was statistically significantly lower than what was expected by the null model (P = 0.010). The U area had a functional richness of 68.67, a functional divergence of 0.45, and its functional traits space area was statistically significantly lower than what was expected by the null model (P = 0.030). The HU area had a functional richness of 47.41, a functional divergence of 0.44, and its functional traits space area was not different from that expected by the null model (P = 0.307). The functional richness of HU was statistically significantly lower than that of U (χ^2 = 3.894, P = 0.048), this was the only statistically significant comparison of these metrics.

Effects of urbanisation on morphological traits

Only few functional traits were statistically different among the urban categories. The PW was statistically significantly higher in SU than HU (Fig. 4A), and the OD was lower in SU than HU (Fig. 4F) (Tab. 2). However, few traits were almost significantly different (P < 0.1) among the categories (Tab. 2). HL was marginally higher in U than HU (Fig. 4B), head AR was marginally higher in SU than U (Fig. 4C), propodeal SL (Fig. 4D) and EA (Fig. 4E) were marginally higher in SU than HU (Tab. 2).

Similarly, only few functional traits were statistically affected by PC1 and PC2 (Tab. 3). OD statistically significantly decreased with PC1 (Fig. 5C), and AL increased with PC2 (Fig. 5E). However, few traits were marginally affected (P < 0.1) (Tab. 3). HL marginally increased with PC2 (Fig. 5A), while EA (Fig. 5B) and AL (Fig. 5D) marginally increased with PC1.

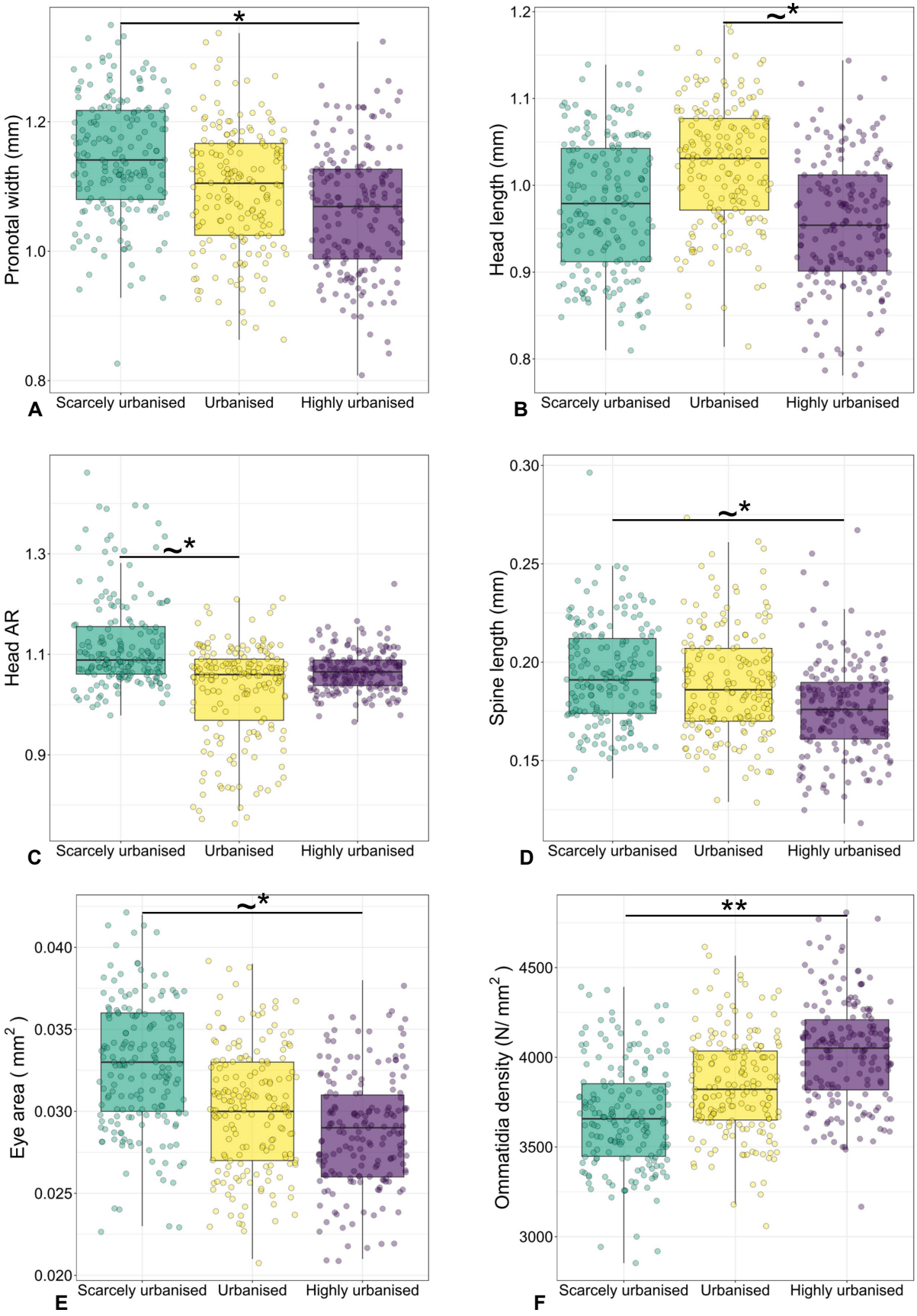

Fig. 4: Boxplots showing the statistically significant (** P < 0.01, * P < 0.05) or marginally significant (~* P < 0.1) results of generalised linear mixed models used to test the variation in functional traits in the three urbanisation categories. A: pronotal width, B: head length, C: Head aspect ratio (AR), D: propodeal spine length, E: eye area, F: ommatidia density.

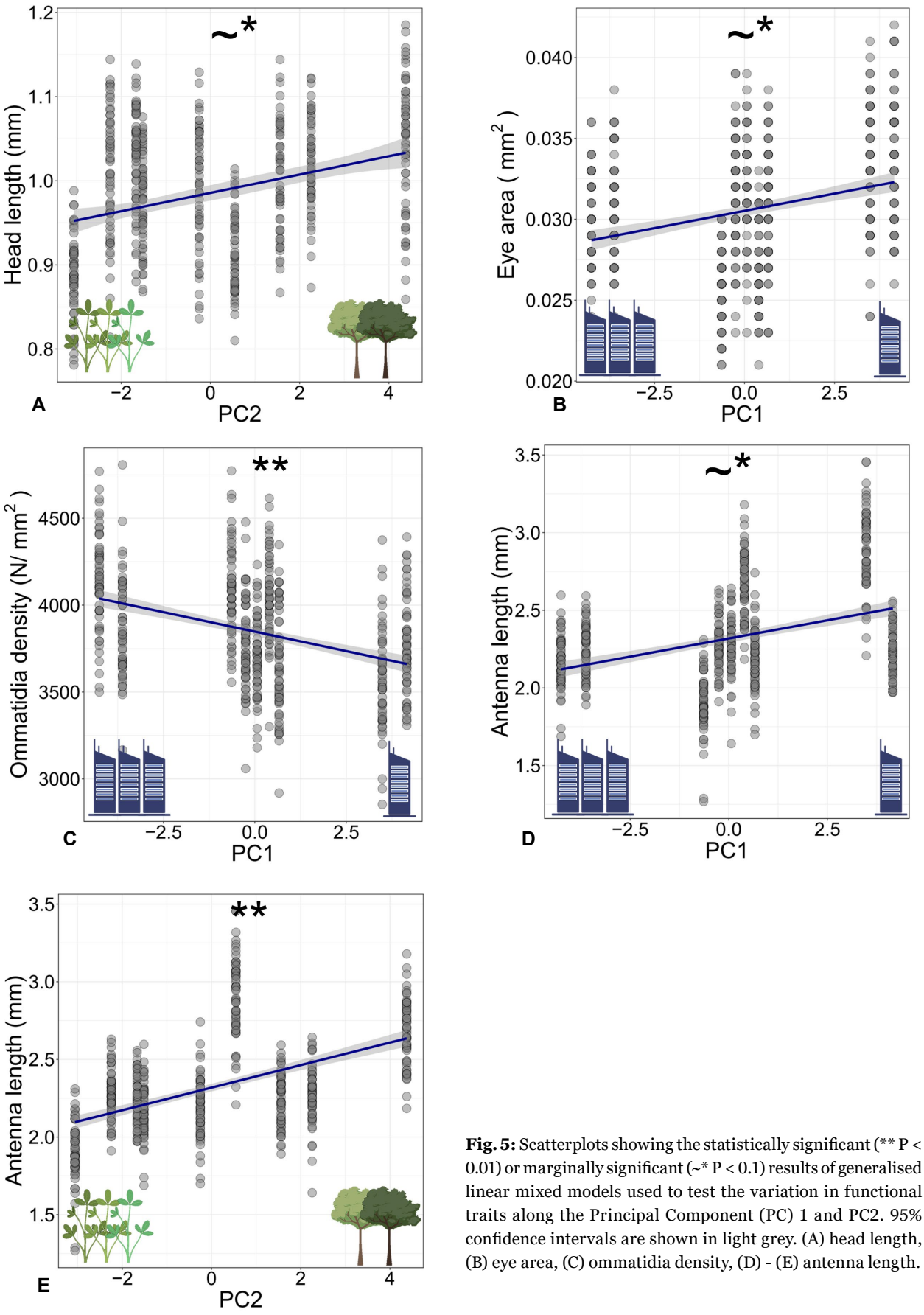

Fig. 5: Scatterplots showing the statistically significant (** P < 0.01) or marginally significant (~* P < 0.1) results of generalised linear mixed models used to test the variation in functional traits along the Principal Component (PC) 1 and PC2. 95% confidence intervals are shown in light grey. (A) head length, (B) eye area, (C) ommatidia density, (D) - (E) antenna length.

Discussion

The morphology of workers of the ant *Crematogaster scutellaris* was studied across a local urbanisation gradient, revealing significant differences in morphology. This suggests that local environmental and land-use characteristics of the urban matrix do indeed influence the morphology of these insects. Overall, both the homogenisation and the filter hypotheses found some support.

Urban functional trait space homogenisation hypothesis

The use of functional trait space is becoming increasingly popular (Violle & al. 2012), providing a useful tool for defining potential "urban phenotype" for insects (Montes de Oca-Aguilar & al. 2022). Here, differences in morphological functional trait space were observed when comparing ants from highly, moderately, and scarcely urban areas. These differences can be interpreted as a morphological response to the selective pressures exerted by highly urbanised areas, consistent with findings in other insect taxa (Ferrari & Polidori 2024, Liao & Lin 2024). For medium and low levels of urbanisation, the functional trait space was smaller than the null expectation, possibly indicating trait clustering and a shift in trait optima (Luo & al. 2023).

The results from the comparison of the functional trait spaces across the three urbanisation categories largely support the homogenisation hypothesis. In line with this hypothesis, ants from highly urbanised areas had the smallest functional trait space, meaning that their morphology is somewhat constrained, supporting the expectation that urbanisation would lead to a homogenisation effect. This is in line with other studies on ants (Luo & al. 2023, da Silva Utta & al. 2024) and is consistent with the biotic homogenisation hypothesis: Biotas become increasingly similar due to anthropogenic pressures such as habitat conversion and simplification (Petsch 2016), further highlighting the ecological consequences of intensive land use. Highly urbanised areas were characterised by higher temperatures, and greater fragmentation and distances between tree patches (suitable nesting sites for *Crematogaster scutellaris*). Higher temperatures may accelerate larval development, which may partially explain the reduction in body size and other morphological structures observed in the functional trait space (discussed in the next section).

Nevertheless, the large overlap of functional spaces towards the centre of the global space (i.e., all individuals) may indicate that *Crematogaster scutellaris* has a "core morphology" that is conserved across sites, colonies, or individuals.

Urban ecological filter hypothesis

Not all functional traits analysed showed significant changes across the urbanisation gradient when considered individually. This highlights the need for an integrated approach that examines morphological changes from multiple perspectives to detect underlying mechanisms. One possible explanation is that as ant size shifted with urbanisation, the strong relationship between body size and the other parameters may have driven changes in other traits. This means that for certain traits, urbanisation does not alter their magnitude but rather scales them in proportion to the size of the organism (Perl & Niven 2016, Tawdros & al. 2020). Nevertheless, the substantial differences (250-meter scale) between sites in terms of temperature and sealed cover (PC1) as well as vegetation (PC2) highlighted some morphological shifts that can be interpreted according to the filtering hypothesis.

Larger ants, with longer heads, and higher head aspect ratio were predominantly found in sites with medium to low levels of urbanisation, in accordance with other studies suggesting that larger ants are favoured by lower levels of urbanisation (Chen & Neoh 2023), even though this pattern does not hold true in all cases (Ossola & al. 2015). Hence, the expectation that urbanisation would overall filter for reduced body size, likely due to resource depletion or the higher temperatures, seems to be true.

Interestingly, propodeal spines were also found to be slightly longer in seminatural areas. Ant spines are thought to be defensive structures, and phylogenetic analyses support the hypothesis that elongated propodeal spines serve as a defence mechanism against both vertebrates and invertebrates (Sarnat & al. 2017). Albeit solid conclusions cannot be drawn, it can be hypothesised that urbanisation reduces the number of ant natural enemies, since habitat loss might lead to a reduction in insect predators (Turrini & al. 2016, Theodorou 2022). Hence, the expectation that urbanisation would filter for enlarged defensive structures, due to increased competition and aggression in urban environments, does not appear to be supported.

Higher ommatidial densities were found in highly urbanised sites (higher visual acuity, see Jelley & Barden 2021), while larger eye areas were observed in less urbanised sites. The first interpretation is that, as shown, larger eyes have also a reduced ommatidia density. However, higher ommatidia density was found in arboreal and epigeic ants (Jelley & Barden 2021) and in bees from more urbanised areas (Ferrari & al. 2024a); two visually demanding landscapes. Therefore, this could be a response to the need to search for food or nesting resources while navigating man-made structures. In addition, smaller eyes in urban landscapes have also been reported in wasps, as response to the Urban Heat Island effect (Ferrari & al. 2024a). Ants may follow this pattern, since highly urbanised areas were also characterised by higher temperatures. These findings support the prediction that urbanisation would filter for improved sensory systems, particularly in the visual domain, to address the challenges of navigation in fragmented habitats.

Antennae are essential organs for perceiving chemical stimuli both from the environment and nestmates (Zube & al. 2008, Knaden & Graham 2016). Antennae were found to be longer in areas with extensive tree cover. This is very similar to what was found in natural habitats, where ants living in tree-rich habitats had longer antennae than those

living in grassland-rich pastures (Yates & al. 2014, Braun & Lortie 2024). Similarly, wasps have been shown to possess shorter antennae in more fragmented urban area, further supporting the prediction that urbanisation filters against antennal size (Ferrari & al. 2024a). Longer antennae may improve ant chemosensory abilities in denser vegetation, which could explain why ants with shorter antennae were found in open, grassland-dominated habitats. Overall, vegetation cover may act as a filter on ant morphology by influencing ant perception, with habitats rich in trees being perceptually more demanding for the species analysed.

Finally, antennal length was negatively correlated with ommatidial density, which was higher in ants from medium to high levels of urbanisation. This was also found in other ant species (Jelley & Barden 2021), suggesting a potential trade-off in resource investment between visual and olfactory / tactile acuity that might be affected by urbanisation.

Conclusion

In conclusion, this work contributes to the growing body of evidence on the phenotypic plasticity of ants and other insects in response to increasing anthropogenic pressures, showing that ants in highly urbanised areas exhibit a more homogeneous morphology, potentially making them more vulnerable to environmental change. If this functional homogenisation would extend to several taxa, then the ecosystem services they provide may be compromised (Hung & al. 2019). However, it remains difficult to resolve whether these shifts in functional traits represent (i) an adaptive response to urban conditions, (ii) simply a manifestation of background phenotypic plasticity, or (iii) changes based on genetic or epigenetic mechanisms. However, alates of *Crematogaster scutellaris* can fly at more than 80 m of altitude (Giannetti & al. 2025b) and have likely high dispersal ability. Additionally, the monogynic propensity, together with the aggressiveness that characterizes this species (Seifert 2018), are further clues that queens would tend to disperse as far as possible from other conspecific colonies. Therefore, we suggest that the variation in their phenotypic traits may be mainly driven by different habitat conditions. Hence, we preliminarily hypothesise that adaptation and phenotype plasticity are the most likely mechanisms for the observed morphological variation. Future studies investigating the genetic relationship between populations will likely help to elucidate the mechanisms behind the response of this species to urbanisation.

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Declaration on use of generative artificial intelligence tools

The authors declare that they did not utilize generative artificial intelligence tools in any part of the composition of this manuscript.

Author contributions

AF: formal analysis, investigation, data curation, writing - original draft, writing - review & editing, visualization; DLC: methodology, investigation, writing - review & editing; DGT: methodology, investigation, writing - review & editing, visualization; EN: methodology, investigation, writing - review & editing, visualization; CP: conceptualization, formal analysis, methodology, validation, resources, writing - review & editing, supervision, funding acquisition.

Conflict of interest

The authors declare that they have no known competing financial interest or personal relationship that could have appeared to influence the work reported in this paper.

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