

DOI: 10.20103/j.stxb.202502270423

曹源源, 苏秋海, 罗昕裕, 尹如意, 黄相钦, 罗怡, 周昭敏. 区域气候对西南山地城市蚂蚁群落体形大小的影响. 生态学报, 2026, 46(10): - .
Cao Y Y, Su Q H, Luo X Y, Yin R Y, Huang X Q, Luo Y, Zhou Z M. Effects of regional climate on body size of urban ant communities in the Southwest Mountains. Acta Ecologica Sinica, 2026, 46(10): - .

区域气候对西南山地城市蚂蚁群落体形大小的影响

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摘要: 体形是生物的基本性状。贝格曼法则、干旱适应假说和季节性假说被广泛用于解释昆虫在自然生境中的体形大小变异。然而, 城市昆虫群落体形大小对区域气候的生态响应仍然缺乏证据。在西南山地 8 个城镇(海拔 510—3380 m)开展了广泛的蚂蚁群落调查和采样。城镇间, 蚂蚁群落体形大小存在显著差异(例如, 康定市的蚂蚁群落加权平均体形大小和群落算术平均体形大小分别比永仁县高出约 136% 和 85%)。线性混合效应模型结果表明, 在区域气温较低或区域气温季节性变化较大的城镇, 蚂蚁群落体形较大; 降水和降水季节性对蚂蚁群落体形大小的影响不显著。上述结果表明, 该地区的城市蚂蚁群落体形大小变异符合贝格曼法则, 但不符合干旱适应假说和季节性假说。因此, 城市蚂蚁群落体形大小可能会受到气候变化和人类活动的双重影响。

关键词: 城市; 群落; 体长; 贝格曼法则; 干旱适应假说; 季节性假说

Effects of regional climate on body size of urban ant communities in the Southwest Mountains

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Abstract: Body size is a fundamental functional trait of organisms, influencing spatial use, lifespan, reproductive capacity, and functional roles within ecological networks. In natural ecosystems, geographical variations in insect body size are often explained by classical ecological hypotheses, such as Bergmann's rule (larger sizes in colder climates), the drought adaptation hypothesis (larger sizes in arid environments to reduce water loss), and/or the seasonality hypothesis (smaller sizes in highly seasonal climates to facilitate rapid reproduction). However, urban ecosystems exhibit distinct microclimates from those in the adjacent natural habitats, characterized by phenomena such as heat islands and altered humidity regimes. A critical, unresolved question is whether these anthropogenic modifications decouple the relationship between regional climate and body size, rendering large-scale geographic patterns unpredictable in urban insect communities. To address this knowledge gap, we conducted a large-scale field study along an extensive elevational gradient (510—3380 m a.s.l.) in the Southwest Mountains at the eastern margin of the Qinghai-Tibet Plateau. We systematically sampled ground-foraging ant communities using pitfall traps from 64 (sub)urban sites across eight counties. A total of 55,890 worker ants, representing 81 species from 31 genera, were collected. Weber's length was measured for each species and used to calculate the community-weighted mean and community mean of body size to characterize the ant assemblages. We employed one-way ANOVA to assess whether the body size of ant communities differed significantly among counties, and performed linear

基金项目: 国家自然科学基金青年项目(31600412); 西华师范大学青年教师科研资助项目(19D044)

收稿日期: 2025-02-27; **网络出版日期:** 2026-00-00

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mixed-effects models to test the potential effects of temperature, precipitation and seasonality on the body size variations. We found that body size of ant communities differed significantly among counties (e.g., the average values of community-weighted mean and community mean were approximately 136% and 85% higher in Kangding than those in Yongren, respectively). Consistent with Bergmann's rule, ant communities exhibited larger body sizes in regions with lower annual mean temperatures. In contrast, neither annual precipitation nor precipitation seasonality had significant effects on body size, which does not support the drought adaptation hypothesis or the precipitation-related aspect of the seasonality hypothesis. Contrary to the seasonality hypothesis, however, the community-weighted mean of body size was positively associated with temperature seasonality. Our study highlights that body size in urban ant communities remains sensitive to regional temperature variation, while also suggesting that land management practices (such as irrigation) may mediate the influence of precipitation regimes. Consequently, we propose that monitoring the responses of ant functional traits such as body size to regional climate gradients can serve as a valuable bioindicator tool. This approach shows great promise for broadly assessing the ecological impacts of land disturbance and urbanization, thereby offering fresh insights into the mechanisms sustaining biodiversity in an era of global change.

Key Words: urban; community; Weber's length; Bergmann's rule; drought adaptation hypothesis; seasonality hypothesis

体形作为生物体的基本性状,与物种的空间利用、寿命及繁殖力等关键生活史特征密切相关^[1-2],进而影响种间互动,乃至生态网络动态^[3]。在自然生境中,蚂蚁等昆虫群落体形大小对区域气候的响应非常灵敏。地理演变模式往往遵循贝格曼法则(Bergmann's rule)(物种在较为寒冷的环境中通常具有更大的体形)^[4-5]、干旱适应假说(drought adaptation hypothesis)(个体在干旱环境中体形趋于更大以减少水分散失并储存更多脂肪)^[6-7]和季节性假说(seasonality hypothesis)(在季节性强的栖息地,较小的物种能够更快完成繁殖周期,从而避开不宜生长的季节,并占据优势)^[8-9]。

城市化是全球变化的主要形式之一,能够快速改造自然景观,并形成独特的微生境。例如,城市热岛效应使城市环境的平均温度明显高于周边自然区域^[10];园艺活动和人工灌溉则增加了城市绿地湿度^[11];树冠层覆盖减少与不透水表面(如沥青、混凝土)扩张,使城市景观的平均环境温度及波动显著高于农村或自然区域^[12]。城市景观对昆虫群落功能性状往往也具有显著影响^[13-14]。例如,在高城市化水平、强热岛效应和高地表温度环境中,城市蜘蛛群落体形更小^[15]。在气候变化与城市化的交互作用下,城市动物群落性状的生态响应机制可能更为复杂^[16-17]。我们之前的研究发现,西南山地城市蚂蚁群落体色性状对区域气候的响应可能还受到其他城市环境因素的调节^[18]。

蚂蚁(Hymenoptera: Formicidae)是在大多数陆地生态系统中占主导地位的动物类群。通过捕食和竞争等形式,蚂蚁参与了多种关键生态过程,包括种子传播、害虫控制、食腐/分解、土壤生物扰动以及无脊椎动物群落结构的塑造,具有重要的生态服务功能^[19]。现有文献往往聚焦于蚂蚁群落体形大小在自然生境的地理变异模式。其中,不同研究对贝格曼法则的支持程度并不一致:一些较大空间尺度的研究发现,在月均温较低或纬度较高的地区,蚂蚁群落体形较大^[4,20];在意大利阿尔卑斯山南部^[21]和美国大烟山^[22]开展的区域性研究则发现,蚂蚁群落体形大小与气温、海拔或纬度未呈显著性差异;此外,在北美地区,蚁属(*Formica*)的体形大小随气温升高而增大^[23]。虽然干旱适应假说缺乏大空间尺度的证据,但得到了一些区域性研究的支持:例如,在美国佛罗里达州^[24]和巴拿马巴洛·科罗拉多岛^[6],冠层和地栖蚂蚁的抗干旱能力均随体重增加而增加;入侵至美国加州的阿根廷蚁(*Linepithema humile*)在干旱环境中也呈现出体形大小越大、个体生存能力越强的趋势^[25]。蚂蚁研究领域尚缺乏支持季节性假说的证据,但提供了反证:在地中海西南部,较高气温季节性区域的蚂蚁群落具有更大的体形^[26]。

蚂蚁在城市中依然具有较高的多样性和生物量,且易于采集,是研究城市生物群落生态响应的理想对象^[27]。本研究旨在基于在较大空间尺度上的采样,检验城市蚂蚁群落体形大小对区域气候的生态响应,即贝

格曼法则、干旱适应假说和季节性假说对城市蚂蚁群落体形大小地理变异的解释有效性。

1 材料与方法

1.1 研究区域

我们选取西南山地 8 个县级行政区(绥江县、平武县、元谋县、九寨沟县、永仁县、玉龙纳西族自治县、康定市和甘孜县)的县级政府所在城镇为研究区域。城镇间,平均地理距离为 473 km,最短为 44 km(永仁县至元谋县),最长为 870 km(九寨沟县至元谋县)。上述城镇大多地处山间盆地或河谷地带,具有面积小和带状延伸的特点。

根据中华人民共和国国家标准《中国气候区划名称与代码 气候带和气候大区》(GB/T17297—1998),8 个城镇分属 5 个气候带 6 个气候大区:暖温带湿润型气候大区(玉龙县)、南亚热带湿润型气候大区(绥江县、元谋县)、北亚热带湿润型气候大区(平武县、永仁县)、高原亚寒带湿润型气候大区(九寨沟县)、高原亚寒带亚湿润型气候大区(甘孜县)和高原温带亚湿润气候大区(康定市)。我们在每个城市设置 8 个样地。城市内样地平均间距约 2 km。我们从 WorldClim 数据集获取 1970—2000 年间的每个样地的年平均气温(BIO1)、年降水量(BIO12)、气温季节性(BIO4)和降水季节性(BIO15)。所有气候变量以 2.5 弧分的分辨率在 ArcMap 10.8 中提取。经共线性检验,这四个气候因子的方差膨胀因子(VIF)小于 3。

1.2 样品采集

在 2021 和 2022 年夏季,我们运用陷阱法在上述城市共计 64 个样地采集觅食工蚁^[18,28]。为提高采样代表性,我们在城镇内及边缘地带的草地(9 个样地)、次生林地(16 个)、非集约化小型农田(13 个)及人造休闲公园(26 个)四种土地利用类型设置样地。每个样地设置了 16 个陷阱,按照 4×4 阵列布局,相邻陷阱间隔 10 m。每个陷阱由两个堆叠的塑料杯(直径 4.5 cm、容量 250 mL)组成。陷阱内装有 150 mL 丙二醇溶液用于捕杀和保存觅食工蚁。陷阱上方设置塑料顶棚减少丙二醇蒸发和雨水渗入。陷阱在野外放置 6 d。采样期间,存在陷阱被人类活动损坏的情形。为确保数据一致性,从每个样地随机选取 12 个陷阱的标本,用于后续研究。徐正会教授(西南林业大学)和冉浩先生(蚂蚁专家)提供了鉴定指导。除了 103 个蚂蚁标本因严重损坏无法鉴定未纳入分析,其余 55890 只工蚁标本分属 5 亚科、31 属和 81 个物种^[28]。标本用 75%乙醇溶液保存,存放于西华师范大学。

1.3 体形大小测量

每个物种最多选取 6 只工蚁用于测量,若不足 6 只则测量全部个体^[29]。选取标本时,采用两个原则:1) 每个物种的标本尽量来自更多的样地;2) 对于二型或多型工蚁种群,优先测量在种群中占数量优势的小体形工蚁。共测量 81 个物种 442 只工蚁。选择韦伯氏长度(Weber's length)作为反映体形大小的指标,其定义为从前胸背板前背缘到前腹节后腹缘的距离^[29—30]。使用 Leica M205C 体视显微镜和 Leica Application Suite 图像分析软件进行测量,精度达到 1.0—1.5 μm 。所有测量均由同一研究人员完成。我们采用群落加权平均指数(community weighted means, CWM)表征随机从群落中抽取一个个体的期望值;鉴于(1)采样方式和蚂蚁巢穴与陷阱的空间关系可能会影响到各物种的相对多度信息,(2)不同城市间可能存在较高度度的物种更替,(3)不同蚂蚁物种间单个繁殖群的个体数可能存在巨大差异,我们还采用无加权的群落算数平均值(community means, CM)反映特定体形大小性状物种殖民或灭绝对群落体形大小性状的影响^[18]。

1.4 数据分析

Shapiro-Wilk 正态性检验和 Levene's 方差齐性检验表明,CWM 和 CM 符合正态分布且满足方差齐性假设。运用单因素方差分析(One-Way ANOVA)检验城镇间 CWM 和 CM 的差异显著性,然后采用 Tukey's HSD 检验进行多重比较。为评估气候因素对蚂蚁体形大小的影响,将 CWM 和 CM 作为因变量,分别构建线性混合效应模型(Linear mixed model, LMM)。其中,气候因子(BIO1、BIO12、BIO4 和 BIO15)作为固定效应,城镇作为随机效应。模型选择基于赤池信息准则(Akaike Information Criterion, AICc),其中 AICc 值最小的模型被

视为最适模型。通过 Type III Wald 卡方检验评估气候变量的显著性,显著性水平设定为 0.05。数据分析在 R 4.2.3 中完成。

2 结果

在 64 个样地中,共记录到 81 种蚂蚁,体长范围从 45.15 μm (中华小家蚁 *Monomorium chinense*) 至 381.51 μm (山大齿猛蚁 *Odontomachus monticola*)。不同城镇间,CWM 和 CM 均存在显著差异(CWM: $F=17.43$, $P<0.001$; CM: $F=15.72$, $P<0.001$)。有 5 个城镇(平武县、玉龙县、康定市、甘孜县及九寨沟县)的 CWM 或 CM 显著高于元谋县($P<0.001$);有 6 个城镇(绥江县、平武县、元谋县、永仁县、玉龙县、甘孜县)的 CWM 或 CM 显著低于康定市($P<0.001$) (图 1)。8 个城镇中,元谋县的区域气温最高(BIO1 为 21.41 $^{\circ}\text{C}$),而康定市最低(5.81 $^{\circ}\text{C}$);绥江县的区域降水量最高(BIO12 为 1156 mm),而九寨沟县

最低(626 mm);九寨沟县的气温季节性最高(BIO4 为 745.92 $^{\circ}\text{C}$),而元谋县最低(456.86 $^{\circ}\text{C}$);平武县的降水季节性最高(BIO15 96.63 mm),而玉龙县最低(62.76 mm)。

解释 CWM ($\text{AICc} = 599.11$, $R^2_m = 0.59$) 和 CM ($\text{AICc} = 572.35$, $R^2_m = 0.59$) 变异的最适模型都包含气候因子 BIO1 (表 1)。BIO1 对 CWM 和 CM 具有显著影响($P<0.001$),而 BIO4 对 CM 具有显著影响($P=0.04$) (表 2)。在 BIO1 更高的城镇,CWM 和 CM 更小;在 BIO4 更高的城镇,CM 更大(图 2);CWM 和 CM 没有随着 BIO12 和 BIO15 发生显著的趋势性变化(图 2)。

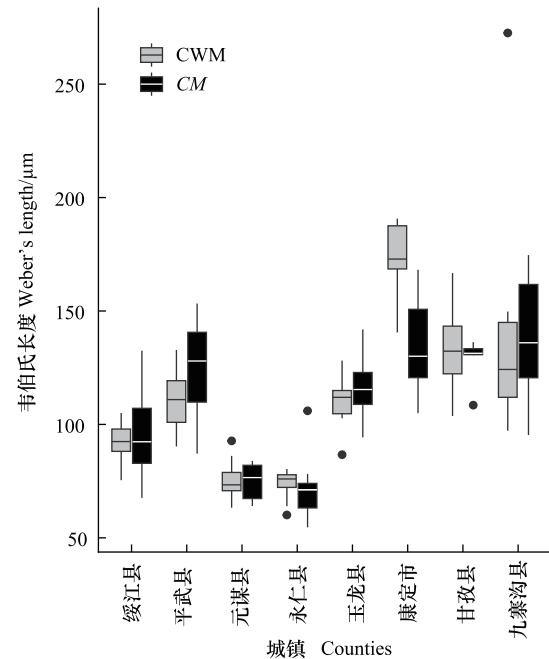


图 1 城镇间蚂蚁群落韦伯氏长度的比较

Fig.1 Comparison of Weber's length of ant communities across counties

通过 Tukey's HSD 检验比较了各城镇间蚂蚁群落体形大小的显著差异;按照字母标记法,采用大小写字母分别标注 CWM 和 CM 的显著差异 ($P<0.05$);CWM: 群落加权平均值 community-weighted mean;CM: 群落算数平均值 community mean

表 1 线性混合效应模型拟合结果对比

Table 1 Comparison of linear mixed models fitting results

类型 Type	模型 Model	自由度 <i>d.f.</i>	最大对数似然 LL	与最适模型的 AICc 差值 ΔAICc	边际 R^2 R^2_m	条件 R^2 R^2_c
群落加权平均值 Community weighted mean (CWM)	~BIO1	4	-292.15	0	0.59	0.64
	~BIO1+BIO4	5	-294.24	2.64	0.58	0.65
	~BIO1+BIO15	5	-292.02	2.65	0.58	0.65
	~BIO1+BIO12	5	-294.76	2.72	0.58	0.64
群落算数平均值 Community mean (CM)	~BIO1+BIO4+BIO15	6	-279.33	0	0.59	0.65
	~BIO1+BIO4	5	-280.18	0.07	0.57	0.65
	~BIO1	4	-279.06	0.66	0.54	0.65
	~BIO1+BIO12+BIO4+BIO15	7	-281.53	1.44	0.60	0.65
	~BIO1+BIO15	5	-278.74	2.76	0.53	0.66

在 CWM 和 CM 的构建模型 ($\Delta\text{AICc}<3$) 中,解释变量包括 BIO1:年平均气温 annual average temperature;BIO12:年降水量 annual precipitation;BIO4:气温季节性 temperature seasonality;BIO15:降水季节性 precipitation seasonality。*d.f.*: 自由度 the degree of freedom;LL: 最大对数似然 maximum log-likelihood; ΔAICc : 与最适模型的 AICc 差值 difference in AICc between models; R^2_m : 边际 R^2 Marginal R^2 ; R^2_c : 条件 R^2 Conditional R^2 ; R^2_m 表示由固定效应解释的变异性, R^2_c 表示由固定效应和随机效应共同解释的变异性

表 2 最适模型的 Type III Wald 卡方检验结果

Table 2 Results of Type III Wald chi-square tests for the best-fitting models

类型 Type	变量 Variable	检验统计量 χ^2	自由度 <i>d.f.</i>	显著性 <i>P</i>
群落加权平均值 Community weighted mean (CWM)	BIO1	48.51	1	<0.001
群落算数平均值 Community mean (CM)	BIO1	18.04	1	<0.001
	BIO4	4.42	1	0.04
	BIO15	2.03	1	0.15

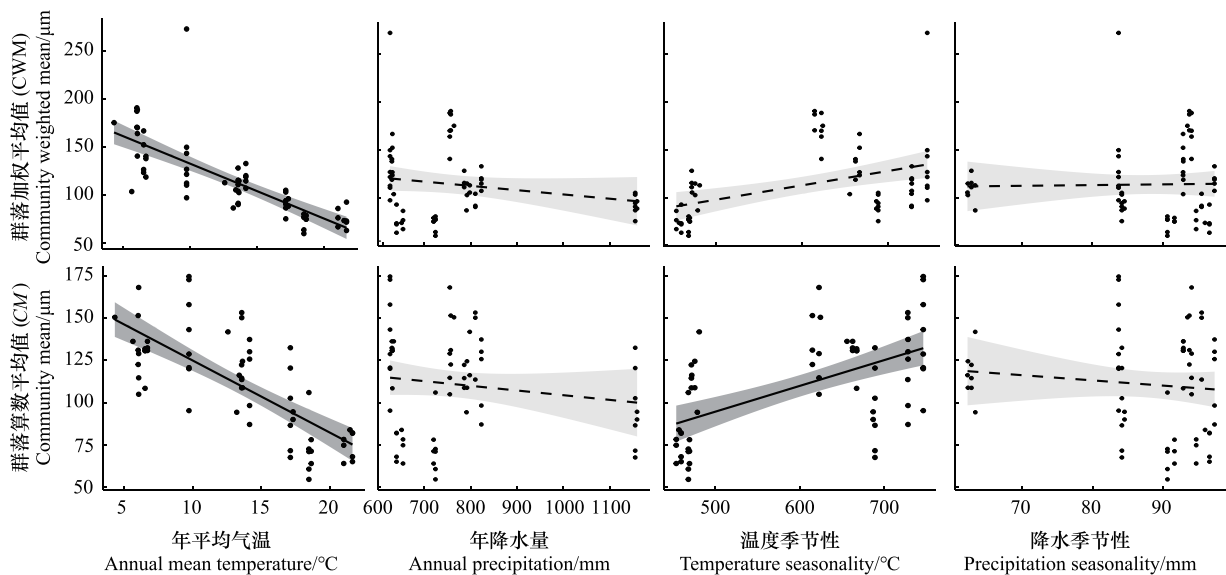
 χ^2 : 检验统计量 Test statistics

图 2 城市蚂蚁群落体形大小 CWM/CM 与年平均气温/年降水量/气温季节性/降水季节性之间的关系

Fig.2 Scatter plot shows the relationship between body size CWM/CM of urban ant community and region climate conditions

灰色区域表示平滑线的 95% 置信区间

3 讨论

本研究揭示了西南山地城市蚂蚁群落体形大小的地理变异及其对区域气候的生态响应。研究表明:区域气温越高,城市蚂蚁群落体形更小,与贝格曼法则相符;区域降水对蚂

蚁群落体形大小没有显著影响,不符合干旱适应假说;区域温度季节性越强,蚂蚁群落体形大小更大,而区域降水季节性对蚂蚁群落体形大小没有显著影响,不符合季节性假说。因此,西南山地的城市蚂蚁群落体形大小性状对区域气温变化存在敏感的生态响应,但其对区域降水和季节性的响应模式可能受到城市中其它因素的调节。

3.1 区域气温对城市蚂蚁群落体形大小的影响

西南山地城市蚂蚁群落的地理变异模式符合贝格曼法则。根据贝格曼法则,工蚁在较高的环境温度下会增加发育过程中的代谢成本,因此体形较小^[4]。虽然大多数鸟类和哺乳动物都符合贝格曼法则^[31],而对外温动物的研究结果则并不一致:蜥蜴、蛇、陆生龟类和北极无脊椎动物大多表现出反贝格曼法则或非线性模式(U形或驼峰形)^[32-33]。先前关于节肢动物体形大小随纬度变异的文献综述指出,有 19 个物种支持贝格曼法则,有 29 个物种表现为反贝格曼法则^[34]。一些大空间尺度的蚂蚁群落研究证实,在自然生境中,寒冷地区的蚂蚁群落体形比温暖地区的更大^[20,35]。本研究的采样点位于山间盆地和河谷地带的小型带状城市,可能受

人为热干扰的影响较小^[18]。大型城市则往往会形成强烈的热岛效应,导致城市局部温度显著升高,进而影响昆虫群落的体形大小^[36-37];例如,大型蚤(*Daphnia magna*)在城市热岛效应形成的高温环境中体形变小,表现出显著的耐热性进化特征^[38]。

3.2 区域降水对城市蚂蚁群落体形大小的影响

西南山地城市蚂蚁群落的地理变异未体现出干旱适应假说的模式。根据干旱适应假说,较大体形昆虫因为表面积体积比较小、储水能力更强以及脂肪储备更丰富,具有更强的抗旱能力^[6]。体壁失水是节肢动物外排水分的重要途径^[39]。体形较小的生物,包括大多数昆虫(<70克),其失水率往往高于代谢率^[40]。相应地,较小体形的蚂蚁可能比较大体形蚂蚁更易死于脱水^[6,24]。有趣的是,新近一项研究发现,可能由于较大体形个体的营养级较高,且运动更依赖土壤颗粒周围较厚的水膜,土壤线虫的体形大小在群落、种群和个体层面均会随干旱胁迫而减小^[41]。与自然生境不同,人类活动和设施能够改变城市区域水循环,进而影响城市昆虫群落的生态响应^[42]。例如,在一些沙漠城市中,因为灌溉的影响,人造休闲公园中蚂蚁群落物种丰富度显著高于城市外的沙漠区域^[37]。因此,城市蚂蚁群落所实际响应的水分条件可能更多来源于灌溉、排水等人为干预所塑造的微环境,而非大空间尺度的年降雨量指标。后续工作还需要收集局部湿度等环境变量,在更精细的尺度上来进一步检验。

3.3 季节性对城市蚂蚁群落体形大小的影响

西南山地城市蚂蚁群落的地理变异未体现出季节性假说的模式。根据季节性假说,在强季节性地区,体形较小物种具有较短的繁殖周期,可以缓解食物和水资源匮乏季节的负面影响,从而在群落中占据优势^[9]。然而,较大体形的动物具有更高的能量利用效率,有助于抵御季节性所导致的极端气候和资源短缺的风险^[43]。例如,一种细胸蚁(*Leptothorax acervorum*)的北极种群比中欧种群体形大10%(未出现细胞生长缓慢或细胞体积增大的现象),并且能在食物匮乏时存活更长时间^[44]。目前,关于季节性对物种更替以及体形大小等功能性状更替的影响,人们了解甚少^[45]。季节性可能通过影响资源可用性来影响物种和功能更替^[46-47]。因此,后续研究需结合物种生活史和城市资源可获得性,进一步探究西南山地城市蚂蚁群落的体形大小对季节变化的生态响应机制。

3.4 其他因素对城市蚂蚁群落体形大小的潜在影响

城市蚂蚁的体形大小还受大气CO₂、基质、土壤粒度和食物资源等多种环境因素影响。大气CO₂浓度上升可能会间接影响蚂蚁的营养来源(改变植物生长模式及其化学组成,如碳氮比),进而作用于其体形和发育^[48]。根据“体形—基质假说”(size—grain hypothesis),较小体形的个体在复杂生境中更有可能受益,而较大体形的个体更有可能在简单生境中受益^[49]。例如,哥斯达黎加拉的一项实验表明,生活在枯叶覆盖的复杂生境中的蚂蚁比生活在没有枯叶覆盖的简单生境个体体形小40%^[50]。土壤粒度的影响可能会对不同体形大小的蚂蚁产生筛选作用:沙质土(保水能力较低)更适宜大体形、抗旱性强的物种^[51],而黏土环境则有利于小体形物种^[52]。此外,城市环境中高蛋白食物(如人类废弃物、昆虫残骸)的富集也可能影响蚂蚁体形大小^[27]。例如,相比城郊森林种群,台中市城区的褐大头蚁(*Pheidole megacephala*)种群具有更高的 $\delta^{15}\text{N}$ 值和更大的体形^[53]。在后续研究还需要扩大样本量并将更多人为因素纳入考量,从而更细致地评估城市蚂蚁群落体形大小对不同环境因素的生态响应。

4 结论

探究动物群落性状在城市生境中的生态响应机制仍然面临诸多问题,例如人为干扰因素的复杂交互作用、物种替代和种内分异对群落性状水平变化的相对贡献以及微生境的生态效应等。然而,全面且深入地量化解析这些问题对研究设计和样本量有更高的要求。检验经典假说在城市蚂蚁群落中的适用性,有助于快速评估城市生境对动物群落性状地理变异的调节作用,并为后续的城市生态学研究提供线索。

全球环境变化的两大核心驱动力—气候变化与城市化,深刻影响昆虫群落在时间和空间上的动态变

化^[48]。部分物种凭借较强适应性在城市生态系统中占据优势,而另一些物种则因环境压力加剧而面临种群衰退甚至局部灭绝风险。这种分异可能导致昆虫群落功能性状显著改变^[14],进而对生态系统的结构与功能产生深远影响^[54]。除气候变化外,城市昆虫群落还受到热岛效应、栖息地片段化及污染等多重胁迫,其适应机制更为复杂。相比区域气候,城市微生境可以更直接地决定蚂蚁的适应性^[55]。因此,揭示城市昆虫群落的生态响应规律,不仅有助于预测未来城市生物多样性演变趋势,还能为城市绿地规划与生态修复提供理论支撑。此外,开展城市动物群落生态响应研究对提升城市生态系统的韧性、优化其生态服务功能,以及应对全球气候变化与快速城市化的双重挑战具有重要的实践意义。

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