

# Flying to greener pastures: Spider ballooning in the city

Marcela Montes<sup>1</sup>  | Raquel M. Gleiser<sup>1,2</sup> 

<sup>1</sup>Centro de Relevamiento y Evaluación de Recursos Agrícolas y Naturales (CREAN), Universidad Nacional de Córdoba (UNC)–CONICET, Instituto Multidisciplinario de Biología Vegetal (IMBIV), Córdoba, Argentina

<sup>2</sup>Departamento de Diversidad Biológica y Ecología, Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Córdoba, Córdoba, Argentina

## Correspondence

Marcela Montes and Raquel M. Gleiser, Centro de Relevamiento y Evaluación de Recursos Agrícolas y Naturales (CREAN), Universidad Nacional de Córdoba (UNC)–CONICET, Instituto Multidisciplinario de Biología Vegetal (IMBIV), Av. Valparaíso S/ N. CC 509, 5000 Córdoba, Argentina. Email: [marcelamontes@gmail.com](mailto:marcelamontes@gmail.com) and [raquel.gleiser@unc.edu.ar](mailto:raquel.gleiser@unc.edu.ar)

## Funding information

Agencia Nacional de Promoción Científica y Tecnológica, Grant/Award Number: PICT-2021-GRFTI-00453; Consejo Nacional de Investigaciones Científicas y Técnicas, Grant/Award Number: 11220200102991CO; Secretaría de Ciencia y Tecnología - Universidad Nacional de Córdoba, Grant/Award Number: 33620180100302CB

Associate Editor: Charles Fox

## Abstract

- Spider ballooning is a phenomenon in which spiders employ silk threads to travel through the air for dispersal. While this behaviour has been extensively studied in agricultural areas, limited research has been conducted in urban environments, where green spaces are highly fragmented. However, in cities, aerial dispersal can be advantageous for spiders as it allows them to move to suitable habitat patches. This study aimed to investigate how the urban landscape affects spider ballooning.
- We collected ballooning spider samples using sticky traps in 10 urban sites within different landscape contexts. By using generalised linear models, we analysed the influence of vegetation cover at both local and landscape scales on spider abundance and family richness.
- Family composition was similar across the city regardless of the landscape context.
- More individuals were collected dispersing aerially in areas with low landscape-level green cover. However, a higher local percentage of vegetation cover led to a substantial increase in aerial dispersal in areas with high landscape-level green cover. Our findings highlight the significance of the interaction between vegetation cover at these two scales on aerial spider abundance.
- Our results support the hypothesis that generalist spiders exhibit increased ballooning in highly fragmented landscapes, actively seeking suitable habitats despite the elevated associated risk. Higher aerial dispersal in areas with greater local vegetation cover suggests an increase in short-distance dispersal, indicating spiders' active search for better habitats nearby upon arrival at a site with potentially greater habitat availability.

## KEYWORDS

aerial dispersal, Araneae, urban

## INTRODUCTION

Animal dispersal is a fundamental ecological process that plays a key role in shaping species distributions and maintaining biodiversity. Dispersal can be defined as any movement of individuals or propagules with potential consequences on gene flow and population dynamics (Ronce, 2007). Many species of spiders have the ability to disperse passively through the air, using silk threads (Bell et al., 2005). This behaviour, called 'ballooning', is generally performed by juveniles, but also regularly by adults in certain small species.

The dispersal ability of different species is associated with their habitat preferences and landscape configuration (Bonte et al., 2006, 2010; Bonte, Vandenbroecke, et al., 2003). In addition, these abilities may also vary between individuals of the same species depending on their genetic composition (Bonte, Deblauwe, & Maelfait, 2003), thermal conditions during juvenile development (Bonte, Deblauwe, & Maelfait, 2003; Bonte, Travis, et al., 2008), habitat disturbance (Entling et al., 2011), food stress (Bonte, Lukáč, & Lens, 2008; Mestre & Bonte, 2012) and conspecific cues (de Meester & Bonte, 2010). In all cases, ballooning can be effective only if weather conditions are suitable for take-off (Reynolds et al., 2007).

Ballooning allows spiders to travel long distances and colonise new, sometimes isolated habitats. Although the propensity for take-off or latency of pre-ballooning behaviour in spiders is influenced by several factors and environmental conditions (see references above), the airborne phase of aerial dispersal is passive, with dispersing individuals having little to no control over flight direction (but see Suter, 1992, 1999). This is why ballooning dispersal is often described as a 'wind lottery' during the airborne phase, preceded by individual-based risk assessment (Bonte, Lukáč, & Lens, 2008; Suter, 1999).

Generalists adapted to disturbed habitats appear to have a higher dispersal propensity than specialists occupying stable habitats (Blandenier et al., 2013; Entling et al., 2011). In highly fragmented environments, suitable habitats for specialist spiders constitute patches in a sometimes inhospitable matrix, and aerial dispersal may result in landing on habitat unsuitable for the species. For eurytopic species that are able to survive in many habitat types, the cost of ballooning is lower than for specialised species (Bonte, Vandenbroecke, et al., 2003). Bonte, Vandenbroecke, et al. (2003) conducted experiments in 29 species of grey dune spiders from seven families (Lycosidae, Linyphiidae, Thomisidae, Araneidae, Tetragnathidae, Gnaphosidae and Dictynidae), each exhibiting varying degrees of habitat specialisation. Their findings indicated that dispersal propensity is selected as being risk spreading in generalist species, while it is selected against in specialist species.

Urbanisation can have a significant impact on spider populations, as it often leads to habitat fragmentation and loss, as well as changes in temperature and humidity and various other environmental factors (Chapman et al., 2017; Gibb & Hochuli, 2002; Parris, 2016). As a result, the ability of spiders to disperse aerially and colonise new areas may be critical for maintaining spider diversity in urban environments. In urban landscapes, green spaces are often distanced and frequently separated by structures such as buildings, which can limit the movement of organisms (Davy et al., 2017), even those with aerial dispersal capabilities (Peralta et al., 2011).

Two opposite processes would be acting in cities. On the one hand, fragmentation selecting against dispersal and favouring the most dispersive species, because it may involve crossing non-habitat (built/impervious) zones, which could be inhospitable or present barriers for movement. On the other hand, turnover further selects fast and good dispersers that are bad competitors (generalists) due to sub-optimal adaptation to the local habitat. As generalists are able to survive in multiple habitat types, the cost of ballooning is certainly lower than for specialised species, and a well-developed ballooning behaviour is evolutionarily favoured. In other words, in urban environments where habitats can be dynamic and subject to frequent changes, species with good dispersal abilities may have an advantage. In this dynamic, selective pressures simultaneously act to limit and promote specific traits among spider populations. Like it is suggested for agricultural spiders (Bell et al., 2005), urban spiders might exhibit random behaviour to enhance adaptability in unpredictable settings. Weyman et al. (2002) proposed a bet-hedging strategy, where the likelihood of initiating ballooning behaviour and the duration of its occurrence are influenced by fluctuating levels of environmental stress (food

availability, patch dynamics, and habitat predictability or other environmental elements perceived by the individual).

While aerial dispersal poses risks, it may be of great advantage to spiders, as it allows them to recolonize managed urban green spaces (Nagy et al., 2018). Theoretically, even in spaces with regular disturbance caused by intensive urban green space management (i.e., lawn mowing), rapid recolonization of spiders from surrounding habitats would be possible. Aerial dispersal could be an important colonisation mechanism of isolated habitats in the city like parks, gardens or green roofs (Vergnes et al., 2017).

Ballooning has been studied mainly in agricultural environments (e.g., Blandenier, 2009; Entling et al., 2011; Hogg & Daane, 2018), grasslands (Bonte, Vandenbroecke, et al., 2003; Morse, 1993) and forests (Bishop, 1990; Larrivé & Buddle, 2011). Very little work has addressed this behaviour in urban environments (e.g., Lagucki et al., 2017; Vergnes et al., 2017), so an exploration of aerial dispersal in these systems is novel. An additional geographical bias is evident within the existing literature concerning ballooning behaviour, particularly focusing on Europe and the United States, with a notable scarcity of studies conducted in the Southern Hemisphere. For example, to the best of our knowledge, the only work on this field in Argentina is Piacentini et al. (2021), describing a forced massive dispersal event of mostly Lycosidae after a flood in a riparian habitat. Conducting additional studies in habitats and geographical regions where ballooning has not been extensively studied may reveal variations in spider ballooning patterns, and eventually aid in differencing context-dependent from general patterns. Calls have been made from different disciplines to reduce the geographic bias that inhibits a balanced understanding of ecological phenomena (Buchholz & Egerer, 2020; Culumber et al., 2019; Pyšek et al., 2008).

Despite its potential relevance for urban spider diversity, spider aerial dispersal has received relatively little attention in urban ecology research. In this study, we attempted to explore the effect of the urban landscape on spider ballooning. We expect that in urban areas, where species are mainly generalists (Kotze et al., 2011), spiders will risk an unsuccessful dispersion to find a suitable habitat. In sites with lower habitat availability (i.e., more fragmented habitat), spiders will balloon more, actively seeking better living conditions. Thus, we expect to find a higher number of spiders, from a lower taxonomic diversity, dispersing aerially in sites with a low percentage of green cover (higher habitat fragmentation) compared with sites with higher green coverage.

## MATERIALS AND METHODS

### Sampling sites and area of study

The study was carried out in Córdoba city (31°25'S 64°11'W), Córdoba province (Argentina). The city elevation at sea level ranges between 352 m (towards the east) and 544 m (towards the south-west) and it belongs to the Espinal ecoregion (Brown et al., 2006). The current climate of Córdoba is subhumid and temperate, with dry winters (Peel et al., 2007).

To detect more clearly the differences in the diversity of spiders dispersing aerially, we selected sites that represented contrasting landscape contexts in the city. To choose these sites, we used a publicly available map created by Infraestructura de Datos Espaciales de Córdoba (IDECOR) that depicts the land cover of Córdoba using five classification categories (details in *Local and landscape characterization*). We created a 500 m buffer around each of 100 randomly distributed points in the city (1000 m apart from each other) using QGIS 3.22 and then extracted the land cover data for each buffer. Finally, we obtained the percentage of green cover for the 500 m buffer area surrounding each site. Since these 100 points are a sample representing the city, the 30th and 70th percentiles were used to select 10 ( $n = 10$ ) sites with low and high vegetation cover, respectively (Figure 1). The vegetation cover of sites 1–5 does not exceed 17% (30th percentile), whereas the percentage of vegetation of sites 6–10 was above 41% (70th percentile). A minimum number of sites were selected to optimise cost and logistics, without losing the representativeness of the samples. We opted for easily accessible sites that could be checked regularly, mostly private gardens. We did not sample in public green spaces due to the risk of vandalism.

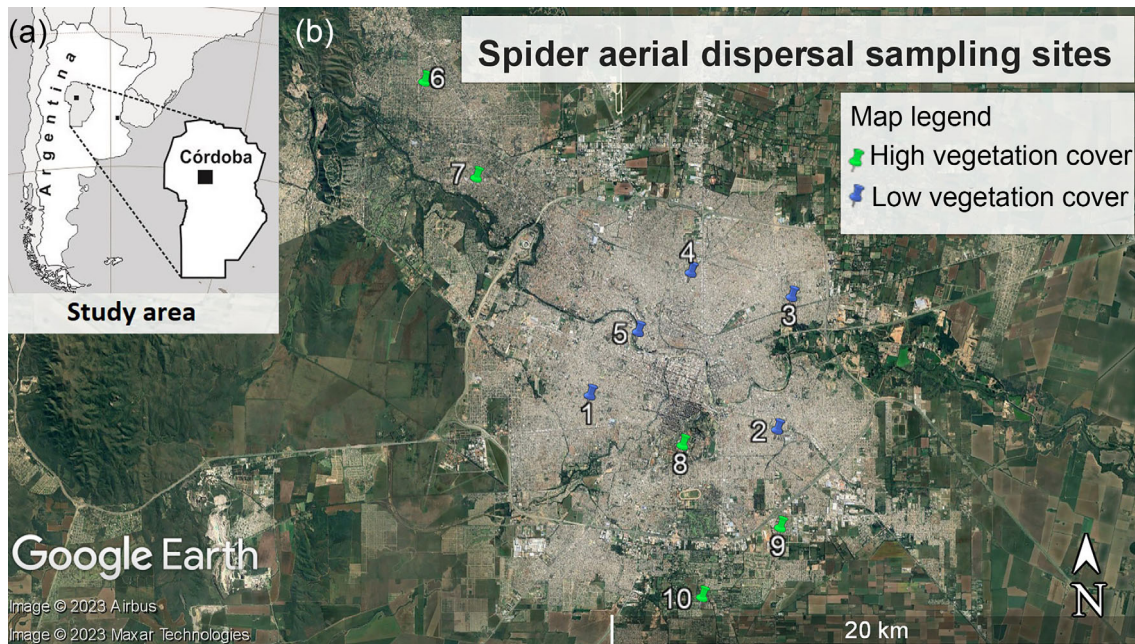
### Spider sampling method and identification

Spider aerial dispersal was sampled in autumn (April–May) and spring (September) 2022 and summer (February) 2023. We placed one sticky trap per site, at similar heights of approximately 1.5–2 m above ground level, mostly from trees (except site 2, which was approximately 5–6 m away from the closest tree). The trap consisted of a hanging corrugated plastic roof, attached to three 42.7 cm long

× 24.3 cm wide sticky plates (Figure 2). Each trap remained exposed for 1 month each season and was checked for spiders once per fortnight. Because most dispersal events occur at relatively low densities,



**FIGURE 2** Hanging sticky trap used in each sampling site.



**FIGURE 1** (a) Study area: Córdoba city, Córdoba province, Argentina. (b) Location of sampling sites in the city. Sites 1–5 represent sites surrounded by low vegetation cover, and 6–10 represent sites surrounded by high vegetation cover at a landscape scale (buffer 500 m).



on the order of hundreds to a single individual per 1000 m<sup>3</sup> (Greenstone et al., 1991), and because it is highly likely that densities are even lower in an urban context, a large sampling effort is necessary to obtain a statistically reasonable number of individuals. For this reason, cumulative data from each trap was used and sampling was carried out over 3 months.

Collected spiders were preserved in 70% alcohol and identified based on morphological characters at the lowest possible taxonomic level using keys (Grismado et al., 2014), specific descriptions and comparisons with laboratory reference material. Because it is generally the juveniles that perform ballooning behaviour, individuals were identified to family level and assigned into genus or morphospecies when possible. For data analysis, only family richness was used to avoid an under or overestimation of species richness, as species determination in juveniles based on morphological characteristics is usually not reliable.

## Local and landscape characterisation

To characterise each site landscape context, we used the publicly available map of urban fragmentation 2021-ongoing (<https://mapascordoba.gob.ar/viewer/#/mapa/383>), made by IDECOR. The metadata describing the creation process can also be found online ([https://obs-idecor-lib.obs.sa-argentina-1.myhuaweicloud.com/Documentos/METADATOS\\_MAPA\\_FRAGMENTACION.pdf](https://obs-idecor-lib.obs.sa-argentina-1.myhuaweicloud.com/Documentos/METADATOS_MAPA_FRAGMENTACION.pdf), last accessed Dec 2023). Briefly, the map was produced using Sentinel 2 images (interval 1 October 2019 to 30 April 2020, resolution 10 m) and processed using Google Earth Engine and QGIS (EPSG:22174, POSGAR 98 and ARGENTINA 4). It classifies the urban landscape into five cover classes, but our study specifically centred on one, the urbanised open spaces (UOS), since we were interested in how the percentage of green cover surrounding sampling sites influenced ballooning spider diversity. The percentages of UOS were extracted for each site from a 50 m buffer (local level cover) and a 500 m buffer (landscape level cover).

It is relevant to mention that, as pixel size is 100 m<sup>2</sup>, courtyards and gardens smaller than this size, which may be suitable habitat for certain spiders, may not have been detected in the classification. To avoid repeating the information, we subtracted the pixels of the 50 m buffer from the 500 m buffer. UOS showed different patterns at both scales, which was reflected in their effects on ballooning spider abundance. We also checked for multicollinearity in the models and verified that they were not correlated (described below).

## Statistical analysis

### Spider diversity estimates

We determined the number of individuals (abundance), families (family richness), and the composition of spider assemblages of each trap. We estimated sample coverage (C, Chao & Jost, 2012), and the coefficient of variation (CV, Chao & Chiu, 2016) for both families and

morphospecies, using the total of ballooning spiders collected. We also calculated an abundance-based coverage estimator (ACE) to estimate the number of families and morphospecies expected for a given number of individuals collected (software SpadeR, Chao et al., 2015). The sample coverage (C) estimated the completeness of the sample, whereas the CV characterised the degree of heterogeneity among families and morphospecies discovery probabilities. Additionally, we checked if numbers of specimens captured differed between seasons using a Chi-square test. For descriptive purposes, we also evaluated seasonal family turnover, calculating the Bray-Curtis index (BCi).

## Local and landscape analysis

We used generalised linear models (GLMs) to test the effect of landscape and local green cover, on ballooning spider abundance and family richness. Furthermore, we also considered the possible interactions between the independent variables. We expected that landscape green cover (UOS\_500 m) and local green cover (UOS\_50 m) would interact. Table 1 describes our working hypotheses for each included variable.

Models were fitted using the package MASS in R 4.1.3. Using AICc and residual deviance on degrees of freedom, we checked for the error distribution that would best fit our count data; for both abundance and family richness, the data were not overdispersed and the Poisson distribution was appropriate. We tried all possible independent variable combinations, to find the best statistical model that minimised AICc but also aligned with our biological hypothesis (Table 1). We checked for multicollinearity in our models by

**TABLE 1** Hypothesis tested using generalised linear models and their respective independent variables (IV) selected.

IV	Hypothesis	Brief description
UOS50 m	Habitat availability at a local scale affects local spider dispersal by ballooning	Percentage of green cover of a 50 m buffer surrounding each site
UOS500 m	Habitat availability at landscape scale affects spider dispersal by ballooning	Percentage of green cover of a 500 m buffer surrounding each site, minus the 50 m buffer.
UOS50 m: UOS500 m	Habitat availability at different spatial scales can interact, resulting in a different effect on the aerial dispersal of spiders than that caused by each scale alone.	Interaction between the percentage of green cover of the two spatial scales.

calculating the variance inflation factor (VIF) using the `vif()` function from the `car` package in R. Best-fitting models were selected using a  $\Delta AICc < 2.0$  criteria. Including the null model, we created eight GLMs for both variables (Tables 4 and 5).

## Assemblage composition

Landscape effects on the family composition of ballooning spider assemblages were tested with PERMANOVA (BCi). Sample size adequacy was checked using a pseudo multivariate dissimilarity-based standard error analysis (MultSE, Anderson & Santanta-Garcon, 2015; R 4.1.3) Since we selected our sites with contrasting landscape and/or local contexts, for each spatial scale we used two categories: 'Low vegetation cover' and 'High vegetation cover'.

## RESULTS

### Spider diversity

We collected a total of 202 spiders, of which 200 belonged to 14 families (Table 2 and Supplementary Material S1). Overall, the most abundant families were Thomisidae (19%), Linyphiidae (14.5%), Dictynidae (14.5%), Anyphaenidae (13%), Theridiidae (13%), Araneidae (9%) and Salticidae (6.5%). Two specimens were in bad condition and could not

be identified. We also assigned 199 specimens to 48 different morphospecies.

For the total spider assemblage, C values were close to 100% (99.5% and 92% for families and morphospecies, respectively) indicating a very good representation of the taxa in the samples. Moreover, the estimated family richness (ACE) was the same as the observed number of families. The CV values (0.855 and 1.22 for families and morphospecies, respectively) indicate a moderate heterogeneity in family-morphospecies discovery probabilities in the samples (Table 2). The number of spiders collected ballooning (abundance) was not significantly different between seasons ( $X^2 = 0.51$ ,  $df = 2$ ,  $p = 0.77$ ) (Table 3). Family composition was very similar between seasons as well. This is reflected in the estimated BCi value (BCi =  $0.84 \pm 0.09$ ).

### Local and landscape variables

For the abundance variable, one of the models (P6) was significantly better than the others (Table 4). It included landscape-level green cover (UOS500 m), which negatively affected ballooning spider abundance, and the interaction between landscape and local green cover (UOS500 m: UOS50 m, Figure 3). Figure 3 shows the effect of the interaction. To facilitate interpretation, we used a two-level factor ('high vegetation cover' and 'low vegetation cover') instead of the quantitative variable 'UOS500 m'. At the landscape level, there is a

**TABLE 2** Summary of families, their abundances and their respective number of morphospecies collected dispersing aerially.

Variables	Family	Specimens	Morphospecies
Families	Amaurobiidae	2	1
	Anyphaenidae	26	4
	Araneidae	18	5
	Cheiracanthiidae	1	1
	Corinnidae	2	2
	Dictynidae	29	3
	Gnaphosidae	6	3
	Linyphiidae	29	7
	Lycosidae	2	1
	Philodromidae	3	2
	Pholcidae	4	1
	Salticidae	13	4
	Theridiidae	27	8
	Thomisidae	38	3
No. of individuals		200	199
No. of taxa		14	48
ACE $\pm$ S.E.		14.42 $\pm$ 0.87	61.39 $\pm$ 6.67
Estimated Cover (C)		0.995	0.926
Estimated CV		0.855	1.22

Note: Completeness of the sample was estimated using sample coverage (C) and the degree of heterogeneity among families and morphospecies discovery probabilities was characterised using the coefficient of variation (CV). ACE is an abundance-based coverage estimator.

**TABLE 3** Seasonal abundance (total and average number of specimens collected per site) and family richness of ballooning spider assemblages.

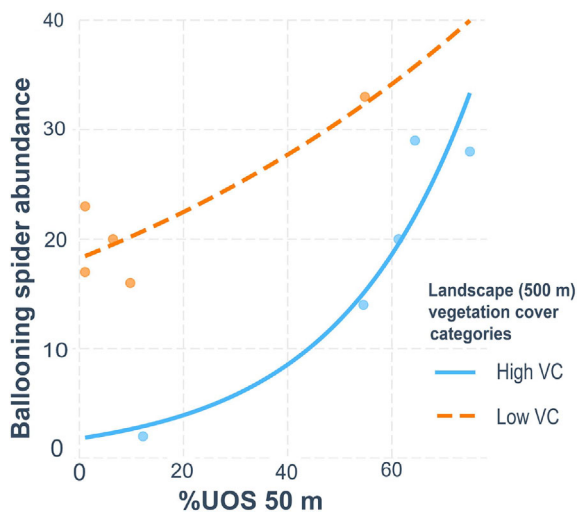
Season	Abundance	Site mean $\pm$ EE	Family richness	Site mean $\pm$ EE
Autumn	66	6.6 $\pm$ 1.03	12	4.3 $\pm$ 0.62
Spring	64	6.4 $\pm$ 1.18	10	3.5 $\pm$ 0.5
Summer	72	7.2 $\pm$ 1.2	12	4.4 $\pm$ 0.67

Note: Neither abundances nor richness differed significantly between seasons ( $p > 0.05$ ).

**TABLE 4** Generalised linear models tested for the abundance variable and their AICc values.

Model	k	AICc	$\Delta$ AICc	%UOS 500 m	%UOS 50 m	UOS500 m: UOS50 m
Null	1	93.3	7.8			
P1	4	72.9	5.30	X	X	X
P2	3	85.5	17.89	X	X	
P3	2	87.2	19.61		X	
P4	2	96.2	28.64	X		
P5	3	91.2	23.62		X	X
<b>P6</b>	<b>3</b>	<b>67.6</b>	<b>0</b>	<b>X</b>		<b>X</b>
P7	2	90.9	23.29			X

Note: UOS500 m = percentage of urban open spaces class for the 500 m buffer; UOS50 m = percentage of urban open spaces class for the 50 m buffer. Bold indicates best model ( $\Delta$ AICc < 2).

**FIGURE 3** Interaction between UOS500 m and UOS50 m on the abundance response variable. We used a two-level factor ('high vegetation cover' and 'low vegetation cover') instead of the quantitative variable 'UOS500 m' to facilitate interpretation. UOS500 m = percentage of urban open spaces class for the 500 m buffer; UOS50 m = percentage of urban open spaces class for the 50 m buffer. VC = vegetation cover.

higher dispersion of individuals in areas with low green cover compared to those with high green cover. In contrast, at a local scale, a higher percentage of vegetation cover is associated with increased aerial dispersal, as opposed to areas with low local green cover. A high

green cover at a local scale significantly increases aerial spider abundance in sites with low green cover at a landscape scale.

For the family richness variable, we found three best models (Table 5): M3 that included local green cover (UOS50 m), M6 that included landscape-level green cover (UOS500 m) and the interaction UOS500 m: UOS50 m, and the Null Model. The effects of the independent variables on richness were similar to those found for the abundance variable but, not only were they not statistically significant, given that the null model was also among the best models, we do not consider the effect of these variables as strong predictors. Moreover, the models were overfitted.

### Family composition

PERMANOVA results comparing the spider assemblages between two conditions of vegetation cover (low or high) were not significant for landscape ( $F = 0.899$ ,  $p = 0.52$ ) nor for local scales ( $F = 0.59$ ,  $p = 0.81$ ). These results show that the family composition of the ballooning spider assemblage was similar across the city regardless of the landscape context.

## DISCUSSION

In this study, we investigated spider ballooning in an urban context, specifically examining the role of vegetation cover locally and in the landscape context on spider aerial dispersal. Our work, while

**TABLE 5** Generalised linear models tested for the family richness variable and their AICc values.

Model	K	AIC	$\Delta$ AICc	%UOS 500 m	%UOS 50 m	UOS500 m: UOS50 m
<b>Null</b>	<b>1</b>	<b>49.6</b>	<b>0.1</b>			
P1	4	55.4	5.9	X	X	X
P2	3	52.0	2.5	X	X	
<b>P3</b>	<b>2</b>	<b>51.3</b>	<b>1.8</b>		<b>X</b>	
P4	2	52.6	3.1	X		
P5	3	54.5	5.0		X	X
<b>P6</b>	<b>3</b>	<b>49.5</b>	<b>0</b>	<b>X</b>		<b>X</b>
P7	2	52.5	3.0			X

Note: UOS500 m = percentage of urban open spaces class for the 500 m buffer; UOS50 m = percentage of urban open spaces class for the 50 m buffer. Bold indicates the best models ( $\Delta$ AICc <2).

preliminary, contributes valuable insights to the scientific understanding of spider aerial dispersal dynamics in urban settings, revealing a significant effect of surrounding vegetation cover at two spatial scales on the abundance of spiders dispersing aerially in urban environments.

Maintaining sampling effort, we found similar numbers of individuals and family composition dispersing across three different seasons. Most collected spiders were captured during ballooning events, but not all. For instance, four pholcid spiders found in traps likely fell accidentally, as Huber (2023) notes no evidence of evolved airborne behaviour in Pholcidae. Instead, they exhibit behaviours like bridging and dropping on a line, occasionally leading to accidental airborne specimens. While acknowledging the possibility of some accidental falls, we still attribute the presence of other spider families to intentional ballooning, given their smaller sizes and documented aerial dispersal abilities. Our trap design aimed to minimise accidental falls, and despite potential errors, we maintain confidence that the majority arrived via intentional ballooning.

Thomisidae was the most abundant family collected, a trend mirrored by their significant presence in urban green spaces of Córdoba city (Argañaraz et al., 2018). We take note that, despite Thomisidae's propensity for ballooning, it rarely takes a leading role as one of the most abundant families engaged in aerial dispersal (e.g., Bishop & Riechert, 1990). Morse (1993) determined that crab spider spiderlings are programmed to seek a new location if they do not quickly find a satisfactory one locally, and also noted that some ballooning events cover only a few meters. Since we sampled at a height of 1.5–2 m, and traps were hung mostly from trees, it is likely that short-distance dispersal is being overrepresented in our study. However, it is interesting to note that the two most frequent families collected from a trap hanged on a building 40 m above the ground were Thomisidae and Linyphiidae (preliminary sampling, Supplementary Material S2).

Linyphiidae, the second most prevalent airborne family in our study along with Dictynidae, was anticipated to secure the prime position, given its frequent citation and collection records in previous ballooning studies (Thorbeck et al., 2002; Woolley et al., 2016). Nonetheless, it is plausible that these disparities stem from differences in habitat—predominantly agricultural—covered in other studies and their geographical locations, particularly focusing on Europe (e.g., Blandenier et al., 2013; Coulson et al., 2003; Rensch et al., 2010;

Woolley et al., 2016) and the USA (e.g., Dean & Sterling, 1985; Hogg & Daane, 2018). This family is the most diversified and abundant family in temperate regions of the Northern Hemisphere (Duffey, 1998) and is particularly abundant in meadows and agroecosystems. Notably, we highlight that Linyphiidae was the most abundant spider family found in urban green spaces vegetation of Córdoba city (Argañaraz et al., 2018). This emphasises that a family's high abundance on land does not necessarily equate to a greater airborne presence, even for a family like Linyphiidae, known for its ballooning propensity.

Family composition did not change significantly between sites with high and low vegetation cover (500 and 50 m), reflecting that most families can be found ballooning across the city. Furthermore, across collected samples, the richness consistently remained remarkably high, with nearly all individuals collected during the same time period with a given trap belonging to different families.

Since ballooning dispersal is a wind lottery preceded by individual-based risk assessment, we hypothesized that spider diversity during ballooning would vary depending on the surrounding landscape context. The risk is higher for specialist spiders (Bonte, Vandenbroecke, et al., 2003), but in the city, generalist (Kotze et al., 2011; Magura et al., 2010) spiders with good dispersal capacities (Piano et al., 2020) are more common. Therefore, we expected to find a higher number of spiders, from a lower taxonomic diversity, dispersing aerially in areas with low percentage of green cover than in areas with a higher green cover percentage. Our results partially support this hypothesis. Although we did not detect differences in richness (i.e., the number of different taxa), we collected more ballooning spiders (i.e., more specimens) in sites with low landscape-level vegetation cover (Figure 3), potentially reflecting a higher need to find suitable habitats. In fact, in a study also conducted in Córdoba city, Argañaraz et al. (2018) reported that spider diversity, measured in terms of abundance and richness, was negatively affected by the prevalence of impervious surfaces in the surrounding landscape. Therefore, our higher abundance in this type of site would indicate a higher dispersal activity, rather than being a consequence of a higher abundance of spiders on the ground.

Landscape-level vegetation cover could not explain ballooning spider diversity on its own, but it became important when considering

its interaction with another variable. We found that local vegetation cover (within a 50 m radius) interacted with landscape-level vegetation cover to affect ballooning spider abundance, with higher local vegetation cover increasing the number of spiders dispersing in sites with high landscape-level vegetation cover. We believe that this happens because there are a higher number of spiders dispersing locally, searching for a better place nearby (since they arrived at a site with potentially higher habitat availability).

In a study of aerial plankton in Paris, Vergnes et al. (2017) found a significant interaction between height and Landscape Greening Index, despite capturing a very small number of spiders. Their Landscape Greening Index showed a strong positive effect on spider abundances at high heights, but a weaker and opposite effect at lower heights (but above 10 m). This result was explained by a barrier effect of buildings that limits dispersion from potential sources of sites. Our results suggest that 1.5–2 m high fencing may not represent significant barriers for ballooning dispersal, but we believe that further research considering taller structures could explore the effects of buildings as barriers for dispersal and their consequences for spider diversity in a vertical gradient.

This study marks a promising starting point in the exploration of aerial dispersal within urban environments by showing that local- and landscape-level plant covers have differential effects on spider ballooning. Understanding the mechanisms and patterns of spider ballooning in urban environments can help us to better understand the factors that influence spider diversity in cities, and may provide insights into how we can promote and support urban biodiversity conservation efforts.

## AUTHOR CONTRIBUTIONS

**Marcela Montes:** Conceptualization; investigation; writing – original draft; methodology; visualization; formal analysis; software; data curation. **Raquel Miranda Gleiser:** Conceptualization; funding acquisition; methodology; writing – review and editing; supervision; resources; project administration; validation.

## ACKNOWLEDGEMENTS

We are especially grateful to each person who allowed us to use their garden as study sites. We also acknowledge taxonomic support received from Drs. Carina I. Aragañaraz. and Gonzalo D. Rubio. We thank three anonymous reviewers and Dr. Charles Fox for their valuable contributions that have greatly improved our manuscript. R. M. Gleiser is a Career researcher from CONICET. M. Montes holds a scholarship from the same institution and is a doctorate of FCEfyN, UNC.

## FUNDING INFORMATION

This work was supported by Secretaría de Ciencia y Tecnología (SECyT) of Universidad Nacional de Córdoba (grant 33620180100302CB), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) grant PIP 2021 (11220200102991CO) and Agencia Nacional de Promoción Científica y Tecnológica (ANPCyT) grant PICT 2021 (PICT-2021-GRFTI-00453).

## CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

## DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available on request from the corresponding author. The data are not publicly available due to privacy or ethical restrictions.

## ORCID

Marcela Montes  <https://orcid.org/0000-0003-4478-9333>

Raquel M. Gleiser  <https://orcid.org/0000-0003-0726-2639>

## REFERENCES

- Anderson, M.J. & Santanta-Garcon, J. (2015) Measures of precision for dissimilarity-based multivariate analysis of ecological communities. *Ecology Letters*, 18(1), 66–73.
- Argañaraz, C.I., Rubio, G.D. & Gleiser, R.M. (2018) Spider communities in urban green patches and their relation to local and landscape traits. *Biodiversity and Conservation*, 27(4), 981–1009. Available from: <https://doi.org/10.1007/s10531-017-1476-8>
- Bell, J.R., Bohan, D.A., Shaw, E.M. & Weyman, G.S. (2005) Ballooning dispersal using silk: world fauna, phylogenies, genetics and models. *Bulletin of Entomological Research*, 95(2), 69–114. Available from: <https://doi.org/10.1079/ber2004350>
- Bishop, L. (1990) Meteorological aspects of spider ballooning. *Environmental Entomology*, 19(6), 1381–1387. Available from: <https://doi.org/10.1093/ee/19.5.1381>
- Bishop, L. & Riechert, S.E. (1990) Spider colonization of agroecosystems: mode and source. *Environmental Entomology*, 19(6), 1738–1745. Available from: <https://doi.org/10.1093/ee/19.6.1738>
- Blandenier, G. (2009) Ballooning of spiders (Araneae) in Switzerland: general results from an eleven-year survey. *Arachnology*, 14(7), 308–316. Available from: <https://doi.org/10.13156/ arac.2009.14.7.308>
- Blandenier, G., Bruggisser, O.T., Rohr, R.P. & Bersier, L.F. (2013) Are phenological patterns of ballooning spiders linked to habitat characteristics? *Journal of Arachnology*, 41(2), 126–132. Available from: <https://doi.org/10.1636/P12-48>
- Bonte, D., Borre, J.V., Lens, L. & Maelfait, J.P. (2006) Geographical variation in wolf spider dispersal behaviour is related to landscape structure. *Animal Behaviour*, 72(3), 655–662. Available from: <https://doi.org/10.1016/j.anbehav.2005.11.026>
- Bonte, D., Deblauwe, I. & Maelfait, J.P. (2003) Environmental and genetic background of tiptoe-initiating behaviour in the dwarfspider *Erigone atra*. *Animal Behaviour*, 66(1), 169–174. Available from: <https://doi.org/10.1006/anbe.2003.2191>
- Bonte, D., Hovestadt, T. & Poethke, H.J. (2010) Evolution of dispersal polymorphism and local adaptation of dispersal distance in spatially structured landscapes. *Oikos*, 119(3), 560–566. Available from: <https://doi.org/10.1111/j.1600-0706.2009.17943.x>
- Bonte, D., Lukáč, M. & Lens, L. (2008) Starvation affects pre-dispersal behaviour of *Erigone* spiders. *Basic and Applied Ecology*, 9(3), 308–315. Available from: <https://doi.org/10.1016/j.baae.2007.03.004>
- Bonte, D., Travis, J.M., De Clercq, N., Zwertvaegher, I. & Lens, L. (2008) Thermal conditions during juvenile development affect adult dispersal in a spider. *Proceedings of the National Academy of Sciences of the United States of America*, 105(44), 17000–17005. Available from: <https://doi.org/10.1073/pnas.0806830105>
- Bonte, D., Vandenbroecke, N., Lens, L. & Maelfait, J.P. (2003) Low propensity for aerial dispersal in specialist spiders from fragmented landscapes. *Proceedings of the Royal Society B: Biological Sciences*, 270 (1524), 1601–1607. Available from: <https://doi.org/10.1098/rspb.2003.2432>



- Brown, A.D., Martínez-Ortíz, U., Acerbi, M. & Corcuera, J. (2006) *La situación ambiental Argentina 2005*. Buenos Aires, Argentina: Fundación Vida Silvestre Argentina.
- Buchholz, S. & Egerer, M.H. (2020) Functional ecology of wild bees in cities: towards a better understanding of trait-urbanization relationships. *Biodiversity and Conservation*, 29, 2779–2801. Available from: <https://doi.org/10.1007/s10531-020-02003-8>
- Chao, A. & Chiu, C.H. (2016) *Species richness: estimation and comparison*. Hoboken, New Jersey: Wiley StatsRef: Statistics Reference Online, pp. 1–26.
- Chao, A. & Jost, L. (2012) Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. *Ecology*, 93 (12), 2533–2547. Available from: <https://doi.org/10.1890/11-1952.1>
- Chao, A., Ma, K., Hsieh, T.C. & Chiu, C.H. (2015) Online program SpadeR (species-richness prediction and diversity estimation in R). Program and user's guide published at [http://chao.stat.nthu.edu.tw/wordpress/software\\_download/](http://chao.stat.nthu.edu.tw/wordpress/software_download/)
- Chapman, S., Watson, J.E., Salazar, A., Thatcher, M. & McAlpine, C.A. (2017) The impact of urbanization and climate change on urban temperatures: a systematic review. *Landscape Ecology*, 32, 1921–1935.
- Coulson, S.J., Hodgkinson, I.D. & Webb, N.R. (2003) Aerial dispersal of invertebrates over a high-Arctic glacier foreland: Midtre Lovnbreen, Svalbard. *Polar Biology*, 26(8), 530–537. Available from: <https://doi.org/10.1007/s00300-003-0516-x>
- Culumber, Z.W., Anaya-Rojas, J.M., Booker, W.W., Hooks, A.P., Lange, E. C., Pluer, B. et al. (2019) Widespread biases in ecological and evolutionary studies. *Bioscience*, 69(8), 631–640. Available from: <https://doi.org/10.1093/biosci/biz063>
- Davy, C.M., Ford, A.T. & Fraser, K.C. (2017) Aeroconservation for the fragmented skies. *Conservation Letters*, 10(6), 773–780. Available from: <https://doi.org/10.1111/conl.12347>
- de Meester, N. & Bonte, D. (2010) Information use and density-dependent emigration in an agrobiont spider. *Behavioral Ecology*, 21(5), 992–998. Available from: <https://doi.org/10.1093/beheco/arq088>
- Dean, D.A. & Sterling, W.L. (1985) Size and phenology of ballooning spiders at two locations in eastern Texas. *Journal of Arachnology*, 13, 111–120.
- Duffey, E. (1998) Aerial dispersal in spiders. In: Selden, P.A. (Ed.) *Proceedings of the 17th European Colloquium of Arachnology, Edinburgh 1997*, Vol. 1937, Burnham Beeches, Bucks: British Arachnological Society, pp. 187–191.
- Entling, M.H., Stämpfli, K. & Ovaskainen, O. (2011) Increased propensity for aerial dispersal in disturbed habitats due to intraspecific variation and species turnover. *Oikos*, 120(7), 1099–1109. Available from: <https://doi.org/10.1111/j.1600-0706.2010.19186.x>
- Gibb, E. & Hochuli, D.F. (2002) Habitat fragmentation in an urban environment: large and small fragments support different arthropod assemblages. *Biological Conservation*, 106, 91–100. Available from: [https://doi.org/10.1016/S0006-3207\(01\)00232-4](https://doi.org/10.1016/S0006-3207(01)00232-4)
- Greenstone, M.H., Eaton, R.R. & Morgan, C.E. (1991) Sampling aerially dispersing arthropods: a high-volume, inexpensive, automobile- and aircraft-borne system. *Journal of Economic Entomology*, 84(6), 1717–1724. Available from: <https://doi.org/10.1093/jee/84.6.1717>
- Grismado, C., Ramírez, M.J. & Izquierdo, M.A. (2014) Araneae: taxonomía, diversidad y clave de identificación de familias de la Argentina. In: Roig-Juñent, S., Claps, L.E. & Morrone, J.J. (Eds.) *Biodiversidad de Artrópodos Argentinos*, Vol. 3. San Miguel de Tucumán, Argentina: Editorial INSUE–UNT, pp. 55–94.
- Hogg, B.N. & Daane, K.M. (2018) Aerial dispersal ability does not drive spider success in a crop landscape. *Ecological Entomology*, 43(5), 683–694. Available from: <https://doi.org/10.1111/een.12641>
- Huber, B.A. (2023) Do pholcid spiders balloon? *Arachnology*, 19(6), 885–887. Available from: <https://doi.org/10.13156/arc.2023.19.6.885>
- Kotze, J., Ven, S., Niemelä, J. & Spence, J. (2011) *Effects of urbanization on the ecology and evolution of arthropods. Urban ecology, patterns, processes and applications*. New York: Oxford University Press, pp. 159–166.
- Lagucki, E., Burdine, J.D. & McCluney, K.E. (2017) Urbanization alters communities of flying arthropods in parks and gardens of a medium-sized city. *PeerJ*, 2017(9), e3620. Available from: <https://doi.org/10.7717/peerj.3620>
- Larrivé, M. & Buddle, C.M. (2011) Ballooning propensity of canopy and understorey spiders in a mature temperate hardwood forest. *Ecological Entomology*, 36(2), 144–151. Available from: <https://doi.org/10.1111/j.1365-2311.2010.01255.x>
- Magura, T., Horváth, R. & Tóthmérész, B. (2010) Effects of urbanization on ground-dwelling spiders in forest patches, in Hungary. *Landscape Ecology*, 25, 621–629. Available from: <https://doi.org/10.1007/s10980-009-9445-6>
- Mestre, L. & Bonte, D. (2012) Food stress during juvenile and maternal development shapes natal and breeding dispersal in a spider. *Behavioral Ecology*, 23(4), 759–764. Available from: <https://doi.org/10.1093/beheco/ars024>
- Morse, D.H. (1993) Some determinants of dispersal by crab spiderlings. *Ecology*, 74(2), 427–432. Available from: <https://doi.org/10.2307/1939304>
- Nagy, D.D., Magura, T., Horváth, R., Debnár, Z. & Tóthmérész, B. (2018) Arthropod assemblages and functional responses along an urbanization gradient: a trait-based multi-taxa approach. *Urban Forestry & Urban Greening*, 30, 157–168. Available from: <https://doi.org/10.1016/j.ufug.2018.01.002>
- Parris, K.M. (2016) *Ecology of urban environments*. Chichester, WestSussex, UK: Wiley-Blackwell.
- Peel, M.C., Finlayson, B.L. & McMahon, T.A. (2007) Updated world map of the Köppen-Geiger climate classification. *Hydrology and Earth System Sciences*, 11(5), 1633–1644.
- Peralta, G., Fenoglio, M.S. & Salvo, A. (2011) Physical barriers and corridors in urban habitats affect colonisation and parasitism rates of a specialist leaf miner. *Ecological Entomology*, 36(6), 673–679. Available from: <https://doi.org/10.1111/j.1365-2311.2011.01316.x>
- Piacentini, L.N., Grismado, C.J., Aisenberg, A., Toscano-Gadea, C.A., Laborda, A., Simó, M. et al. (2021) Massive spider web aggregations in South American grasslands after flooding. *Ecological Entomology*, 46(6), 1333–1341. Available from: <https://doi.org/10.1111/een.13080>
- Piano, E., Giuliano, D. & Isaia, M. (2020) Islands in cities: urbanization and fragmentation drive taxonomic and functional variation in ground arthropods. *Basic and Applied Ecology*, 43, 86–98.
- Pyšek, P., Richardson, D.M., Pergl, J., Jarošík, V., Sixtová, Z. & Weber, E. (2008) Geographical and taxonomic biases in invasion ecology. *Trends in Ecology & Evolution*, 23(5), 237–244. Available from: <https://doi.org/10.1016/j.tree.2008.02.002>
- Rensch, M., Volkmar, C. & Spilke, J. (2010) Aerial dispersal of spiders in central east Germany: modelling of meteorological and seasonal parameters. In: Nentwig, W., Entling, M. & Kropf, C. (Eds.) *Proceedings of the 24th European colloquium of arachnology*, Vol. 2008. Bern: Natural History Museum, pp. 147–152.
- Reynolds, A.M., Bohan, D.A. & Bell, J.R. (2007) Ballooning dispersal in arthropod taxa: conditions at take-off. *Biology Letters*, 3(3), 237–240. Available from: <https://doi.org/10.1098/rsbl.2007.0109>
- Ronce, O. (2007) How does it feel to be like a rolling stone? Ten questions about dispersal evolution. *Annual Review of Ecology, Evolution, and Systematics*, 38, 231–253. Available from: <https://doi.org/10.1146/annurev.ecolsys.38.091206.095611>
- Suter, R.B. (1992) Ballooning: data from spiders in freefall indicate the importance of posture. *Journal of Arachnology*, 20(2), 107–113.
- Suter, R.B. (1999) An aerial lottery: the physics of ballooning in a chaotic atmosphere. *Journal of Arachnology*, 27(1), 281–293.

- Thorbek, P., Topping, C.J. & Sunderland, K.D. (2002) Validation of a simple method for monitoring aerial activity of spiders. *Journal of Arachnology*, 30(1), 57. Available from: [https://doi.org/10.1636/0161-8202\(2002\)030\[0057:VOASMF\]2.0.CO;2](https://doi.org/10.1636/0161-8202(2002)030[0057:VOASMF]2.0.CO;2)
- Vergnes, A., Le Saux, E. & Clergeau, P. (2017) Preliminary data on low aerial plankton in a large city center, Paris. *Urban for Urban Green*, 22, 36–40. Available from: <https://doi.org/10.1016/j.ufug.2017.01.012>
- Weyman, G.S., Sunderland, K.D. & Jepson, P.C. (2002) A review of the evolution and mechanisms of ballooning by spiders inhabiting arable farmland. *Ethology, Ecology and Evolution*, 14, 307–326.
- Woolley, C., Thomas, C.G., Blackshaw, R.P. & Goodacre, S.L. (2016) Aerial dispersal activity of spiders sampled from farmland in southern England. *Journal of Arachnology*, 44(3), 347–358.

## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**Supplementary Material S1.** Abundance of families and morphospecies collected dispersing aerially.

**Supplementary Material S2.** Total spiders and most abundant families dispersing aerially, collected with a trap placed on a building 40 m above the ground (31°25'10.2"S 64°10'46.1"W). Cumulative data is shown. Sampling was carried out over two and a half months during the summer (November 2019–January 2020), samples collected biweekly.

**How to cite this article:** Montes, M. & Gleiser, R.M. (2024)

Flying to greener pastures: Spider ballooning in the city.

*Ecological Entomology*, 49(3), 397–406. Available from: [https://](https://doi.org/10.1111/een.13313)

[doi.org/10.1111/een.13313](https://doi.org/10.1111/een.13313)