

Physical barriers and corridors in urban habitats affect colonisation and parasitism rates of a specialist leaf miner

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Abstract. 1. Urban environments are fragmented habitats characterised by the presence of physical barriers, which may negatively affect dispersal and colonisation by insect herbivores and their natural enemies. Conversely, plants growing along pavements may function as dispersal corridors, helping to moderate the harmful effects of resource patch isolation on organism movement and population persistence.

2. We experimentally tested the effects of walls as physical barriers to the dispersal of the leaf miner *Liriomyza commelinae* Frost and colonisation of its host plant, *Commelina erecta* L., in urban habitats. We also evaluated whether plants along pavements could act as corridors for this species.

3. We exposed experimental host plants to the leaf miner in houses with front gardens and back yards, the latter being completely surrounded by walls. The front gardens had walls but none separating them from the pavement. Previously mined plants were also exposed to parasitoids in the yards to determine parasitoid attack.

4. *Liriomyza commelinae* took longer to colonise back yards with higher walls, and the abundance of mined plants along pavements reduced the colonisation time. Leaf-miner abundance was marginally affected by the yard type, and was lower in back yards. Cumulative parasitism rates decreased with increasing distance at which mined plants were placed from pavements.

5. Constructions act as physical barriers, having a negative impact on colonisation of host plants by leaf miners. The function of pavements as corridors seems to depend on the abundance of mined plants. Parasitism may be affected by distance from the corridor rather than physical barriers or other potential hosts.

Key words. Biological control, dispersal, herbivore insect, parasitoid, predator–prey, urbanisation.

Introduction

Insect herbivore populations are often structured as metapopulations, as a consequence of habitat fragmentation or patchy distribution of their plant resources (Tschardt & Brandl, 2004). In urban landscapes, patches of plants are often small and distant from each other, immersed in a matrix

of built environment (Niemelä, 1999; Zipperer *et al.*, 2000), which additionally promotes the occurrence of metapopulation dynamics in phytophagous insects. In this context, distance of non-occupied plant patches from source habitats can be one of the most important factors affecting their probability to be colonised (Hanski, 1999). Moreover, in cities the presence of horizontal (e.g. streets) and/or vertical (e.g. walls) physical barriers may make insect dispersal difficult and risky, and present an obstacle for insects searching for suitable habitats for their development (Wratten *et al.*, 2003; Raupp *et al.*, 2010).

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Connectivity between habitat patches is thus an important factor determining species occurrence in urban areas, which is critical to maintaining metapopulations (Zipperer *et al.*, 2000).

One way to moderate the negative effects of resource isolation on organism movement and persistence is the preservation of corridors (Haddad, 2000; Tewksbury *et al.*, 2002), which can increase immigration and emigration by functioning as movement conduits between patches (Rosenberg *et al.*, 1997; Beier & Noss, 1998). In cities, green areas bordering roads, pavements, and streets are habitats that could operate as biological corridors (Haddad *et al.*, 2003), as they facilitate movement and ensure colonisation of isolated semi-natural areas (Savard *et al.*, 2000). Moreover, these habitats can facilitate dispersal of herbivorous insects, maintaining their distribution, diversity, and abundance (Gonzalez *et al.*, 1998; Hopwood, 2008). Corridors could also affect herbivore mortality by enhancing circulation and dispersal of their natural enemies (Nicholls *et al.*, 2001). However, top-down control exerted by generalist predators could be unaffected by corridors, because generalists can prey on different species within isolated patches (Tschamtko *et al.*, 2002).

Recently, natural landscape elements have been evaluated as barriers and corridors for dispersal of hymenopterans (Krewenka *et al.*, 2011). In human modified habitats, many studies have shown detrimental effects of urbanisation on the diversity and abundance of insects (Weller & Ganzhorn, 2004; Rango, 2005; Fenoglio & Salvo, 2010), but there is no empirical evidence on how vertical barriers influence the colonisation of habitat patches by herbivorous insects, or whether vegetation alongside pavements can function as corridors. Moreover, it is unknown whether urban barriers can disrupt the regulation of herbivores by natural enemies. Here, we experimentally examine the effects of vertical physical barriers (i.e. walls of buildings) on the colonisation time of plant patches by a specialist leaf miner (*Liriomyza commelinae* Frost, Diptera: Agromyzidae). As parasitoid insects are one of the main mortality sources of leaf-mining herbivores (Parrella, 1987; Hespeneheide, 1991) we focused on this group to evaluate whether there are changes in the top-down control according to several urban habitat variables. Dispersal ability of leaf-mining insects (Nash *et al.*, 1995; Eber, 2004) has been scarcely studied, particularly within the context of ever-increasing urban environments. However, evidence suggests that this group of insects prefers to fly at low heights (Chandler, 1985; Weintraub & Horowitz, 1996). On this basis, we hypothesised that walls represent physical barriers that negatively affect herbivore colonisation of unoccupied patches and that pavements could act as biological corridors for the leaf miner, since their host plant is usually abundant in this habitat. In contrast, pavements would not necessarily constitute corridors for the parasitoids, since they are mostly generalist species (Salvo & Valladares, 1998, 2004), with the potential to attack other species of leaf miners in the surroundings. For this reason, we expect that parasitism rates would be more affected by the availability of other potential hosts for parasitoids rather than physical barriers. In those cases where pavements act as corridors, distance of plant patches from these sources is expected to have an effect on the studied variables.

Materials and methods

Study system

Here we focus on the species *Liriomyza commelinae* (Diptera: Agromyzidae), a neotropical leaf miner that feeds exclusively on the genus *Commelina* (Commelinaceae) (Valladares, 1984), and in the study region is specialised on *Commelina erecta* L. This perennial herbaceous plant is patchily distributed, occurs in natural, cultivated and urban habitats, throughout the north and centre of Argentina (Sérsic *et al.*, 2006). *Liriomyza commelinae* pupates within the leaf parenchyma (Smith, 1987), and 50% of its mortality is caused by parasitism (Fenoglio & Salvo, 2009). Twenty-five parasitoid species (Hymenoptera) have been associated with *L. commelinae* in the study area (Fenoglio & Salvo, 2009), most of them being solitary and polyphagous (Salvo & Valladares, 1999). The fragmented distribution of its host resource in the city apparently does not negatively affect the leaf miner, as higher abundance has been observed as the degree of urbanisation increases (Fenoglio *et al.*, 2009). The degree of urbanisation was also found to have no effect on parasitoid species richness or parasitism rates of *L. commelinae* at the site scale (Fenoglio *et al.*, 2009). Mined *C. erecta* plants have even been observed in building terraces (M. S. Fenoglio, pers. obs.), suggesting that *L. commelinae* has the ability to disperse among highly fragmented host plant populations in an urban environment.

Experiment

In Córdoba city, central Argentina (31°20'S, 64°10'W, elevation 440 m), we selected six houses with front garden and back yard completely separated by walls. Back yards were completely isolated by walls of at least 1.8 m height, whereas front gardens had walls on three of their sides (0.45 m minimum), but there was no wall separating them from the pavement (Fig. 1). Prior to the experiment, all *C. erecta* plants were eliminated from both yards of all houses in order to avoid plant colonisation by individuals reared in the same sites.

We used 24 pots (30 cm × 12.5 cm, 13 cm deep), each containing two to four *C. erecta* plants (depending on size, to maintain approximately consistent leaf area), for the

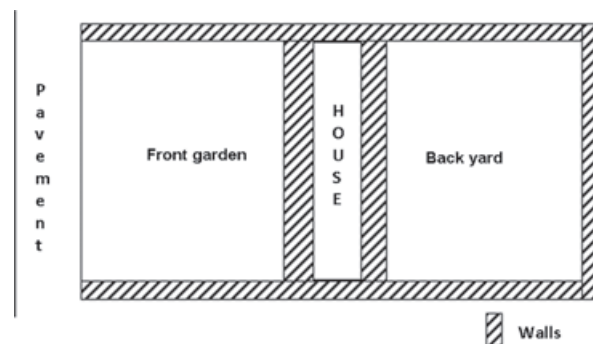


Fig. 1. Schematic representation of a house with its front garden and back yard and the walls surrounding them.

experiment. In the laboratory, 12 pots were placed in cages (cardboard and voile, 60 cm × 36 cm × 36 cm deep, three pots per cage) with adults of *L. commelinae* (seven females and seven males per cage) for 48 h, at room temperature, to allow mating and oviposition.

We took four plant pots to each house (two with mined leaves, at the first larval stage, and two with entirely non-mined leaves), placing one mined and one non-mined plant at both the front garden and the back yard. As the configuration of the houses differed, plants in front gardens were located between 1.5 and 7 m away from pavements, while those situated in back yards were between 3.6 and 15 m apart from pavements. Plants without mines were intended to assess leaf miner colonisation whereas mined plants were used to evaluate parasitism rates of the leaf miner. The experimental plant exposure times were insufficient to allow leaf miners from the mined plants to mature and colonise the non-mined plants. We visited the houses every 8 days, during 10 weeks, collecting all mined leaves from the originally non-mined plants at each visit (to estimate leaf-miner abundance), and leaves with pupae from the mined plants (to estimate parasitism rates). The leaves were placed in plastic bags, transported to the laboratory, and kept until flies and parasitoids emerged. Adult leaf miners and parasitoids were stored in glass vials and, when full emergence had ceased, were counted and identified according to Salvo (1996). The extraction of all mined leaves from initially non-mined plants on each visit ensured that mines observed in the next visit resulted from new colonising females. In addition, because *L. commelinae* adults live for 4 days on average (M. S. Fenoglio, unpublished), observations of new mines in each visit are good estimators of new colonisations. Since we removed mined leaves from the non-mined plants on each visit, this reduced the number of leaves available for colonisation. To control for this potential confounding effect, we performed ANOVAS to test for differences in the number of leaves available for oviposition between front gardens and back yards in each visit. We found no significant differences in any case ($P > 0.05$), indicating no bias in the availability of leaves across yard treatments.

From non-mined plant treatments, two variables were calculated after exposure in the yards: leaf-miner abundance (number of mines) and colonisation time (number of days until the first observation of mines). In order to estimate cumulative parasitism rates, we added data obtained during the whole sampling period, estimating parasitism from adults obtained from the mined plants as the proportion of larvo-pupal parasitoids relative to the total number of adults (leaf miners plus parasitoids). We used the cumulative parasitism because no adults emerged in several visits in different houses.

All natural patches of *C. erecta* along the pavement surrounding the block in which each sampling house was located (total length of approximately 800 m of 2 m wide pavement) were counted and checked to register presence or absence of mined leaves. We used the percentage of host-plant patches containing mines as an estimator of the surrounding leaf-miner density (neighbourhood leaf-miner abundance). At each experimental house site, we quantified plant species richness in the yards as an estimator of the number of

other potential hosts for parasitoids, and also measured the height of the walls (m) and the distance at which potted plants were placed from pavements (m) as characteristics with potential impact on insect colonisation. No significant correlation between height of walls and the distances at which potted plants were placed from pavements was observed in any yard type (all cases $P > 0.05$).

Statistical analysis

We used generalised linear mixed models (GLMMs) with Poisson error to detect differences in the colonisation time between yards (front versus back), and to estimate the effect of wall height, neighbourhood leaf-miner abundance, and distances at which potted plants were placed from pavements. We checked for overdispersion using the dispersion scale factor, which was < 1.5 . For herbivore abundance (number of mines) we tested the same variables but using a negative binomial distribution because the equidispersion assumption of the Poisson model was not achieved (Zuur *et al.*, 2009). The interaction of yard type × wall height was also included in these models to test for differences in the effect of wall height between front gardens and back yards. These variables were all incorporated into the models as fixed effects, whereas house was incorporated as a random effect to account for the non-independence of front gardens and back yards in the same house (front garden and back yard nested within house). For the herbivore abundance model, date within yard was included as an additional random effect because the 10 temporal measures from each yard were not independent. A similar model was constructed for cumulative parasitism rates using binomial error distribution, with a logit link function. In this case, we tested yard type, wall height, plant richness, distances at which potted plants were placed from pavements, and the interaction between yard type and wall height as fixed effects.

We began with a maximal model containing all the above variables, and this was then simplified by first removing non-significant interactions and then main effects, until no further reduction in residual deviance (measured using the Akaike Information Criterion, AIC) was observed (Bolker *et al.*, 2009). Parameter estimates for fixed effects were tested for significance using a *Z*- or *t*-test (depending on the underlying error distribution), as these provide a more robust test than the alternative likelihood ratio test when sample sizes are small (Bolker *et al.*, 2009). Mixed models were conducted using the lme4 (Bates & Maechler, 2009) and glmmADMB (Skaug *et al.*, 2008) packages in the R 2.9.2 environment (R Development Core Team, 2009), with glmmADMB being used in instances where a negative binomial distribution was needed.

Results

Colonisation time

The mean colonisation time of *L. commelinae* in back yards was almost twice (mean = 17.33, SE = 3.82 days, $n = 6$) as that for front gardens (mean = 9.33, SE = 1.33 days,

Table 1. Results of generalised linear mixed effects model to compare leaf-miner colonisation time (with Poisson error, Z-test), leaf-miner abundance (with negative binomial error, *t*-test), and parasitism rates (with binomial error, Z-test) in front garden and back yard feeding patches. The back yard parameter is the difference between the front garden intercept and the back yard intercept. Interaction terms show the difference in slopes of the front gardens and back yards graphs according to the continuous variable under analysis.

Response variable	Fixed effects	Estimate ± SE	Z-/t-value	P-value	Random effects (variance)
A Leaf-miner colonisation time	Intercept (front garden)	4.110 ± 0.756	5.438	<0.0001	1.253 e-15
	Back yard	-3.718 ± 1.640	-2.267	0.023	
	Wall height	-0.124 ± 0.420	-0.294	0.768	
	Neighbourhood abundance	-0.019 ± 0.008	-2.223	0.026	
	Wall height × back yard	1.582 ± 0.676	2.339	0.019	
B Leaf-miner abundance	Intercept (front garden)	-2.673 ± 1.120	-2.386	0.140	0.001
	Back yard	-3.480 ± 0.879	-3.958	0.058	
	Wall height	1.332 ± 0.502	2.655	0.117	
	Neighbourhood abundance	0.041 ± 0.014	2.968	0.097	
	Distance from potted plants to pavements	0.089 ± 0.046	1.942	0.192	
C Parasitism rates	Intercept	1.582 ± 0.343	4.614	<0.0001	0.254
	Back yard	0.318 ± 0.411	0.774	0.439	
	Distance from potted plants to pavements	-0.172 ± 0.054	-3.193	0.001	

$n = 6$). The effect of wall height on the colonisation time of *L. commelinae* significantly depended on the yard type (yard type × wall height interaction), having only significant effects on colonisation time of back yards (Table 1, A). Specifically, *L. commelinae* needed more time to colonise plants located in back yards with higher walls (Fig. 2).

Out of 121 *C. erecta* patches checked along pavements of all houses and adjacent blocks (neighbourhood leaf-miner abundance), 92.56% were occupied by the leaf miner. Neighbourhood leaf-miner abundance also had a significant effect on the leaf-miner colonisation time, with the leaf miner taking

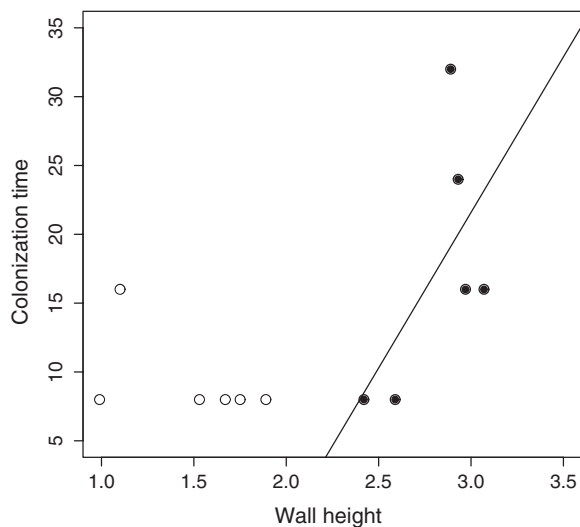


Fig. 2. Relationship between colonisation time (days) of *Liriomyza commelinae* and wall height (m) in front gardens (white points) and back yards (black points, continuous line). Although generalised linear mixed-effects models were performed (see Results), the least-squares trend line is shown to illustrate the direction of the significant relationship.

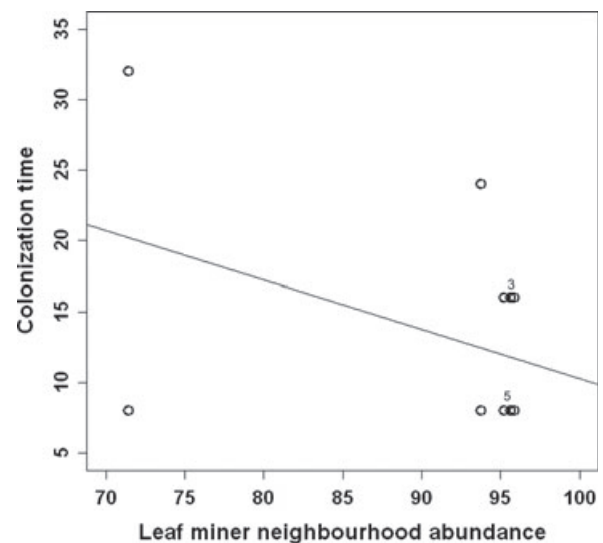


Fig. 3. Relationship between colonisation time (days) of *Liriomyza commelinae* and leaf-miner neighbourhood abundance (percentage of mined *Commelina erecta* patches on the houses surroundings). Although generalised linear mixed-effects models were performed (see Results), the least-squares trend line is shown to illustrate the direction of the relationship. The numbers in the plot indicate the number of data points at 95–96% of leaf-miner neighbourhood density that were superimposed.

more time to colonise houses situated in neighbourhoods with lower leaf-miner abundance (Fig. 3).

Leaf-miner abundance

A total of 1006 mined leaves were obtained from the exposed initially non-mined *C. erecta* plants across all the samples, and more than 70% of these came from front gardens.

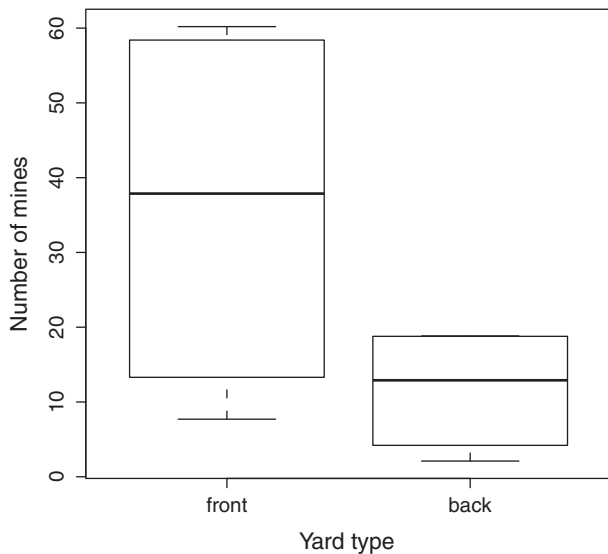


Fig. 4. Abundance of *Liriomyza commelinae* (median number of mines per visit) in front gardens and back yards ($n = 6$ houses).

On average, front gardens had 35.88 (SE = 4.15, min = 0, max = 140, $n = 57$) mines per sampling date, and back yards had 11.49 (SE = 1.63, min = 0, max = 41, $n = 59$) mines.

Yard type had a marginally significant effect on the number of mines, being higher in front gardens compared to back yards (Fig. 4; Table 1, B). None of the other variables tested in the model had a significant effect on the leaf-miner abundance, although they were retained in the best model except for the yard type \times wall height interaction.

Parasitism

Of the 591 leaf miners reared from the collected leaves, 58.71% were parasitised, representing eight larvo-pupal hymenopteran species (Table 2). They varied in abundance, with *Chrysocharis flacilla* being the most abundant species. In front gardens, six species were able to parasitise leaf-miner larvae in experimental plants by the first sampling round, whereas just two species were found in plants located in back yards

Table 2. Larvo-pupal parasitoid species (Hymenoptera) attacking experimental patches of *Liriomyza commelinae* in front gardens and back yards.

Superfamily	Family	Species
Chalcidoidea	Eulophidae	<i>Chrysocharis</i> Förster sp. A
		<i>Chrysocharis</i> sp. B
		<i>Chrysocharis</i> sp. C
		<i>Chrysocharis flacilla</i> (Walker)
		<i>Chrysocharis vonones</i> (Walker)
		<i>Chrysocharis caribea</i> (Boucek)
Ichneumonoidea	Braconidae	<i>Phaedrotoma luteoclypealis</i> (Van Achterberg & Salvo)
Cynipoidea	Figitidae	<i>Agrostocynips enneatoma</i> (Diaz)

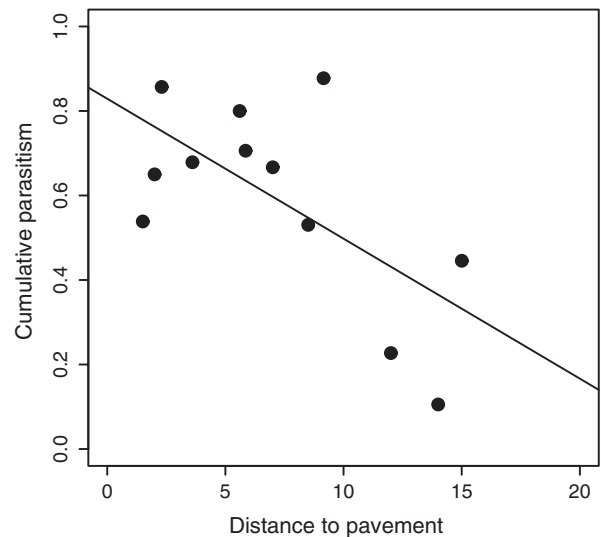


Fig. 5. Relationship between cumulative parasitism rates and distance (m) at which mined-potted plants were placed from pavements. Although generalised linear mixed-effects models were performed (see Results), the least-squares trend line is shown to illustrate the direction of the significant relationship.

during the same period. Parasitoids were found in all the front gardens and in three of the back yards in the first visit, while the other back yards were colonised by parasitoids in 16 days.

Cumulative parasitism rates of *L. commelinae* varied from 10% to 88% and they were significantly negatively affected by distance at which mined potted plants were placed from pavements (Fig. 5; Table 1, C). Although yard type did not have a significant effect on the cumulative parasitism rates, this variable was retained in the best-fitting model.

Discussion

Our results show that vertical physical barriers negatively affected leaf-miner colonisation of experimental plant patches. Dispersal barriers are of special interest when organisms exhibit a patchy distribution pattern (Tilman & Kareiva, 1997), such as that of *L. commelinae*, driven by the fragmented distribution of its feeding resource in urban environments. The pattern observed for colonisation time of the leaf miner in response to wall height depended on the yard type. Even though all experimental patches located in back yards were colonised in less than 32 days, vertical physical barriers substantially slowed the colonisation of host plants by *L. commelinae*, which needed more time to colonise plants located in back yards, especially those with higher walls. This highlights the importance of studying not only the effects of horizontal physical barriers, such as roads (Forman & Alexander, 1998), but also vertical ones, especially in urban environments where the latter are widespread. Colonisation time was also significantly longer when *L. commelinae* neighbourhood abundance was lower, probably because there were fewer leaf miners in the surroundings that could colonise the host plants. Leaf-miner

colonisation time did not depend on the distance of experimental potted plants to the pavements, even when the latter seem to be acting as corridors for the leaf miner.

If insect dispersal is disrupted by barriers, this could have negative consequences for species richness and their abundance in urban areas. We found that yard type had a marginally significant effect on the number of mines, which was lower in back yards. This result could probably be due to fewer individuals reaching back yards, or could also be observed if female leaf miners that reach back yards invested large amounts of energy in dispersal, and subsequently had less energy left for host-plant location and ovipositioning (Ellers *et al.*, 1998). In contrast to back yards, no walls existed between pavements and front gardens, so leaf miners did not need to overcome a vertical barrier when colonising experimental plants located in front gardens. The lack of an interaction effect between yard type and wall height confirms that the simple presence of barriers could limit the population abundance of the leaf miner.

We hypothesised that parasitism rates of *L. commelinae* would be more affected by the availability of other potential hosts, since almost all its parasitoids also attack other leaf-miner species of ornamental and aromatic plants, such as those usually found in yards (Salvo & Valladares, 1996; Valladares & Salvo, 1999). However, contrary to our expectations, cumulative parasitism was mainly affected by the distance at which potted plants were placed from pavements. With increasing distance, rates of parasitism were lower, suggesting that more isolated patches were more difficult for parasitoids to locate and colonise (Cronin & Strong, 1999), leading to a decrease of cumulative parasitism rates. Furthermore, since parasitoids have in pavements an abundant feeding resource, they may tend to remain there rather than investing a large amount of energy in looking for other habitats. Besides, this result is in agreement with other studies, which showed a decrease in parasitism rates with increasing patch isolation (Faeth & Simberloff, 1981; Kruess & Tschamtkke, 2000). Parasitoids in the superfamily Chalcidoidea (to which most parasitoid species of *L. commelinae* belong) have been observed to reach high altitudes (between 27 and 36 m) when flying (Compton *et al.*, 2000), which is probably the reason why, in our study, parasitoid dispersal was not limited by the presence or height of barriers.

Urbanisation is increasing worldwide, making ecological studies in urban environments critical in order to understand how species respond to urban structures (McKinney, 2002). We have shown that buildings represent physical barriers to the detection and colonisation of new feeding patches in urban habitats, and that the height of urban structures such as walls can represent a dispersal constraint, even for mobile species such as leaf miners. It can also be inferred from our results that city pavements can function as corridors, not only for the leaf miner but also for its parasitoids, which declined with the distance of the mined plants from the pavements.

Overall, our results reinforce the importance of maintaining greenways and front gardens in urban areas for the conservation of biological diversity (Botkin & Beveridge, 1997). The management of urban ecosystems sometimes requires small actions, which may have a great effect on biodiversity (Savard

et al., 2000). Ecosystem services provided by some species, such as pest control by natural enemies, should be an important consideration of urban planning. Several parasitoid species studied here also attack a globally important leaf-miner pest species (Fenoglio & Salvo, 2009), highlighting the potential benefits of conservation measures (such as the promotion of green corridors) for natural enemies in urban habitats.

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