

# Host–parasitoid interactions on urban roofs: an experimental evaluation to determine plant patch colonisation and resource exploitation

IVONE QUISPE and MARIA S. FENOGLIO Facultad de Ciencias Exactas, Físicas y Naturales, Centro de Investigaciones Entomológicas de Córdoba – Instituto Multidisciplinario de Biología Vegetal (CONICET), Universidad Nacional de Córdoba, Córdoba, Argentina

**Abstract.** 1. In cities, green roofs may favour an increase in the local diversity, although the role they play on host–parasitoid interactions is still unclear. Here, we tested the hypothesis that the specialist leaf-miner *Liriomyza commelinae* and its parasitoid assemblage are able to colonise and exploit patches located on roofs, but with a lower efficiency than at ground level. We also predicted that parasitoid species may differ in their abilities to colonise patches on roofs due to traits related to their life strategy (idio/koinobionts) and morphology (body size).

2. Through experimental exposure of non-mined and mined host plants located at ground level and on the bare roofs of houses, we determined colonisation levels for the leaf-miner and its parasitoids respectively. Changes in leaf-miner abundance, parasitism rates and parasitoid species richness were also investigated.

3. *L. commelinae* was able to locate host plants on rooftops, but revealed a lower rate of colonisation and abundance than on the ground. A few species of the parasitoid assemblage were associated with the leaf-miner in plants on roofs, resulting in decreasing colonisation rates, less species richness and lower parasitism. Interestingly, parasitoid species categorised as ‘small’ did not colonise plants on roofs.

4. Our results provide evidence on how habitats at height influence host–parasitoid interactions in cities, representing one of the first approaches to the biological role that green roofs might have on them.

**Key words.** Cities, dispersal at roof height, green roofs, leaf-miner insect, parasitism.

## Introduction

The management and conservation of natural resources within cities is improving day by day as a reaction to the rapid expansion of both urban and suburban areas (Dear-

born & Kark, 2010). Among the sustainable urban innovations that have recently been developed are green roofs, which act as ‘patches of nature’ by favouring an increase in local diversity, among other benefits (Oberndorfer *et al.*, 2007). There is a small but growing body of evidence on the positive role that green roofs can play in the conservation of insect biodiversity in cities (Kadas, 2006; Colla *et al.*, 2009; MacIvor & Lundholm, 2011; Tonietto *et al.*, 2011; Madre *et al.*, 2013; Braaker *et al.*, 2014). In general these studies, however, have focused on describing patterns of diversity, with there still being a poor understanding of the colonisation process itself (Madre *et al.*,

Correspondence: Maria S. Fenoglio, Facultad de Ciencias Exactas, Centro de Investigaciones Entomológicas de Córdoba – Instituto Multidisciplinario de Biología Vegetal (CONICET), Físicas y Naturales, Universidad Nacional de Córdoba, Av. Vélez Sarsfield 1611 (X5016 GCA), Córdoba, Argentina.  
E-mail: mfenoglio@efn.uncor.edu

2013) or how species interact (Ksiazek *et al.*, 2012) in these novel habitats.

In an increasingly urban world, green roofs can provide an interesting management tool to reconcile the greening of cities with the ecosystem services provided by insects. Pest control has been mentioned among the ecological benefits that insect diversity can render to urban systems (Hunter & Hunter, 2008). Therefore, the potential of insect herbivores to colonise and successfully exploit plants on rooftops and of parasitoids to track their hosts on these newly created habitats is an area that deserves further attention (Cook-Patton & Bauerle, 2012).

For herbivorous insects and their parasitoids, the probability of locating the host plant is largely determined by spatial factors (Cronin & Reeve, 2005; Schoonhoven *et al.*, 2005). Finding the plant can be difficult in the urban landscape, since patches are scattered across an inhospitable matrix (Raupp *et al.*, 2010; Fenoglio *et al.*, 2013), thus insects can be affected by habitat fragmentation. In this context, it is expected that insect diversity will be lower in smaller and more isolated habitat patches, with species of higher trophic levels being the most susceptible (Kruess & Tschrantke, 1994; Holt *et al.*, 1999). Colonisation, extinction and population abundance have also been predicted to be affected by urban fragmented vegetation (Hanski, 1999; Niemelä, 1999). Nevertheless, this situation may be reverted if a network of patches on both the horizontal and vertical dimensions can be established. In fact, a recent study has demonstrated that green roofs can favour connectivity for highly mobile species (Braaker *et al.*, 2014). But prior to any further speculation, it is necessary to examine if hosts and parasitoids are able to colonise and exploit elevated habitats.

Here, we present an experimental study on host–parasitoid interactions on urban roofs. The model system we used to determine patch colonisation and exploitation was the specialist leaf-miner *Liriomyza commelinae* (Frost) (Diptera: Agromyzidae), its host plant *Commelina erecta* (Commelinaceae) and the associated parasitoid assemblage (Hymenoptera). Leaf-miners are ideal organisms to study colonisation due to mines offering a precise record of new arrivals and parasitoids constituting their main source of mortality (Parrella, 1987; Hespeneheide, 1991). Feeding patches were placed at the ground level and on the bare roofs of houses in Córdoba city (Argentina). In Argentina, the implementation of green roofs is a very recent trend in urban planning and developed principally in its capital city Buenos Aires (Saint Criq, 2012).

There is evidence that a variety of insects, including many bees and beetles, have been able to colonise green roofs (Kadas, 2006; Colla *et al.*, 2009; MacIvor & Lundholm, 2011; Tonietto *et al.*, 2011; Ksiazek *et al.*, 2012; Braaker *et al.*, 2014). Regarding leaf mining insects, although there is information on their horizontal dispersal ability from studies on urban habitat fragmentation (Denys & Schmidt, 1998; Rickman & Connor, 2003), agricultural pests (Chandler, 1985; Jones & Parrella, 1986; Minkenberg, 1988; Weintraub & Horowitz, 1996) or inva-

sive species (Nash *et al.*, 1995; Augustin *et al.*, 2009; Gebiola *et al.*, 2013), little is still known about their mobility at height within cities (Davis *et al.*, 2010; Peralta *et al.*, 2011). It has been suggested that individuals of the genera *Liriomyza* prefer to fly at low heights (Chandler, 1985; Weintraub & Horowitz, 1996), with Peralta *et al.* (2011) having detected that walls of concrete have a negative impact on the colonisation of host plants by *L. commelinae*. However, a recent study reported Agromyzidae flies in the pasture of living roofs (Davis *et al.*, 2010), and our preliminary observations have indicated the presence of *C. erecta* mined plants on the terraces and balconies of buildings (M. S. Fenoglio, pers. obs.). Therefore, the system suggested above is suitable for the present study.

Although it is known that parasitoids can reach considerable heights to attack herbivores that develop on trees (Hawkins, 1994; Compton *et al.*, 2000), there is little evidence on their ability to exploit resource patches placed on the roofs of buildings (Schindler *et al.*, 2011). Parasitoid colonisation usually depends on cues associated with the host itself, on the presence of plants with nectar and overwintering and mating sites (Shaw, 2006), as well as on patch size and isolation (Cronin, 2004; Elzinga *et al.*, 2007). Particularly for parasitoids of *L. commelinae* in cities, it has been shown that they can be more affected by distance from corridors rather than physical barriers or other potential hosts (Peralta *et al.*, 2011).

The parasitic complex of *L. commelinae* is comprised of idiobiont (prevents further host development at the time of parasitoid attack) and koinobiont (permits continued host development) species (Fenoglio & Salvo, 2009). This dichotomy could be a practical criterion in the absence of detailed rearing records for distinguishing between parasitoids that tend to be specialists (koinobionts) and parasitoids that are potentially more generalists (idiobionts) in terms of the host range attacked (Askew & Shaw, 1986; Hawkins *et al.*, 1990; Godfray, 1994; Memmott *et al.*, 1994). As in the study region Agromyzidae are mainly associated with koinobionts (Salvo, 1996), this group of parasitoids would be expected to search at low altitudes due to the increased concentration there of herbaceous plants, where leaf-miners could attain their maximum diversity (Memmott *et al.*, 1994; Lewis *et al.*, 2002). In contrast, as idiobionts tend to be more generalist species, they might have the potential to search for hosts located on plants of differing heights (Salvo, 1996). Another attribute that may influence the dispersal ability of parasitoid species is their body size (Roland & Taylor, 1997). In this sense, it would be expected that larger species are dispersed over greater distances than smaller ones (Tscharntke & Brandl, 2004).

Considering the above, we tested two hypotheses: (i) The leaf-miner *L. commelinae* and its parasitoids are able to colonise and exploit patches located at roof height, but with a lower efficiency than on the ground. Thus, we predict that patches localised on the roofs of houses would have lower colonisation rates and a longer colonisation time for both the leaf-miner and parasitoids, as well as

lower leaf-miner abundance, less parasitoid species richness and lower overall parasitism rates than patches on the ground (ii) The parasitoid species differ in their abilities to colonise the patches located on roofs due to traits related to their life strategy and body size. Thus, we predicted that there would be differences in parasitoid frequency association between host locations, with koinobionts and small species being mainly associated with hosts at ground level.

## Materials and methods

### Study system

The *L. commelinae* species is a neotropical and oligophagous leaf-miner that in the region of study is specialised on *C. erecta* (Valladares, 1984). The larvae burrow into the leaf parenchyma, forming distinct serpentine mines visible on the upper surface of the leaves, within which they pupate (Smith, 1987). Adults of *L. commelinae* live for 4 days on average and attain a peak abundance in the summer, especially during February and March in the study area (M. S. Fenoglio, unpubl. data). Its host plant *C. erecta* is a herbaceous perennial plant (leaves available only in summer, but rhizomes present all year) that grows in dry sandy soils of the north and centre of Argentina (Sérsic *et al.*, 2006). In urban systems, it is frequently detected on sidewalks, forming patches of different sizes at various distances from other patches (Fenoglio *et al.*, 2010) due its ruderal habitats. It is important to mention that *C. erecta* has been selected as one of the plant species suitable to be used in green roofs of Buenos Aires city (GCBA, 2012).

Parasitoids are the main source of mortality in *L. commelinae*, with 25 native Hymenopteran species being recorded in central Argentina, which cause on average a 50% mortality (Fenoglio & Salvo, 2009). Most of these parasitoids are solitary and polyphagous, feeding on various leaf-miner species in the study region (Salvo & Valladares, 1999; Fenoglio & Salvo, 2009). There are no

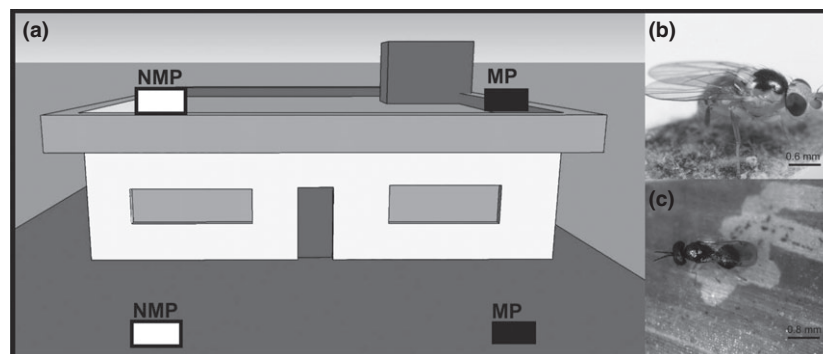
existing records of hyperparasitoids being associated with *L. commelinae*.

### Experiment

Eight houses located in different neighbourhoods of Córdoba city (31°21'S, 64°10'W) were selected for the study. In each house, non-mined and mined potted plants of *C. erecta* were placed in the front garden at ground level and on roofs, and the colonisation by the leaf-miner and its parasitoids was assessed respectively. The average height of the roofs of the houses was 3.25 m ( $\pm 0.57$ ).

The general methodology used here followed the one proposed by Peralta *et al.* (2011). Thirty-two pots (30 × 12.5 cm, 13 cm deep), each with three or four *C. erecta* plants were used for the experiment. Sixteen of these were exposed to field-collected *L. commelinae* adults in the laboratory. Two or three pots were placed in a cage (cardboard and voile, 60 × 36 × 36 cm deep) with adults of *L. commelinae* (seven females and nine males per cage) for approximately 48 h, at room temperature, to allow mating and oviposition. After 3–4 days, the approximate time taken for eggs to hatch, the total number of leaves, the number of mined leaves and the number of mines per leaf per pot were recorded to be able to expose both locations to a similar density of the leaf-miner.

Once this procedure was completed, four pots were placed in each house, two of which (a mined and non-mined) were separated by a distance of 3 m and put at ground level in the front garden with the remaining two (mined and non-mined) being placed on the roof directly above the bottom two (Fig. 1). The four pots were placed such that the distance from the sidewalks was the same. The structure of the vegetation in the gardens was in general very simple, predominantly with grass and a low diversity of plant species with flowers (0–3 spp.). To prevent the colonisation of plants by individuals reared at the same sites, all *C. erecta* plants were removed from gardens before starting the experiment, and it was checked that no plants had any other leaf-miner species



**Fig. 1.** (a) Schematic representation of a house typical from Argentina with its front garden and roof. Non-mined plants (NMP) and mined potted plants (MP) of *Commelina erecta* were placed at both locations to evaluate (b) *Liriomyza commelinae* colonisation and (c) parasitoid colonisation (i.e. *Chrysocharis flacilla*), respectively.

present. The houses were visited once a week over a period of 6 weeks (from 18th March to 22nd April, 2013), and at each visit all mined leaves from originally non-mined plants were collected to estimate the leaf-miner abundance. All leaves with pupae and/or larvae visibly parasitised from previously mined potted plants were used to estimate species richness and parasitism rates. The experimental plant exposure times selected were insufficient to allow leaf-miners from the mined plants to mature and colonise the non-mined plants. All the collected leaves were placed individually in plastic bags, transported to the laboratory, and kept until the flies and parasitoids emerged. Adult leaf-miners and parasitoids were stored in glass vials plugged with cotton wool. Then, once emergence had ceased, they were counted and identified (Salvo & Valladares, 1999).

The collection on each visit of all mined leaves from initially non-mined plants and all leaves with pupae and/or larvae visibly parasitised from previously mined potted plants ensured that individuals observed on the subsequent visit resulted from new colonising females. Since mined leaves were removed from the non-mined plants on each visit, this reduced the number of leaves available for colonisation. Therefore, an ANOVA test was performed to evaluate if the number of leaves available for oviposition differed between the ground and roof for each visit. No significant differences were found in any case ( $P > 0.05$ ), indicating no bias in the availability of leaves across treatments. Furthermore, it was statistically confirmed that the total number of exposed mines was similar in plants at ground level and on roofs (paired  $t$ -test,  $P = 0.81$ , ground: mean = 36.37, SE = 9.97; roof: mean = 34.75, SE = 6.30), which assured a similar amount of resources being available for parasitoids. At the end of the experiment, it was checked that the number of mines available (averaged per visit) did not change between gardens and roofs (paired  $t$ -test  $P = 0.09$ ). Differences in the daily mean temperature between plants on the ground and roof were also discarded (paired  $t$ -test,  $P = 0.70$ ).

At each sampling site, other variables were measured which may also influence the abundance and colonisation of *L. commelinae* and their parasitoids in urban environments (Fenoglio *et al.*, 2009; Peralta *et al.*, 2011). Previous evidence (Fenoglio *et al.*, 2009) has shown that the leaf-miner abundance increases with higher urbanisation within the city, and the specific composition of parasitoid species changes along the urbanisation gradient. Thus, we decided to take into account the level of urbanisation at each site, the abundance of the leaf-miner, as well as the abundance of one of the main alternative resources for parasitoids in each neighbourhood. The urbanisation level was estimated by measuring the vehicular traffic (mean number of vehicles/minute at maximum vehicular traffic time: 10 a.m.–12 p.m., for four replicates), due to this variable having been previously found to be correlated to other variables indicative of urbanisation (Fenoglio *et al.*, 2009). Neighbourhood leaf-miner abundance was estimated as the proportion of mined patches in the

surroundings of the focal house (total sidewalk length studied approximately 800 m long by 2 m wide) by counting all the patches (mined and non-mined) present on the sidewalks. In addition, the total number of *Jacaranda mimosifolia* Don. (Bignoniaceae), a common urban tree in Córdoba city, was determined in the surroundings of each house as a proxy for the presence of the specialist leaf-miner *Phytoliriomyza jacarandae* Steyskal and Spencer, 1978. It is known that this species is attacked by parasitoids, all Hymenoptera and mostly generalist species (Salvo & Valladares, 1997). Thus, this fact should be taken into account when analysing the data, since it is possible that experimental *C. erecta* plants on roofs represent a favourable resource for parasitoid species developing on *J. mimosifolia* trees.

Two response variables were calculated for the leaf-miner on non-mined plants and its parasitoid assemblage on mined plants: colonisation rate (number of visits where at least one new mine or parasitised mine was recorded/total number of visits), and colonisation time (number of days until the first mine or parasitised mine was observed). In addition, leaf-miner abundance (number of mines) from originally non-mined plants, and parasitoid species richness and parasitism rates (the total number of parasitoids divided by leaf-miner abundance) from mined ones were estimated. We also calculated the parasitoid species richness by rarefaction, since this method enables samples with different numbers of individuals to be compared (Magurran, 2004). The estimate of species richness was calculated from the lowest number of parasitoids among all samples by using the rarefy function of the vegan package of R software. For all variables, we added data obtained from the whole sampling period.

Parasitoids were categorised as idiobionts or koinobionts according to Salvo (1996) and in relation to their body size. Life strategy was used as a proxy of host range, since we had insufficient information about the number of herbivore species used by all the reared parasitoid species (Salvo & Valladares, 1999, 2004). Three categories of body size were defined using the terciles of the distribution of body length estimated by Fenoglio *et al.* (2010) for species of parasitoids associated with *L. commelinae*. The 'small' category included the first tercile, with species between 0.82 and 1.13 mm, while the 'large' category corresponded to the last tercile, with species from 1.60 to 1.77 mm. The 'medium' category comprised species with intermediate values.

#### Statistical analyses

*Leaf-miner.* General Linear Mixed Models were used to evaluate possible differences in the leaf-miner colonisation rate, colonisation time and leaf-miner abundance between patches located on the ground and roof. The house was included in the models as a random effect to account for the non-independence of the plants on the

ground and the roof of the same house. Vehicular traffic (log transformed) and neighbourhood leaf-miner abundance were added to the models as covariates. Multicollinearity was checked between covariates using the variance inflation vector, which was  $<5$  in all cases, indicating a good diagnosis (Logan, 2010). Conditional  $F$ -tests were used to assess the overall significance of fixed-effects terms in each model (Pinheiro & Bates, 2004). Pairwise interactions between the patch location and covariates were not included because of the limited degrees of freedom. Mixed models were conducted using the nlme package (Pinheiro *et al.*, 2007) of the R 2.15.1 environment (R Development Core Team, 2012). The model parameters were estimated by using maximum likelihood, and the model's assumptions were validated. Only data of leaf-miner abundance needed to be log transformed to achieve residual normality.

**Parasitoid assemblage.** The same model structure and procedure was used to detect differences in parasitoid colonisation rates, species richness and parasitism rates. As well as the covariates mentioned above, the abundance of *J. mimosifolia* (log  $x + 1$  transformed) was also incorporated into the models. The colonisation time for parasitoids could not be statistically analysed due to a lack of parasitoids in some of the roofs (see Results).

Parasitoid traits were studied using the exact  $G$ -tests, which allowed analysing the frequency associations of individuals classified according to their life strategy and body size in different patch locations. We decided to determine significant variations from expected values in

the parasitoid community between ground level patches and roofs, because few roofs had parasitoids.

## Results

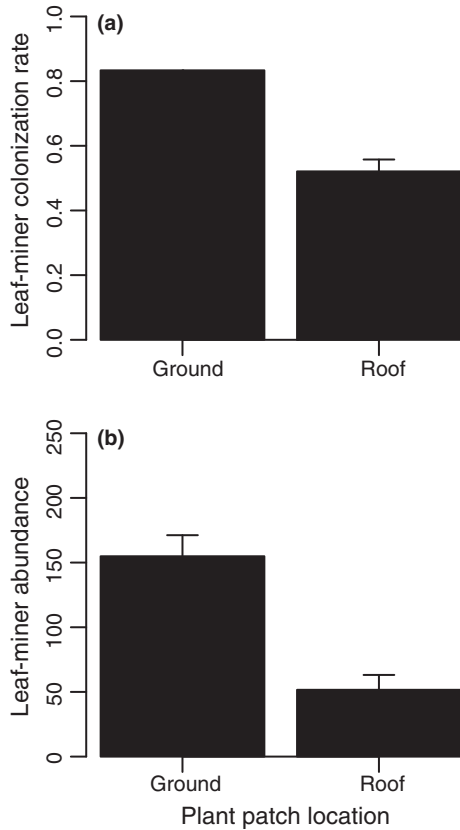
### Leaf-miner

The colonisation rate for *L. commelinae* was significantly affected by plant patch location (Table 1), with roofs having lower rates of colonisation (Fig. 2a). It is interesting to note that, however, on average, new mines were detected on roofs for half of the visits, which is not a negligible value. The times the leaf-miner took to colonise plants on roofs (mean = 14.87, SE = 0.88) and plants at ground level (mean = 14, SE = 0) were similar (Table 1). For all houses, the leaf-miner was first detected after the 14th day, with the exception of one house in which the herbivore colonised the plants located on the roof from day 21. Although we registered variations among sites in the vehicular traffic (range = 0.67–36.75) and in the proportion of mined patches in the neighbourhood (range = 0.55–1), neither of the covariates influenced the rate or time of colonisation (Table 1).

Throughout the study, 35.9% of the exposed leaves of *C. erecta* were mined by *L. commelinae*, with a total of 1652 mines being registered. The leaf-miner abundance per location varied between 10 and 291 larvae, which was significantly higher (Table 1) in plants situated at the ground level than on the roof (Fig. 2b). The number of mines detected in the experimental patches was indepen-

**Table 1.** Summary of  $F$  – ratios of main fixed effects from GLMMs of the factors affecting the colonisation rate, colonisation time and abundance of the leaf-miner as well as the colonisation rate by the parasitoid assemblage, parasitoid species richness, and parasitism rates. Model parameters were estimated by maximum likelihood (ML).

| Response variable                       | Fixed effects                          | $F_{(n.d.f., d.d.f.)}$  | $P$    |
|---|--|-------------------------|--------|
| Leaf-miner colonisation rate            | Patch location                         | 19.51 <sub>(1,7)</sub>  | 0.003  |
|   | Vehicular traffic                      | 0.22 <sub>(1,5)</sub>   | 0.65   |
|   | Neighbourhood abundance                | 0.09 <sub>(1,5)</sub>   | 0.77   |
| Leaf-miner colonisation time            | Patch location                         | 0.94 <sub>(1,7)</sub>   | 0.36   |
|   | Vehicular traffic                      | 0.95 <sub>(1,5)</sub>   | 0.37   |
|   | Neighbourhood abundance                | 0.20 <sub>(1,5)</sub>   | 0.67   |
| Leaf-miner abundance                    | Patch location                         | 14.29 <sub>(1,7)</sub>  | 0.006  |
|   | Vehicular traffic                      | 1.72 <sub>(1,5)</sub>   | 0.25   |
|   | Neighbourhood abundance                | 2.87 <sub>(1,5)</sub>   | 0.15   |
| Parasitoid assemblage colonisation rate | Patch location                         | 24.35 <sub>(1,7)</sub>  | 0.002  |
|   | Vehicular traffic                      | 3.06 <sub>(1,4)</sub>   | 0.15   |
|   | Neighbourhood abundance                | 0.07 <sub>(1,4)</sub>   | 0.80   |
|   | <i>Jacaranda mimosifolia</i> abundance | 2.44 <sub>(1,4)</sub>   | 0.19   |
| Parasitoid species richness             | Patch location                         | 40.97 <sub>(1,7)</sub>  | 0.0004 |
|   | Vehicular traffic                      | 2.33 <sub>(1,4)</sub>   | 0.20   |
|   | Neighbourhood abundance                | 0.0007 <sub>(1,4)</sub> | 0.97   |
|   | <i>J. mimosifolia</i> abundance        | 0.11 <sub>(1,4)</sub>   | 0.75   |
| Parasitism rate                         | Patch location                         | 46.55 <sub>(1,7)</sub>  | 0.0002 |
|   | Vehicular traffic                      | 3.93 <sub>(1,4)</sub>   | 0.11   |
|   | Neighbourhood abundance                | 0.97 <sub>(1,4)</sub>   | 0.38   |
|   | <i>J. mimosifolia</i> abundance        | 3.51 <sub>(1,4)</sub>   | 0.13   |



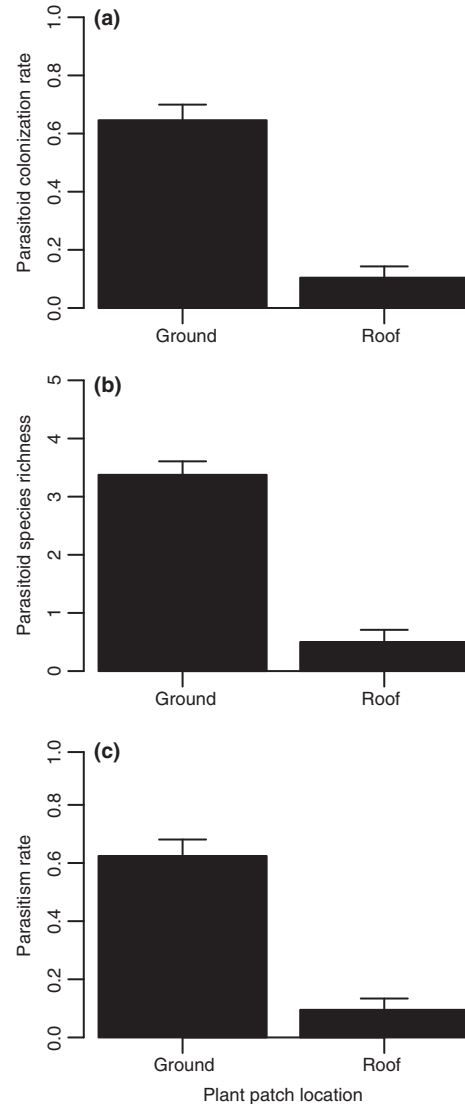
**Fig. 2.** (a) Colonisation rate (number of visits where at least one new mine was recorded over the total number of visits) and (b) abundance (mean  $\pm$  SE) of the leaf-miner *Liriomyza commelinae* in experimental patches of *Commelina erecta* located at ground level and on the roofs of houses ( $n = 8$ ).

dent of neighbourhood leaf-miner abundance and vehicular traffic (Table 1).

#### Parasitoid assemblage

The colonisation rate by parasitoids of the leaf-miner was significantly lower (Table 1) in patches located on roofs than that at the ground level (Fig. 3a). This pattern arose since only two of the eight houses evaluated had parasitoids associated with roofs. Of these two roofs, parasitoids were detected on the first and third visits respectively, indicating a short colonisation time, which was similar to the mean colonisation time for plants on the ground (mean = 12.25, SE = 1.75).

Of 465 adults (flies and parasitoids) reared from potted mined plants, 31% were parasitoids that represented 12 species of Hymenoptera, being mainly from the family Eulophidae (Table 2). Only four parasitoid species reached the roofs, which was reflected in the mean number of parasitoid species at this location and the mortality rate inflicted on the host being in line with the scarce colonisation rate present at this trophic level (Table 1). The



**Fig. 3.** (a) Colonisation rate by parasitoids (number of visits where at least one new parasitised mine was recorded over the total number of visits) (b) parasitoid species richness (c) overall parasitism rate of the leaf-miner (mean  $\pm$  SE) in experimental patches of *Commelina erecta* located at ground level and on the roofs of houses ( $n = 8$ ).

species richness of parasitoids varied between 0 and 5 species, and was significantly lower in plants on the roof than that at the ground level (Fig. 3b). Similar results were obtained for the rarefied species richness ( $F_{\text{patch location}} = 41.97$ ,  $P = 0.003$ ). Of the species colonising roofs, only one is known to attack *P. jacarandae* (Table 2). No effects of the abundance of *J. mimosifolia* tress (range = 0–11) and the rest of the covariates, however, were detected in parasitoid richness (Table 1). The overall percentage of parasitism suffered by the leaf-miners on roofs did not exceed 10%, marking a clear difference with patches at ground level, where parasitism increased by

**Table 2.** Taxonomic position, body size, life strategy, and total abundance of parasitoid species associated with *Liriomyza commelinae* in experimental plant patches at ground level and on the roofs of houses.

| Parasitoid species                       | Body size | Life strategy | Abundance |      |
|--|-----------|---------------|-----------|------|
|  |           |               | Ground    | Roof |
| Chalcidoidea–Eulophidae                  |           |               |           |      |
| <i>Chrysocharis caribea</i> (Boucek)     | Medium    | Koinobiont    | 3         | –    |
| <i>Chrysocharis flacilla</i> (Walker)    | Large     | Koinobiont    | 36        | –    |
| <i>Chrysocharis vonones</i> (Walker)     | Medium    | Koinobiont    | 20        | 1    |
| <i>Chrysocharis</i> Forster sp. A        | Small     | Koinobiont    | 27        | –    |
| <i>Chrysonotomyia</i> Ashmead sp. A*     | Small     | Idiobiont     | 5         | –    |
| <i>Chrysonotomyia</i> sp. B              | Small     | Idiobiont     | 7         | –    |
| <i>Diglyphus websteri</i> (Crawford)*    | Small     | Idiobiont     | 2         | –    |
| <i>Elachertini</i> sp. A                 | Medium    | Idiobiont     | 8         | 4    |
| <i>Elachertini</i> sp. B                 | –         | Idiobiont     | 1         | –    |
| Chalcidoidea–Pteromalidae                |           |               |           |      |
| <i>Halticoptera</i> sp. A*               | Large     | Koinobiont    | –         | 21   |
| <i>Herbertia</i> nr. <i>brasiliensis</i> | –         | Idiobiont     | –         | 1    |
| Cynipoidea–Figitidae                     |           |               |           |      |
| <i>Agrostocynips clavatus</i> (Diaz)     | Medium    | Koinobiont    | 1         | –    |

\*Species shared with *Phytoliriomyza jacarandae* (Salvo & Valladares, 1997).

**Table 3.** Total number of parasitoid individuals, classified according to their life strategy and body size, obtained from each patch location.

| Parasitoid trait | Ground level | Roof        |
|------------------|--------------|-------------|
| Life strategy    |              |             |
| Idiobiont        | 23 (22.48)   | 5 (5.52)    |
| Koinobiont       | 87 (87.52)   | 22 (21.48)  |
| Body size        |              |             |
| Small            | 41 (33.1)*   | 0 (7.9)*    |
| Medium           | 32 (29.87)   | 5 (7.13)    |
| Large            | 36 (46.02)*  | 21 (10.98)* |

The expected figures from a random distribution are indicated in brackets.

\*Values significantly deviated from those expected according to adjusted residuals ( $G$ -test,  $P < 0.0001$ ).

more than 50% (Fig. 3c). The same pattern found for species richness was detected for covariates and parasitism (Table 1).

Considering the whole community, a similar representation of idiobiont and koinobiont species was observed in plants on the roof and ground (Table 2), being the number of individuals of each category independent ( $G = 0.08$ ,  $P = 0.78$ ) of host location (Table 3). Of the parasitoid species colonising roofs, half were idiobionts (with 5 individuals) and the rest were koinobionts (with 22 individuals). Two species of parasitoids (both koinobionts) were found to be associated with the leaf-miner only on roofs, with *Halticoptera* sp. A being the most abundant and the fastest at colonising habitat patches at roof height.

Regarding body size, four species of the complex were classified as 'small', four as 'medium', with only two being 'large' (Table 2). Strong departures from expected values were observed for the abundance of parasitoids of differ-

ent sizes ( $G = 27.96$ ,  $P < 0.0001$ ). Interestingly, no individual of the 'small' category colonised roofs, and more individuals of this size than expected were associated with the leaf-miner in plants at ground level. Conversely, more individuals of 'large' species were observed on roofs and less on the ground compared to that expected under independence (Table 3).

## Discussion

The results of the present study revealed that the leaf-miner *L. commelinae* was able to locate *C. erecta* plants on rooftops, but with a lower rate of colonisation and abundance than at ground level. The leaf-miner, however, took the same period of time to find its host plant at both locations. For parasitoids, our results showed that only a few species of the assemblage were associated with the leaf-miner in plants on roofs. This resulted in decreasing colonisation rates, less species richness and lower parasitism rates, with body size being the only trait that seemed to be related to the ability of parasitoid species to colonise roofs.

The rate of colonisation by *L. commelinae* on feeding patches on roofs was lower, indicating that the leaf-miner searches for its host plant at a higher frequency on the ground, which is where herbaceous plants usually develop. A recent study on the vertical distribution and the effective height for insect flight has shown that *L. trifolii* (Burgess), a species closely related to *L. commelinae*, moves in altitudes lower than a metre (Byers, 2011). This may explain why patches located on the roofs of houses at an average height of three metres showed less colonisation by the leaf-miner. However, taking into account the overall picture, all the houses studied presented mines in plants

on roofs over time, thus reflecting the potential of *L. commelinae* to inhabit new habitats at roof height in the urban system. Monophagous herbivores, such as the species investigated, feed on a single plant-resource. Consequently their niche requirements in the urban environment are met by the presence of a single patch (Herrmann *et al.*, 2012), which might explain why the leaf-miner was capable of exploiting plants on roofs, despite these possibly being perceived as an isolated resource.

The pattern found for colonisation was also reflected in the pattern of resource exploitation by *L. commelinae*, being in the two cases independent of the level of urbanisation and the proportion of mined patches at the site. It is likely that the high abundance of larvae in plants at ground level was due to several flies having simultaneously arrived on plants in the gardens, or as a result of females that were able to reach roofs spending much of their energy in dispersal, and consequently leaving little for oviposition (Ellers *et al.*, 1998; Peralta *et al.*, 2011). This idea is supported by the fact that changes in dispersal patterns in Diptera probably involve changes in the reproductive potential of females (Roff, 1977).

For the parasitoid assemblage of *L. commelinae*, the results were in line with what was expected, indicating that although certain species of parasitoids were able to colonise habitat patches at roof height, these parasitoids usually searched for hosts at ground level, where the leaf-miners concentrated. Although previous studies have shown that the richness of Hymenoptera insects found on green roofs was similar to that at ground level (Kadas, 2006; MacIvor & Lundholm, 2011), it is important to emphasise that these insects belonged to Aculeata, a group with larger and fast moving species than those of Parasitica.

The overall parasitism rates of *L. commelinae* at ground level were more than double those on roofs, indicating a greater efficiency of attack at this location, even though the availability of resources was similar at both locations. As for the herbivore, no relationship was evident between the urbanisation level and the variables referring to the parasitoid community, which reinforces the importance of height in the colonisation process of these insects. Although the parasitoids studied here strongly attack *L. commelinae*, the most abundant resource in urban habitats (Fenoglio *et al.*, 2013), this variable did not have a significant impact on the community. The same result was found for the abundance of *J. mimosifolia* trees, discarding the idea that all houses with abundant trees have a higher species richness of parasitoids on rooftops.

In this investigation, we proposed that differences would be found in the ability of parasitoid species to colonise patches on roofs due to traits related to their life strategy and morphology. Evidence, however, was only obtained regarding the latter aspect. Although the representation of parasitoid species of ‘large’ and ‘small’ sizes was uneven in the complex, it is interesting that any individual of the ‘small’ category, which was well represented,

colonised plants on roofs even when the regional abundance was known to be higher than that of species categorised as ‘large’ (Fenoglio *et al.*, 2009). *Halticoptera* sp. A, classified as ‘large’, was only found at height and at a higher frequency than expected. Considering that this parasitoid also attacks *P. jacarandae*, we discarded the possibility that individuals of *Halticoptera* sp. A may have come from *J. mimosifolia* trees, as they were absent at the site where this plant species was registered. These results indicate a potential role of body size on the flight height that parasitoids can reach. Nevertheless, since small organisms can be displaced by air currents (Corbett & Rosenheim, 1996), further studies are necessary to discriminate active from passive dispersal.

Regarding our expectation that koinobionts, which tend to be specialists, would concentrate their search at the lower levels of vegetation (Salvo, 1996), the results were inconclusive since a similar richness and abundance of the koinobiont and idiobiont species were recorded. Nevertheless, these findings should be considered carefully, taking into account the exceptions that exist for the idiobiont–koinobiont dichotomy in relation to the host range of parasitoids (Arnaud, 1978; Mills, 1992). Once this information is available, the host range itself could be a better predictor of parasitoid colonisation. Many of the parasitoids of *L. commelinae* which attack other leaf-miners present on herbaceous plants (Salvo & Valladares, 1999) are likely to concentrate their search at ground level, due to an increased availability of alternative hosts in contiguous areas (Fenoglio *et al.*, 2009) as well as of food and resting sites (Shaw, 2006). Therefore, it is possible that the creation of green roofs with a larger structure, with a greater diversity of plant and host resources, would be capable of providing a better habitat for generalist species (Madre *et al.*, 2013).

In conclusion, our findings represent a first approximation of one of the potential biological roles that the implementation of green roofs might have on host–parasitoid interactions. The leaf-miner *L. commelinae* was capable of colonising and exploiting plant patches on roofs, albeit at a lower efficiency than for ground level patches. Therefore, it is possible that an increase in the number of plant patches available on roofs would favour the conservation of native specialist herbivore communities (Herrmann *et al.*, 2012). Agricultural weeds or ruderals common to disturbed sites are the main species involved in the spontaneous colonisation of plants on living roofs (Francis & Lorimer, 2011), thus the nature of the herbivore and plant species involved in the present study indicates the relevance of the ecological system when designing green roofs.

Regarding parasitoids, our results suggested that certain species have the ability to track their host on roofs. In spite of the short length of the present experiment, this is not insignificant and may be in fact auspicious since the number of parasitoid species inhabiting patches on roofs may increase over a longer time scale, and with different niches that provide habitat and resources (Brenneisen,



2006). Future studies that consider real green roofs, larger parasitoid species, as well as different altitudinal strata are required to strengthen the results of this investigation. This might also help to improve the understanding of the possible mechanisms of insect dispersal at roof height and whether green roofs can provide habitat compensation for species of beneficial insects that are negatively affected by the patchiness of their resources in urban areas (Denys & Schmidt, 1998; Fenoglio *et al.*, 2013).

### Acknowledgements

We thank Adriana Salvo, Guadalupe Peralta and two anonymous reviewers for helpful comments on the manuscript. Thanks are also due to all those who generously allowed us to conduct the experiments in their houses. Special thanks to Dr. Paul Hobson, native speaker, for reviewing the manuscript. This work was supported by FONCyT and CONICET. M. S. Fenoglio belongs to CONICET (Consejo Nacional de Investigaciones Científicas y Técnicas).

### References

- Arnaud, P.H. (1978) *A host-parasite catalog of North American Tachinidae (Diptera)*. United States Department of Agriculture, Miscellaneous Publication 1319.
- Askew, R.R. & Shaw, M.R. (1986) Parasitoid communities: their size, structure and development. *Insect Parasitoids* (ed. by J. Waage and D. Greathead), pp. 225–264. Academic Press, London, UK.
- Augustin, S., Guichard, S., Heitland, W., Freise, J., Svatos, A. & Gilbert, M. (2009) Monitoring and dispersal of the invading Gracillariidae *Cameraria ohridella*. *Journal of Applied Entomology*, **133**, 58–66.
- Braaker, S., Ghazoul, J., Obrist, M.K. & Moretti, M. (2014) Habitat connectivity shapes urban arthropod communities: the key role of green roofs. *Ecology*, **95**, 1010–1021.
- Brenneisen, S. (2006) Space for urban wildlife: designing green roofs as habitats in Switzerland. *Urban Habitats*, **4**, 27–36.
- Byers, J.A. (2011) Analysis of vertical distributions and effective flight layers of insects: three-dimensional simulation of flying insects and catch at trap heights. *Entomological Society of America*, **40**, 1210–1222.
- Chandler, L.D. (1985) Flight activity of *Liriomyza trifolii* (Diptera: Agromyzidae) in relationship to placement of yellow traps in bell pepper. *Journal of Economic Entomology*, **78**, 825–828.
- Colla, S.R., Willis, E. & Packer, L. (2009) Can green roofs provide habitat for urban bees (Hymenoptera: Apidae)? *Cities and the Environment*, **2**, 1–12.
- Compton, S.G., Ellwood, M.D.F., Davis, A.J. & Welch, K. (2000) The flight heights of chalcid wasps (Hymenoptera, Chalcidoidea) in a low land Bornean rain forest: fig wasps are the high fliers. *Biotropica*, **32**, 515–522.
- Cook-Patton, S.C. & Bauerle, T.L. (2012) Potential benefits of plant diversity on vegetated roofs: a literature review. *Journal of Environmental Management*, **106**, 85–92.
- Corbett, A. & Rosenheim, J.A. (1996) Quantifying movement of a minute parasitoid, *Anagrus epos* (Hymenoptera: Mymaridae), using fluorescent dust marking and recapture. *Biological Control*, **6**, 35–44.
- Cronin, J.T. (2004) Host-parasitoid extinction and colonization in a fragmented prairie landscape. *Oecologia*, **139**, 503–514.
- Cronin, J.T. & Reeve, J.D. (2005) Host-parasitoid spatial ecology: a plea for a landscape-level synthesis. *Proceedings of the Royal Society B*, **272**, 2225–2235.
- Davis, R., Simcock, R. & Toft, R. (2010) *Islands in the sky: urban biodiversity enhancement in NZ on indigenous living roof landscapes*. 44th Annual Conference of the Architectural Science Association, ANZAScA, Unitec Institute of Technology.
- Dearborn, D.C. & Kark, S. (2010) Motivations for conserving urban biodiversity. *Conservation Biology*, **24**, 432–440.
- Denys, C. & Schmidt, H. (1998) Insect communities on experimental mugwort (*Artemisia vulgaris* L.) plots along an urban gradient. *Oecologia*, **113**, 269–277.
- Ellers, J., Van Alphen, J.J.T. & Sevenster, J.G. (1998) A field study of size-fitness relationship in the parasitoid *Asobara tabida*. *Journal of Animal Ecology*, **67**, 318–324.
- Elzinga, J.A., van Nouhuys, S., van Leeuwen, D.J. & Biere, A. (2007) Distribution and colonization ability of three parasitoids and their herbivorous host in a fragmented landscape. *Basic and Applied Ecology*, **8**, 75–88.
- Fenoglio, M.S. & Salvo, A. (2009) *Liriomyza commelinae* (Diptera: Agromyzidae): an alternative host for parasitoids of the pest leafminer *Liriomyza huidobrensis*. *International Journal of Pest Management*, **55**, 299–305.
- Fenoglio, M.S., Salvo, A. & Estallo, E. (2009) Effects of urbanisation on the parasitoid community of a leafminer. *Acta Oecologica*, **35**, 318–326.
- Fenoglio, M.S., Salvo, A., Videla, M. & Valladares, G. (2010) Plant patch structure modifies parasitoid assemblage richness of a specialist herbivore. *Ecological Entomology*, **35**, 594–601.
- Fenoglio, M.S., Videla, M., Salvo, A. & Valladares, G. (2013) Beneficial insects in urban environments: parasitism rates increase in large and less isolated plant patches via enhanced parasitoid species richness. *Biological Conservation*, **164**, 82–89.
- Francis, R.A. & Lorimer, J. (2011) Urban reconciliation ecology: the potential of living roofs and walls. *Journal of Environmental Management*, **92**, 1429–1437.
- GCBA (2012) *Cubiertas verdes en edificios públicos*. Informe técnico. Gerencia Operativa de Cambio Climático y Energías Sustentables. Dirección General de Estrategias Ambientales. Agencia de Protección Ambiental. Ministerio de Ambiente y Espacio Público. Gobierno de la Ciudad de Buenos Aires, 25 pp.
- Gebiola, M., Lopez-Vaamonde, C., Nappo, A.G. & Bernardo, U. (2013) Did the parasitoid *Phaenocarpa mediterranea* (Hymenoptera: Eulophidae) track the invasion of the horse chestnut leafminer? *Biological Invasions*, **16**, 843–857.
- Godfray, H.C.J. (1994) *Parasitoids, Behavioral and Evolutionary Ecology*. Princeton University Press, Princeton, New Jersey.
- Hanski, I. (1999) *Metapopulation Ecology*. Oxford University Press, New York City, New York.
- Hawkins, B.A. (1994) *Pattern and Process in Host-Parasitoid Interactions*. Cambridge University Press, Cambridge, UK.
- Hawkins, B.A., Askew, R.R. & Shaw, M.R. (1990) Influences of host feeding-niche and food plant type on generalist and specialist parasitoids. *Ecological Entomology*, **15**, 275–280.
- Herrmann, D.L., Pearse, I.S. & Baty, J.H. (2012) Drivers of specialist herbivore diversity across 10 cities. *Landscape and Urban Planning*, **108**, 123–130.
- Hespenheide, H.A. (1991) Bionomics of leaf-mining insects. *Annual Review of Entomology*, **36**, 535–560.

- Holt, R.D., Lawton, J.H., Polis, G.A. & Martinez, N.D. (1999) Trophic rank and the species area-relationship. *Ecology*, **80**, 1495–1504.
- Hunter, M.R. & Hunter, M.D. (2008) Designing for conservation of insects in the built environment. *Insect Conservation and Diversity*, **1**, 189–196.
- Jones, V.P. & Parrella, M.P. (1986) The movement and dispersal of *Liriomyza trifolii* (Diptera: Agromyzidae) in a chrysanthemum greenhouse. *Annals of Applied Biology*, **109**, 33–39.
- Kadas, G. (2006) Rare invertebrates colonizing green roofs in London. *Urban Habitats*, **4**, 66–86.
- Kruess, A. & Tscharntke, T. (1994) Habitat fragmentation, species loss, and biological control. *Science*, **264**, 1581–1584.
- Ksiazek, K., Fant, J. & Skogen, K. (2012) An assessment of pollen limitation on Chicago green roofs. *Landscape & Urban Planning*, **107**, 401–408.
- Lewis, O.T., Memmott, J., Lasalle, J., Lyal, C.H.C., Whitefoord, C. & Godfray, H.J.C. (2002) Structure of a diverse tropical forest insect-parasitoid community. *Journal of Animal Ecology*, **71**, 855–873.
- Logan, M. (2010) *Biostatistical Design and Analysis Using R: A Practical Guide*. John Wiley & Sons, Oxford, UK.
- MacIvor, J.S. & Lundholm, J. (2011) Insect species composition and diversity on intensive green roofs and adjacent level-ground habitats. *Urban Ecosystems*, **14**, 225–241.
- Madre, F., Vergnes, A., Machon, N. & Clergeau, P. (2013) A comparison of three types of green roof as habitats for arthropods. *Ecological Engineering*, **57**, 109–117.
- Magurran, A.E. (2004) *Measuring Biological Diversity*. Blackwell Publishing, Malden, Massachusetts.
- Memmott, J., Godfray, H.J.C. & Gauld, I.D. (1994) The structure of a tropical host–parasitoid community. *Journal of Animal Ecology*, **63**, 521–540.
- Mills, N.J. (1992) Parasitoid guilds, life-styles, and host ranges in the parasitoid complexes of tortricoid hosts (Lepidoptera: Tortricidae). *Environmental Entomology*, **21**, 230–239.
- Minkenberg, P.J.M. (1988) Dispersal of *Liriomyza trifolii*. *Bulletin OEPP/EPPO Bulletin*, **18**, 173–182.
- Nash, D.R., Agassiz, D.J.L., Godfray, H.C.J. & Lawton, J.H. (1995) The pattern of spread of invading species: two leaf-mining moths colonizing Great Britain. *Journal of Animal Ecology*, **64**, 225–233.
- Niemelä, J. (1999) Ecology and urban planning. *Biodiversity & Conservation*, **8**, 119–131.
- Oberndorfer, E., Lundholm, J., Bass, B., Coffman, R.R., Doshi, H., Dunnett, N., Gaffin, S., Köhler, M., Liu, K.K.Y. & Rowe, B. (2007) Green roofs as urban ecosystems: ecological structures functions, and services. *Bio Science*, **57**, 823–833.
- Parrella, M.P. (1987) Biology of *Liriomyza*. *Annual Review of Entomology*, **32**, 201–224.
- Peralta, G., Fenoglio, M.S. & Salvo, A. (2011) Physical barriers and corridors in urban habitats affect colonization and parasitism rates of a specialist leaf miner. *Ecological Entomology*, **36**, 673–679.
- Pinheiro, J.C. & Bates, D. (2004) *Mixed Effects Models in S and S-Plus*. Springer, New York City, New York.
- Pinheiro, J., Bates, D., Debroy, S. & Sarkar, D., The R Core Team (2007) *nlme: Linear and Nonlinear Mixed Effects Models. R Package Version 3.1-86*. <http://CRAN.R-project.org/package=nlme> 20th July 2014.
- R Development Core Team (2012) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Raupp, M.J., Shrewsbury, P.M. & Herms, D.A. (2010) Ecology of herbivorous arthropods in urban landscapes. *Annual Review of Entomology*, **55**, 19–38.
- Rickman, J.K. & Connor, E.F. (2003) The effect of urbanization on the quality of remnant habitats for leaf-mining Lepidoptera on *Quercus agrifolia*. *Ecography*, **26**, 777–787.
- Roff, D. (1977) Dispersal in dipterans: its costs and consequences. *Journal of Animal Ecology*, **46**, 443–456.
- Roland, J. & Taylor, P.D. (1997) Insect parasitoid species respond to forest structure at different spatial scales. *Nature*, **386**, 710–713.
- Saint Ciriq, F.I. (2012) *Un bar en las alturas. Diseño de un local gastronómico ubicado en la terraza ajardinada de un edificio*. Tesis final de grado, Facultad de Diseño y Comunicación. Universidad de Palermo, Buenos Aires, Argentina. 89 pp.
- Salvo, A. (1996) *Diversidad y estructura en comunidades de parasitoides (Hymenoptera: Parasitica) de minadores de hojas (Diptera: Agromyzidae)*. Tesis Doctoral, Universidad Nacional de Córdoba, Córdoba, Argentina, 355 pp.
- Salvo, A. & Valladares, G.R. (1997) Regulación de *Phytoliriomyza jacarandae* (Diptera: Agromyzidae) por parasitoides (Hymenoptera: Chalcidoidea) en Córdoba, Argentina. *Acta Entomológica Chilena*, **18**, 113–118.
- Salvo, A. & Valladares, G.R. (1999) Parasitoid assemblage size and host ranges in a parasitoid (Hymenoptera)–agromyzid (Diptera) system from Central Argentina. *Bulletin of Entomological Research*, **89**, 193–197.
- Salvo, A. & Valladares, G.R. (2004) Looks are important: parasitic assemblages of agromyzid leafminers (Diptera) in relation to mine shape and contrast. *Journal of Animal Ecology*, **73**, 494–505.
- Schindler, B.Y., Griffith, A.B. & Jones, K.N. (2011) Factors influencing arthropod diversity on green roofs. *Cities and the Environment*, **4**, 1–20.
- Schoonhoven, L.M., vanLoon, J.J.A. & Dicke, M. (2005) *Insect-Plant Biology*. Oxford University Press, Oxford.
- Sérsic, A., Cocucci, A., Benítez Vieyra, S., Díaz, L., Glinos, E., Grosso, N., Lazarte, C. Y., Medina, M., Moré, M., Moyano, M., Nattero, J., Paiaro, V., Trujillo, C. & Wiemer, P. (2006) *Flores del centro de Argentina: una guía ilustrada para conocer 141 especies típicas*. Academia Nacional de Ciencias, Córdoba, Argentina.
- Shaw, M.R. (2006) Habitat considerations for parasitic wasps (Hymenoptera). *Journal of Insect Conservation*, **10**, 117–127.
- Smith, D.C. (1987) *The population dynamics in Jamaica of Liriomyza commelinae (Frost) (Diptera: Agromyzidae)*. Doctoral thesis, The University of West Indies, Trinidad y Tobago.
- Tonietto, R., Fant, J., Ascher, J., Ellis, K. & Larkin, D. (2011) A comparison of bee communities of Chicago green roofs, parks and prairies. *Landscape & Urban Planning*, **103**, 102–108.
- Tscharntke, T. & Brandl, R. (2004) Plant-insect interactions in fragmented landscapes. *Annual Review of Entomology*, **49**, 405–430.
- Valladares, G.R. (1984) Sobre el Género *Liriomyza* Mik 1894 (Diptera, Agromyzidae) en la República Argentina. *Revista Sociedad Entomológica Argentina*, **43**, 13–36.
- Weintraub, P.G. & Horowitz, A.R. (1996) Spatial and diel activity of pea leafminer (Diptera: Agromyzidae) in potatoes, *Solanum tuberosum*. *Environmental Entomology*, **25**, 722–726.

Accepted 25 February 2015

First published online 21 March 2015

Editor: Leather R. Simon

Associate editor: Broad Gavin