# Edge effects on insect–plant food webs: assessing the influence of geographical orientation and microclimatic conditions

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**Abstract.** 1. Geographical orientation affects the magnitude of microclimatic edge effects, mainly by altering the exposure to solar radiation. There is considerable evidence available concerning the influence of microclimatic edge effects on organisms at the population level, although little is known about effects at the community level, and variations with edge geographical orientation have barely been addressed. The present study investigated the influence of microclimatic conditions at the forest interior and edges with different geographical orientation on plant–leafminer–parasitoid food webs in the fragmented Chaco Serrano forest located in Central Argentina.

2. Microclimatic variables were measured in three locations: interior, north, and south-facing edges of six forest fragments. In each location, plant resource availability was assessed and mined leaves were collected to investigate plant–leafminer–parasitoid communities by rearing leafminer and parasitoid adults.

3. The results obtained revealed changes in the specific composition of plant, leafminer and parasitoid communities among locations, although they failed to detect location influences on most variables linked to abundance (except for leafminers), richness or food web structure. Leafminer abundance was negatively related to temperature, whereas their richness was related, also negatively, to moisture. Instead, parasitoids were favoured by higher temperatures and light levels, stronger winds, and lower humidity.

4. The results of the present study indicate that the effects of microclimatic conditions may depend on the trophic level considered. Moreover, the findings suggest that possible trade-offs between direct and indirect effects (such as plant quality, floral resources, etc.) of microclimatic conditions could influence plant and insect responses to location.

**Key words.** Communities, edge orientation, leafminers, microclimate, parasitoids.

## Introduction

The creation of edges, one of the main consequences of forest fragmentation, involves changes in microclimatic conditions at these new habitats as a result of the proximity of a structurally dissimilar matrix (Murcia, 1995; Ewers *et al.*, 2013). Taken together, these changes are termed 'microclimatic edge effects' and involve increased temperature levels and fluctuations, lower

humidity, and stronger winds, which in turn affect forest biodiversity, structure, and functioning (da Silva *et al.*, 2018).

Geographical orientation may influence the magnitude of microclimatic edge effects, through changes in the amount of exposure to solar radiation (Chen *et al.*, 1995; Murcia, 1995; Gehlhausen *et al.*, 2000; Heithecker & Halpern, 2007; Bernaschini *et al.*, 2019). In the southern hemisphere, south-facing edges experience milder microclimatic conditions compared with north-facing edges because the former receive lower insolation, which results in lower temperature and higher moisture levels (Matlack, 1993; Chen *et al.*, 1995; Murcia, 1995). The availability of habitats with favourable microclimates at local scale may buffer the impact of climate at regional scale, and

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the occurrence of such habitats should be considered for a better understanding of species distributions and their responses to global climate change (Bennie *et al.*, 2008; De Frenne *et al.*, 2013; Herrera *et al.*, 2014).

Microclimatic edge effects on organisms, at individual and population levels, have been shown by changes in physiology, behaviour, phenology, dispersion, and geographical distribution (Raghu *et al.*, 2004; Ries *et al.*, 2004; Harper *et al.*, 2005; Van der Putten *et al.*, 2010; van Halder *et al.*, 2011; Peyras *et al.*, 2013). However, little is known about the effects at the community level (Souza *et al.*, 2016). Even fewer studies, mostly focused on plant species, have considered the effects of microclimatic conditions in edges with different geographical orientation (Burton, 2002; Tomimatsu & Ohara, 2004; Hylander, 2005; Porensky, 2011; Eldegard *et al.*, 2015). Changes in microclimatic conditions associated with geographical orientation have been studied mainly in relation to mountain slopes, with reported effects on various vegetation aspects (Auslander *et al.*, 2003; Ortiz-Pulido & Pavón, 2010), as well as on development time, density, and activity of insect species (Auslander *et al.*, 2003; Pen-Mouratov *et al.*, 2009; Wu *et al.*, 2015).

Insects are ectothermic organisms whose physiological processes are highly sensitive to environmental temperature; therefore, they respond rapidly to thermal variations (Robinet & Roques, 2010; Colinet *et al.*, 2015). Insect performance increases progressively from a minimum critical temperature to an optimum, and then decreases quickly to a maximum critical temperature (Deutsch *et al.*, 2008). Indeed, temperatures outside the optimal developmental thresholds for insect species have been demonstrated to dramatically alter their performance parameters such as developmental time, size, morphology, longevity, fecundity, and sex ratio, as well as their distribution, abundance, and population structure (Bale *et al.*, 2002; Hance *et al.*, 2007; Menéndez, 2007; Robinet & Roques, 2010; Abram *et al.*, 2015; Sinclair *et al.*, 2016; Sentis *et al.*, 2017; CaraDonna *et al.*, 2018). In this context, and because of the relevance of herbivorous insects as crop pests (Bonebrake *et al.*, 2010) and their associated parasitoids as natural agents of biological control (Klapwijk *et al.*, 2010), plant–herbivore–parasitoid constitute particularly relevant food webs for investigation.

Together with temperature, other microclimatic variables such as humidity, wind velocity, and solar radiation can have both direct and indirect effects on insect performance (Hance *et al.*, 2007; Stoepler *et al.*, 2013). For example, solar radiation affects folivorous insects directly, as well as indirectly through changes in the quality of plant tissues resulting from variations in habitat temperature and humidity (Pincebourde *et al.*, 2007; Winter & Rostás, 2008; Klapwijk *et al.*, 2010; Lomelí-Flores *et al.*, 2010). Both humidity and temperature play an important direct role on the development time, longevity, and fecundity of parasitoids, with significant indirect effects on host location efficiency through changes on plant emission of signalling volatile compounds (Duale, 2005; Emana, 2007; Martínez & Hardie, 2009). In addition, light intensity affects host location by parasitoids because they are mainly guided by visual clues (Gu & Dorn, 2001). Wind speed can affect mating behaviour, oviposition, and leaf colonisation by herbivorous insects (Quiring & McNeil, 1987; Yamazaki, 2011), and also influences the movement of natural enemies, which could alter their dispersion and host search ability (Pasek, 1988; Marchand & McNeil, 2000; Gu & Dorn, 2001).

The response to microclimate differs among organisms according to their specific life-history traits (Robinet & Roques, 2010; Huey *et al.*, 2012). Species belonging to higher trophic levels are the most affected, being directly influenced by microclimatic changes, and also indirectly through the capacity of their hosts to adapt to such changes (Hance *et al.*, 2007; Huey *et al.*, 2012). Additionally, specialists tend to be more sensitive than generalist species to harsh microclimatic conditions, because they are unable to survive if their feeding resources are strongly diminished or locally extinct by such conditions (Cagnolo *et al.*, 2009; Valladares *et al.*, 2012).This differential response of species to microclimate could lead to destabilisation of the food webs in which they are involved (Dell *et al.*, 2014; Tylianakis & Binzer, 2014; Flores-Mejia *et al.*, 2016; Sagata & Gibb, 2016).

Chaco Serrano is a seasonally dry subtropical forest from Central Argentina, which has lost over 90% of its original cover in the last 30 years (Zak *et al.*, 2004). With the ongoing advance of agriculture and urbanisation, the forest has been reduced to a fragmented landscape comprising remnants of different sizes. A previous study reported that interior (I), north (NE), and south-facing edges (SE) of these forest remnants differ in microclimatic variables, particularly in summer, showing a gradient NE > SE > I from more extreme and variable to more stable conditions (Bernaschini *et al.*, 2019). Subsequent to those results, we aim now to analyse the influence of microclimatic conditions at forest interior and edges with different geographical orientation, on plant–leafminer–parasitoid food webs in fragmented Chaco Serrano. Descriptions of these food webs have been provided by Cagnolo *et al.* (2009, 2011) and Valladares *et al.* (2012).

Specifically, we evaluated the effects of microclimatic conditions on the abundance, species richness and composition at each level of the plant–insect food web. In addition, we assessed microclimate-related changes in food web parameters such as vulnerability (consumer load) and generality (range of resources exploited), focusing separately on plant–leafminer and host-parasitoid food-webs. We expected species richness and abundance to decrease with harsher microclimate (NE < SE < I) where conditions may reach beyond optimal development thresholds for most species. Moreover, as a result of the higher susceptibility of specialist species and those belonging to higher trophic levels, we predict lower vulnerability and higher generality in NE food webs, followed by those in SE and ultimately in I.

## Materials and methods

### Study area

The study was carried out in a fragmented Chaco Serrano landscape, with a predominantly agricultural matrix (31°09'S to 31°13'S and 64°13'W–64°17'W) in Córdoba, central Argentina (Zak *et al.*, 2004). This area has an average annual rainfall

of 750 mm concentrated mainly in the warm season (October to April), with average maximum and minimum temperatures between 26 and 10 °C, respectively (Luti *et al.*, 1979). The vegetation comprises an arboreal stratum (8–15 m) dominated by *Aspidosperma quebracho-blanco* Schltdl., *Prosopis* spp., *Fagara coco* Engl., and *Lithraea molleoides* (Vell.); a shrub layer (1.5–3 m) with *Celtis ehrenbergiana* (Klotzsch) Liebm. and *Acacia* spp; herbs and grasses (0–1 m); and several vine species (Luti *et al.*, 1979). Six forest remnants (hereafter 'sites') ranging between 10 and 20 ha in size and distant on average 300 m from each other, were selected through digital satellite images (Landsat TM) and field observations (see Supporting information, Figure S1). Three forest locations were delimited in each site: interior ('I') located 30 to 35 m from the dividing matrix−forest line, a north edge ('NE') and a south edge ('SE') located 2 m from the dividing matrix-forest line and geographically oriented towards the north and south, respectively (see Supporting information, Figure S1).

*Microclimatic measurements*

At each site and location, during 20–31 March 2013, 20−30 January, and 7–17 March 2014, point measurements of air temperature ($T_p$), humidity ($H$), and wind velocity ($V$) were taken every 5 min during a 20 min period using a weather station 'SINUS' 31.1095 placed 1 m above ground level. Additionally, 10 measurements of photosynthetically active radiation under the canopy (PARuc) were recorded by means of a ceptometer LICOR (LI-COR Environmental, Lincoln, Nebraska) (Stoutjesdijk & Barkman, 1992) along a linear 50-m long transect. Simultaneously, we measured values in places without vegetation (PARwv) to estimate (by the difference PARwv-PARuc) the percentage of photosynthetically active radiation intercepted by foliage (IPAR). All these point measurements were taken with a maximum difference of 90 min in the three locations of each site, during the period of greater solar radiation (12–13:30 h), when the temperature and moisture are comparatively steady (Davies-Colley *et al.*, 2000; Denyer *et al.*, 2006). The order in which data were taken at each location was randomly chosen for each site. Additionally, we took continuous records of air temperature through data-loggers suspended on tree trunks, 1 m high above the ground (iButton DS- 1921G-F5; iButtonLink, LLC, Whitewater, Wisconsin), which registered measurements every 1 h during 7 days in January 2013 and February 2014. Using these data, we calculated daily temperature range (DTR) and mean daily temperature ($T_m$).

*Biological measurements*

At each site and location, in coincidence with microclimatic measurements, two transects were delimited, one to evaluate the available plant resource for leafminers and the other to analyse plant−leafminer−parasitoid food web traits. On the first linear transect, a 50-m rope was held at a height of 1 m, and all leaves touching it were collected to assess the number of leaves per plant species and the foliar area available for herbivore consumption. For the latter measurement, each leaf was photographed on a white background using a digital camera (PS SX30; Canon, Tokyo, Japan) and then processed with the IMAGEJ (NIH, Bethesda, MD, U.S.A.). The second transect consisted of a strip (width 2 m, height 2 m, length 50 m length), superimposed to the linear transect, where all mined leaves were collected. Leaves were conditioned in the laboratory at room temperature within plastic bags to obtain leafminer and parasitoid adults (Salvo & Valladares, 1998). Afterwards, the insects were identified to morphospecies using dichotomous keys. Variables corresponding to the each trophic level in the food web were calculated for (i) plants (lower trophic level): mined plant richness, species composition, and indicator species; (ii) leafminers (mid trophic level) and (iii) parasitoids (higher trophic level): abundance, richness, species composition, and indicator species. Leafminer abundance was estimated as the total number of reared adults (leafminers plus parasitoids).

*Statistical analysis*

Richness of available plants, mined plants, leafminers and parasitoids were compared among locations through generalised linear mixed models (GLMMs) with Poisson error distribution, whereas, to compare abundance data (number of leaves, leafminers and parasitoids), we used the negative binomial function *glmer.nb* from the lme4 package to account for overdispersion (Bates & Sarkar, 2007). Likelihood ratio tests were employed to determine the significance of predictor variables in GLMMs (Bolker *et al.*, 2009). Foliar area available was compared among locations through linear mixed models (LMMs), previous log transformation of the variable. In all cases, sampling date and site, nested within sampling date, were included as random effects to contemplate temporal and spatial dependence of the data. Pairwise comparisons between locations were performed using Tukey's test with the *glht* function in the multcomp package (Hothorn *et al.*, 2019). We conducted GLMMs to evaluate the influence of microclimatic variables (mean temperature, point temperature, daily temperature range, humidity, wind speed, and IPAR) on the richness and abundance of each trophic level (plant, leafminers, and parasitoids), including resource variables in each case (plant richness, number of leaves, and foliar area available for mined plants and leafminers; leafminer abundance and richness were also included for parasitoids) as covariables; sampling date and site within sampling date were also included as random effects. Previously, we checked for correlations between predictor variables through the variance inflation factor (VIF), and excluded variables with VIF > 10. We used *dredge* and *model average* functions in the MuMIn package (Barton, 2013) to select the variables that best explained abundance and richness of each trophic level. Candidate models obtained by dredge function, were compared through the corrected Akaike information criterion (AICc) resulting from model average function (Burnham & Anderson, 2002), only including models with AICc values < 2. Because continuous temperatures were registered only once in 2014, data of biological variables from January and March of that year were averaged for analyses.

To test for effects of microclimatic conditions and resource variables on the composition of mined plants, leafminers and parasitoids, partial redundancy analyses (pRDA) were performed. The site was included as conditional variable to account for spatial dependence. Prior to the analyses, the species matrices were transformed using the Hellinger transformation, which reduces the importance of large abundances (Borcard *et al.*, 2011). Predictor variables with VIF > 10 were excluded, and pseudo-*F* and their *P* values were calculated by permutation tests based on 999 permutations. To evaluate the effect of location on species composition, we performed a permutational multivariate analysis of variance (PERMANOVA) using *adonis* function (with 999 permutations) of the vegan package (Oksanen *et al.*, 2010). Afterwards, we tested differences between locations through a pairwise multilevel comparison.

Quantitative parameters (generality and vulnerability) of plant–leafminer and host-parasitoid food-webs were calculated for each location and site (Bersier *et al.*, 2002; Tylianakis *et al.*, 2008), using the function *networklevel* of the bipartite package (Dormann *et al.*, 2008). Subsequently, we conducted LMMs to compare food web generality and vulnerability among locations, adding site as random effect to contemplate location dependence within each site.

We applied species indicator analysis to identify species of mined plants, leafminers and parasitoids that could be considered as indicators of each location, using *indval* function of the labdsv package (Dufrêne & Legendre, 1997; Roberts, 2013). All analyses were performed using R, version 3.3.1 (R Development Core Team, 2018).

## Results

### Plant, leafminer, and parasitoid richness and abundance

Overall, 203 species composed the studied food webs, including 63 plant species (see Supporting information, Table S1), 58 leafminer species (see Supporting information, Table S2), and 82 species of parasitoids (see Supporting information, Table S3). We collected a total of 18 471 mined leaves, from which 2788 were leafminers and 37.59% parasitoids. The collected mined leaves belonged largely to Solanaceae (41.85%), followed by Rhamnaceae (12.87%) and Malvaceae (8.26%). Leafminers were dominated by Lepidoptera (61.55% of all adults obtained), followed by Diptera (35.11%) and, to a lesser extent, Coleoptera (3.33%). Lepidoptera were represented by nine families, from which Gelechiidae was the most abundant (80%), whereas Diptera and Coleoptera were represented by one family each: Agromyzidae and Chrysomelidae, respectively. Parasitoids belonged to nine families of Hymenoptera, with Braconidae (37.69% of all parasitoids emerged) and Eulophidae (28.15%) being the most abundant.

No significant differences were detected among locations in terms of number of leaves and foliar area available for leafminers (Fig. 1b,c and Table 1), whereas plant richness was marginally higher in SE with respect to NE (Fig. 1a and Table 1). Mined plant richness was marginally higher in the forest interior than in NE (Fig. 2a and Table 1). Leafminer abundance was lower in edges than in the forest interior, without differences between
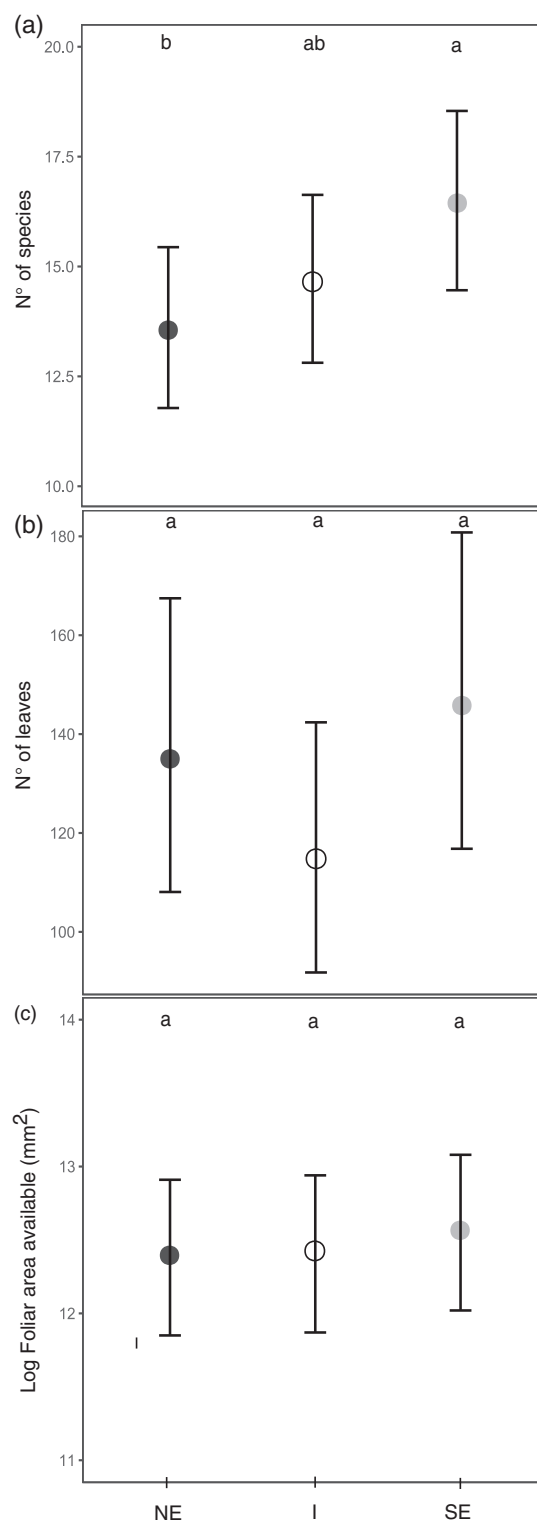


**Fig. 1.** Comparison of the available plant resource in three locations in fragmented Chaco Serrano, measured as (a) plant richness, (b) number of leaves, and (c) foliar area available. The mean of three sampling dates in six sites is shown. Error bars represent 95% confidence intervals. Different lowercase letters above bars indicate significant differences (*P* ≤ 0.05) among locations according to Tukey'd test.

**Table 1.** Results of generalized linear mixed models (GLMM) (through likelihood ratio test) and linear mixed model (LMM) comparing the available plant resources (estimated as plant richness, number of leaves and foliar area available), and the three trophic levels in plan-insect food webs (mined plant, leafminer and parasitoid richness and abundance) among locations (NE, I and SE).

| Response variable | d.f. | Statistic | P |
|---|---|---|---|
| Available plant resources | | | |
| Plant richness | 2 | $\chi^2 = 5.12$ | 0.08 |
| Number of leaves | 2 | $\chi^2 = 4.63$ | 0.10 |
| Foliar area available (log) | 2,34 | $F = 0.53$ | 0.59 |
| Trophic level richness | | | |
| Mined plants | 2 | $\chi^2 = 5.30$ | 0.07 |
| Leafminers | 2 | $\chi^2 = 0.50$ | 0.78 |
| Parasitoids | 2 | $\chi^2 = 0.63$ | 0.73 |
| Trophic level abundance | | | |
| Leafminers | 2 | $\chi^2 = 10.37$ | **0.006** |
| Parasitoids | 2 | $\chi^2 = 3.84$ | 0.15 |

Significant *P*-values are shown in bold.

SE and NE (Fig. 2b and Table 1); no significant effect of location was detected neither in leafminer and parasitoid species richness, nor in parasitoid abundance (Fig. 2 and Table 1).

According to the GLMMs evaluating the influence of microclimatic variables on each trophic level, the best model for mined plant richness included only the available plant richness as a significant predictor (Table 2). Instead, humidity and point temperature had a negative effect on leafminer richness (Table 2) and mean temperature negatively affected leafminer abundance (Table 2), which was also positively (but marginally) associated with DTR (Table 2). Parasitoids were affected by mean (richness) and point (abundance and richness) temperature measurements, positively in both cases (Table 2). Wind velocity only affected parasitoid abundance, with a positive effect (Table 2). Additionally, parasitoid species richness was negatively related to humidity and IPAR, albeit marginally in the latter case (Table 2). Regarding resource availability, parasitoid richness directly depended on leafminer richness and abundance, whereas their abundance was positively related to leafminer abundance (Table 2).

*Plant, leafminer, and parasitoid species composition*

Resource variables did not affect species composition of either of the trophic levels in the studied food webs (plant−leafminer−parasitoid) (P > 0.05 in all cases). However, the microclimatic pRDA revealed a significant relationship between microclimatic variables and the specific composition of plant community attacked by leafminers ($F_{6,18} = 1.55$, $P = 0.01$, F distribution based on 999 permutations, $r^2 = 0.39$, $r^2$ adjusted = 0.23). The first two ordination axis explained 30% of the total variance in mined plant composition. The ordination plot (Fig. 3a) clearly separated mined plant assemblages on locations. These findings were supported by PERMANOVA that showed significant differences in mined plant composition among the three locations (Table 3). For leafminers and parasitoids, microclimatic variables failed to explain differences

in species composition through pRDA ($F_{6,18} = 1.07$, 1.23, respectively; $P > 0.05$, F distribution based on 999 permutations) (Fig. 3b,c). However, a significant difference in species composition between SE and I was detected in the PERMANOVA analysis for both leafminer (Fig. 3b and Table 3) and parasitoid communities (Fig. 3c and Table 3).

*Interactions in plant−leafminer and leafminer−parasitoid food webs*

The studied organisms integrated complex bitrophic food webs (plant−leafminer and leafminer−parasitoid) in the fragmented Chaco Serrano (Figs 4 and 5). Leafminer species (Fig. 4) were clearly more specialised than parasitoids species (Fig. 5), as shown by the larger number of links from most parasitoid species as compared with those from each leafminer species.

Food web parameters did not vary among locations neither in the bitrophic food web integrated by plants and leafminers (generality $F_{2,10} = 1.42$, $P = 0.29$; vulnerability $F_{2,10} = 0.32$, $P = 0.73$), nor in the leafminer−parasitoid food web (generality $F_{2,10} = 2.39$, $P = 0.14$; vulnerability $F_{2,10} = 1.59$, $P = 0.25$).

*Indicator species*

Indicator species analysis revealed that 14 species showed greater affinity for a particular location. Within the first trophic level, we found that *Gomphrena pulchella*, *Malvastrum coromandelianum*, and *Janusia guaranitica* were the species of mined plants most strongly linked to north-facing edges (Table 4), whereas *Fleischmannia prasiifolia*, *Bidens subalternans*, *Iresine diffusa*, and *Anredera cordifolia* were associated with south-facing edges (Table 4). The interior locations were mainly represented by *Setaria oblongata* and *Sida dyctiocarpa* (Table 4). The leafminers *Tischeria* sp2 and *Haplopeodes near tigrensis* were preferentially found in the forest interior (Table 4). Finally, parasitoids *Phaedrotoma* sp1 and *Copidosoma* sp1 were mostly associated with interior locations (Table 4), with the parasitoid *Mirax* sp1 acting as indicator of south-facing locations (Table 4).

## Discussion

The present study, involving interior and differently oriented edges in a fragmented Chaco Serrano forest, revealed changes in the taxonomic composition of plant, leafminer and parasitoid communities, although it failed to show changes in their abundance (except for leafminers), richness or food web structure among those habitats. Nonetheless, we found differential influences of microclimatic variables depending on the trophic level of the studied food webs. These findings provide relevant evidence on the effects of location and microclimatic influences on plant−insect food webs.

*Species richness and abundance*

The results appear to be representative of similar systems in the same region, with comparable percentages of adults
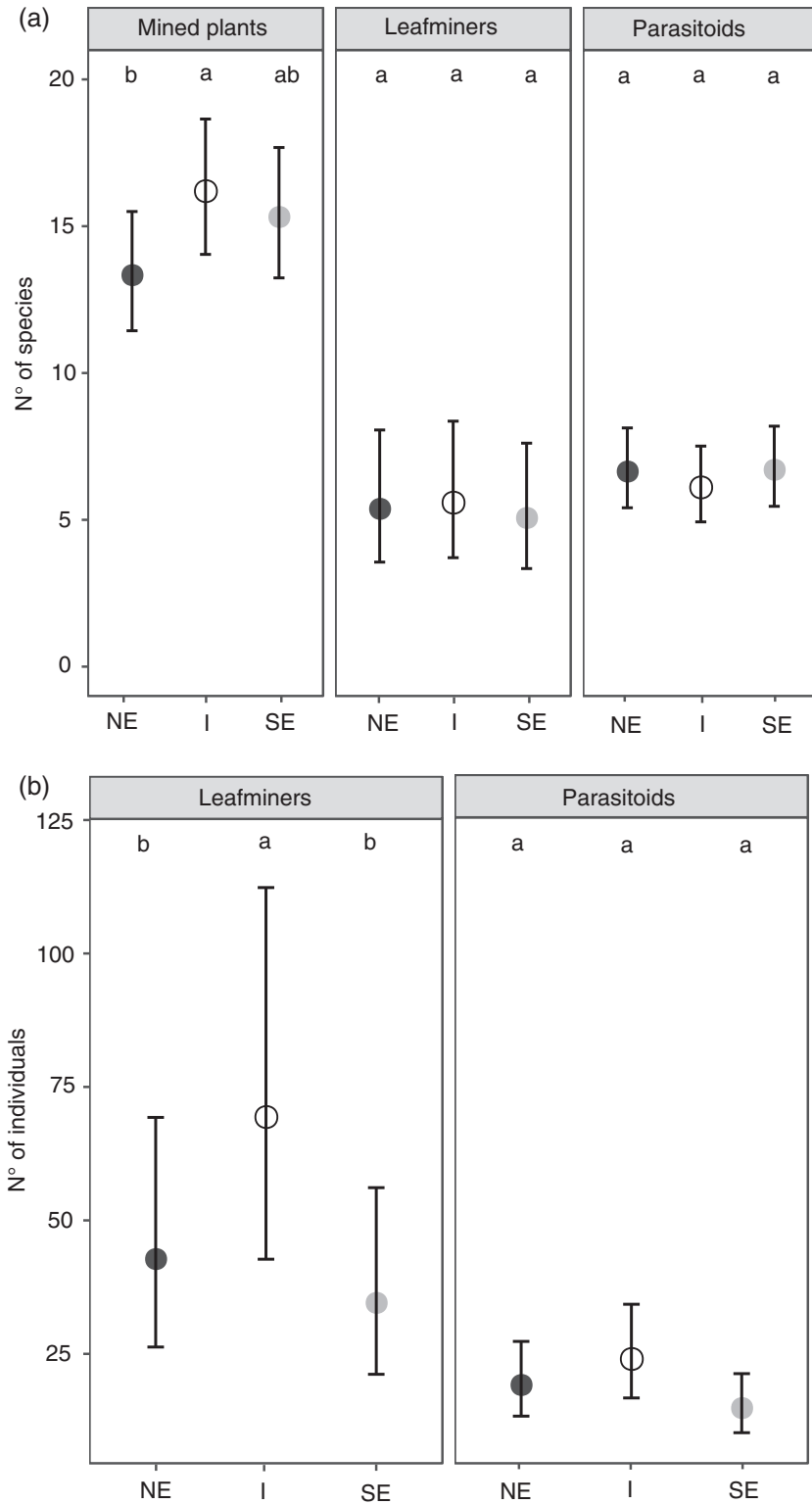
**Fig. 2.** Comparison of (a) species richness of mined plants, leafminers and parasitoids, and (b) leafminer and parasitoid abundance, in the studied locations. The mean of three sampling dates in six sites is shown. Error bars represent 95% confidence intervals. Different lowercase letters above bars indicate significant differences ($P \leq 0.05$) among locations according to Tukey's test.

**Table 2.** Model average parameter estimates, standard error (SE), and *Z* and *P* values for the predictors (microclimatic and plant resource variables) included in the best models (ΔAICc < 2) explaining species richness (1) and abundance (2) in each trophic level of insect-plant food webs (a = mined plants, b = leafminers and c = parasitoids) from three locations in fragmented Chaco Serrano.

| Model average parameters | Estimate | SE | Z | P |
|---|---|---|---|---|
| **Richness** | | | | |
| Mined plants | | | | |
| Intercept | 2.742 | 0.042 | 62.018 | <0.001 |
| Number of leaves | −0.052 | 0.045 | 1.107 | 0.268 |
| Plant richness | 0.136 | 0.043 | 3.011 | **0.003** |
| $T_m$ | −0.050 | 0.043 | 1.069 | 0.285 |
| Leafminers | | | | |
| Intercept | 1.809 | 0.069 | 26.065 | <0.001 |
| H | −0.293 | 0.074 | −3.975 | **<0.001** |
| $T_p$ | −0.262 | 0.068 | −3.830 | **<0.001** |
| Parasitoids | | | | |
| Intercept | 1.899 | 0.073 | 25.004 | <0.001 |
| Leafminer richness | 0.192 | 0.087 | 2.140 | **0.032** |
| $T_p$ | 0.165 | 0.073 | 2.186 | **0.029** |
| Leafminer abundance | 0.198 | 0.094 | 2.041 | **0.041** |
| IPAR | −0.133 | 0.073 | 1.744 | 0.081 |
| $T_m$ | 0.159 | 0.082 | 1.864 | 0.062 |
| *H* | −0.153 | 0.070 | 2.094 | **0.036** |
| **Abundance** | | | | |
| Leafminers | | | | |
| Intercept | 4.000 | 0.100 | 38.492 | <0.001 |
| DTR | 0.167 | 0.090 | 1.776 | 0.076 |
| $T_m$ | −0.336 | 0.132 | 2.460 | **0.014** |
| Parasitoids | | | | |
| Intercept | 2.876 | 0.045 | 59.086 | <0.001 |
| Leafminer abundance | 0.526 | 0.040 | 12.553 | **<0.001** |
| $T_p$ | 0.137 | 0.047 | 2.785 | **0.005** |
| *V* | 0.115 | 0.042 | 2.594 | **0.009** |
| Plant richness | −0.070 | 0.043 | 1.541 | 0.123 |

DTR, daily temperature range; H, humidity; IPAR, interception of photosynthetically active radiation; $T_m$, mean temperature; $T_p$, point temperature; *V*, wind velocity.

successfully reared (15%) from the collected mined leaves, overall parasitism rates (37%) (Valladares *et al.*, 2006), and specific composition (Salvo *et al.*, 2011).

In terms of species richness, only the number of plant species (available plants as well as mined ones) was influenced by the orientation of edges in our study, with north-facing edges displaying an impoverished vegetal community. Survival and germination of trees and herbs can be negatively affected by sun exposed edges (Burton, 2002; Tomimatsu & Ohara, 2004), which could consequently reduce plant species richness. Because the number of plants species consumed by leafminers was also lowest at north facing-edges and directly related to available plant richness, a relatively constant proportion of the available species appears to be exploited by these herbivores, as observed in other studies (Coley *et al.*, 1985).

Although differences in species richness of herbivore (including leafminers) and parasitoid insects between forest interior and edge habitats have been reported from Chaco Serrano (Cagnolo *et al.*, 2006; Rossetti *et al.*, 2013; González *et al.*, 2016; Rossi

Rotondi *et al.*, 2019), the present study did not corroborate those results, nor did we find differences related to edge orientation. Other studies have also found similar herbivore species richness between forest interior and edges (Wirth *et al.*, 2008) or between differently oriented edges (Maeto *et al.*, 2002). One possible explanation is that species were physiologically, as well as genetically, adapted to each location conditions (Huey *et al.*, 2012). In addition, ectothermic organisms are able to adapt their behaviour to cope with stressful environments (Abram *et al.*, 2017); for example, searching for shaded places when they are exposed to high insolation levels. As far as we know, there are no available data about parasitoid and leafminer communities in relation to the geographical orientation of edges.

Notwithstanding their lack of differences among locations, leafminer and parasitoid richness showed links to particular microclimatic conditions. Thus, in contrast to the literature (Fernandes *et al.*, 2004; Kalyebi *et al.*, 2005, 2006; Emana, 2007; Schirmer *et al.*, 2008), both leafminer and parasitoid communities showed more species under lower moisture levels. This could be attributed to an indirect effect, operating through drought stress of host plants, which could promote colonisation by different herbivore species (Kautz *et al.*, 2013; da Silva *et al.*, 2018) and, consequently, influence parasitoid richness. Also, leafminer and parasitoid populations in semi-arid systems, such as the one investigated in the present study, might be physiologically and behaviourally better adapted to colonise and reproduce on plants growing under low moisture conditions. Parasitoid richness was also favoured by higher (mean and point) temperatures and solar radiation levels. More luminous habitats may improve host searching by parasitoids through enhancement of visual cues, whereas higher temperatures may facilitate muscular activity and consequently improve locomotor abilities (Barbosa & Frongillo, 1977; Gu & Dorn, 2001; Stoepler *et al.*, 2013).

As we expected, leafminers were more abundant at the interior than at the forest edges, a result consistent with records of herbivory levels by leafminers in the same region (Valladares *et al.*, 2006). Similar results were reported by McGeoch and Gaston (2000) and were attributed to a higher mortality of mining-larvae by desiccation at edges, a possibility supported by the negative effects of mean temperature on leafminer abundance found in our study. In Chaco Serrano edges, temperature values may have reached above the optimal development thresholds for these organisms (Deutsch *et al.*, 2008), leading to greater larval mortality with respect to the forest interior. Temperature differences between edges with different orientation may not have been sufficiently large to cause significant changes in leafminer abundance (Bernaschini *et al.*, 2019).

By contrast, parasitoid abundance was favoured by greater point temperatures and stronger winds, as well as by a higher availability of leaf-mining larvae (as estimated by the total number of reared adults). Surprisingly, differences in the number of parasitoids between locations were not detected, even when the affecting microclimatic variables differed among them, as was reported by Bernaschini *et al.* (2019). These findings suggest that factors other than abiotic conditions ones and host availability underlie changes in parasitoid abundance in the studied locations. For example, parasitoids could be affected
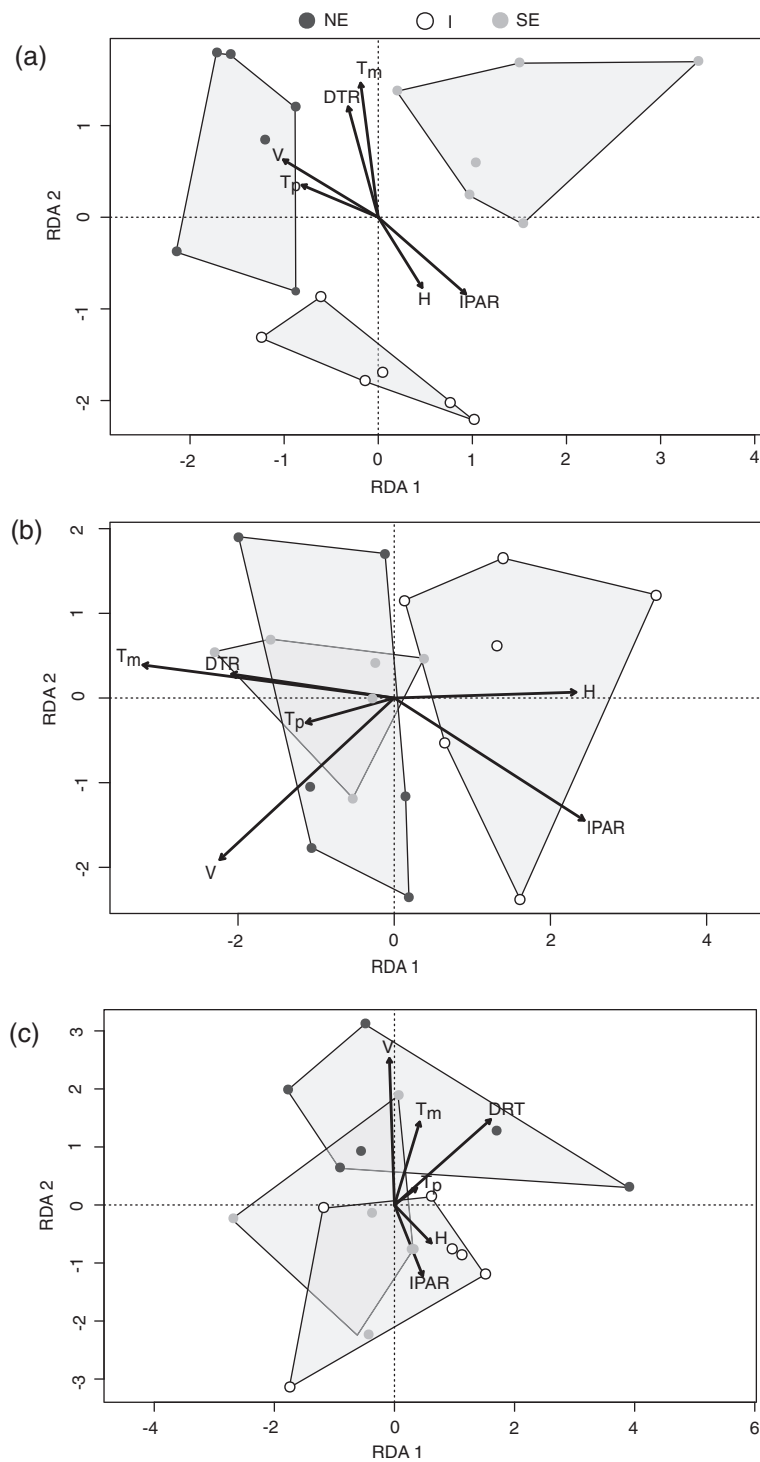
**Fig. 3.** Partial redundancy analyses (RDA) biplots showing the effect of microclimatic variables on the species composition of (a) mined plants, (b) leafminers, and (c) parasitoids. DTR, daily temperature range; H, humidity; IPAR, interception of photosynthetically active radiation; $T_m$, mean temperature; $T_p$, point temperature; $V$, wind velocity.

by the quality and quantity of floral resources (pollen and nectar) whose availability, in turn, might differ among locations (Tylianakis *et al.*, 2004; Lee *et al.*, 2006).

The positive link between parasitoid abundance and point temperature suggests that temperature range may be optimal for these species, so that higher temperatures allow faster development rates (Deutsch *et al.*, 2008). An independent research in the same study system reported greater number of parasitoids captured by yellow water traps in forest edges with respect to forest interior, with such differences being explained by positive links to temperature and light levels (Rossi Rotondi *et al.*, 2019). The positive relationship between

**Table 3.** Results of permutational multivariate analysis of variance comparing species composition within each trophic level (mined plants, leafminers and parasitoids) among forest interior (I) and north and south-facing edges (NE, SE).

| Trophic level locations compared | d.f. | $F$ | $r^2$ | $P$ |
|---|---|---|---|---|
| Mined plants | 2 | 2.41 | 0.24 | **0.001** |
| NE versus SE | | 2.51 | 0.20 | **0.004** |
| NE versus I | | 2.11 | 0.17 | **0.017** |
| SE versus I | | 2.65 | 0.21 | **0.002** |
| Leafminers | 2 | 1.55 | 0.17 | **0.073** |
| NE versus SE | | 1.08 | 0.10 | 0.329 |
| NE versus I | | 1.45 | 0.13 | 0.178 |
| SE versus I | | 2.21 | 0.18 | **0.019** |
| Parasitoids | 2 | 1.67 | 0.18 | **0.02** |
| NE versus SE | | 1.17 | 0.10 | 0.278 |
| NE versus I | | 1.58 | 0.14 | 0.080 |
| SE versus I | | 2.43 | 0.19 | **0.022** |

Results of pairwise multilevel comparison are provided.

parasitoid abundance and faster winds observed in the present study, disagrees with studies showing negative wind effects on parasitoid populations via changes in mate searching behaviour or host searching activities (Messing *et al.*, 1997; Marchand & McNeil, 2000; Gu & Dorn, 2001). Also, our data suggest that parasitoid abundance was strongly associated with leaf-mining larvae availability, as predicted by the 'resource concentration hypothesis' (Root, 1973). Further research will be necessary to disentangle direct microclimate effects on parasitoid abundance from those mediated by changes on host populations. Finally, it is important to note that some parasitoid species have the potential to mitigate climate variability through acclimation, diapause and/or innate resistance to thermal extremes (Thomson *et al.*, 2010).

*Species composition*

Location influence on specific composition of the assemblages found at each individual trophic level was possibly the most consistent trend in our results. In particular, the composition of mined plants, the basal trophic level in the studied food webs, differed among locations and between differently oriented edges, and was also associated with changes in microclimatic variables. Differential preferences of plant species for habitats with different microclimatic conditions could alter resource availability for herbivores (Auslander *et al.*, 2003; Rae *et al.*, 2006). Because leafminers tend to be highly specialised, changes in the assemblage of mined plants may reflect a combination of changes in herbivore composition and changes in the plant community itself.

Leafminer and parasitoid species composition also varied among locations, although our data failed to link such variations to microclimatic conditions. Nevertheless, locations are likely to differ in attributes other than microclimate, including plant resource quality and defences against herbivores (Cronin, 2003; Bidart-Bouzat & Imeh-Nathaniel, 2008; Barber & Marquis, 2011; Kautz *et al.*, 2013; Bagchi *et al.*, 2018; da Silva *et al.*, 2018), exposure to insecticides from the adjacent cultivated

matrix, movement of organisms between matrix and forest (González *et al.*, 2016) or the availability of floral resources and nesting sites (Chacoff & Aizen, 2006; Hagen & Kraemer, 2010; Bailey *et al.*, 2014), amongst others. These factors, which could in turn be affected by microclimatic conditions, may finally influence the composition of herbivore and parasitoid communities, either directly or indirectly through cascading effects. Furthermore, leafminer and parasitoid adults could be moving from one location to another in search of places with suitable conditions, leading to species replacement among locations.

Changes in community composition may reflect species-specific differences in tolerance to particular conditions and/or preference for particular habitats. According to our analysis of indicator species, interior conditions were apparently more generally benign for leafminer species (with no species preferring edges), whereas plants and parasitoids showed species-specific links to interior habitats and edges with different orientation. Species tolerance range to particular environmental conditions can be a relevant factor for explaining biological responses to habitat degradation (Jiguet *et al.*, 2006) and to edge conditions in fragmented landscapes (Peyras *et al.*, 2013).

*Interactions in plant−leafminer and leafminer−parasitoid food webs*

The above discussed influences of location and microclimatic conditions on plant and insect communities did not translate into changes in species interactions, as indicated by vulnerability and generality, for either plant−leafminer or leafminer−parasitoid food webs. According to several studies, changes in the structure of trophic networks can be associated with reductions in the number of species, changes in species composition, disruption of interactions, and extreme sensitivity of species at higher trophic levels (Tylianakis *et al.*, 2007; Valladares *et al.*, 2012; Tylianakis & Binzer, 2014; Flores-Mejia *et al.*, 2016). For example, vulnerability in leafminer−parasitoid food webs was previously shown to decrease with forest size reduction, accompanied by a marked loss of species (Valladares *et al.*, 2012). In the present study, the lack of changes in species richness may explain, at least partially, the similarity of food web parameters among locations: after all, generality indicates how many different resources are consumed and vulnerability shows the number of consumers supported by each species. Nonetheless, generality in plant−leafminer as well as in leafminer−parasitoid food webs might have been expected to change among locations because the identity of the species at the resource level (plants/leafminers), as well as that of the consumers (leafminers/parasitoids), was different. The occurrence of a pair of leafminer species (*Gelechiidae* sp1 and *Haplopeodes near tigrensis*) equally dominant in the three locations may have masked some subtle differences in plant and leafminer interactions. In addition, a lack of variation in food web generality suggests that microclimate effects were independent of feeding strategy, despite the higher susceptibility shown by specialist species in these fragmented landscapes (Cagnolo *et al.*, 2009). These results provide the first available evidence about
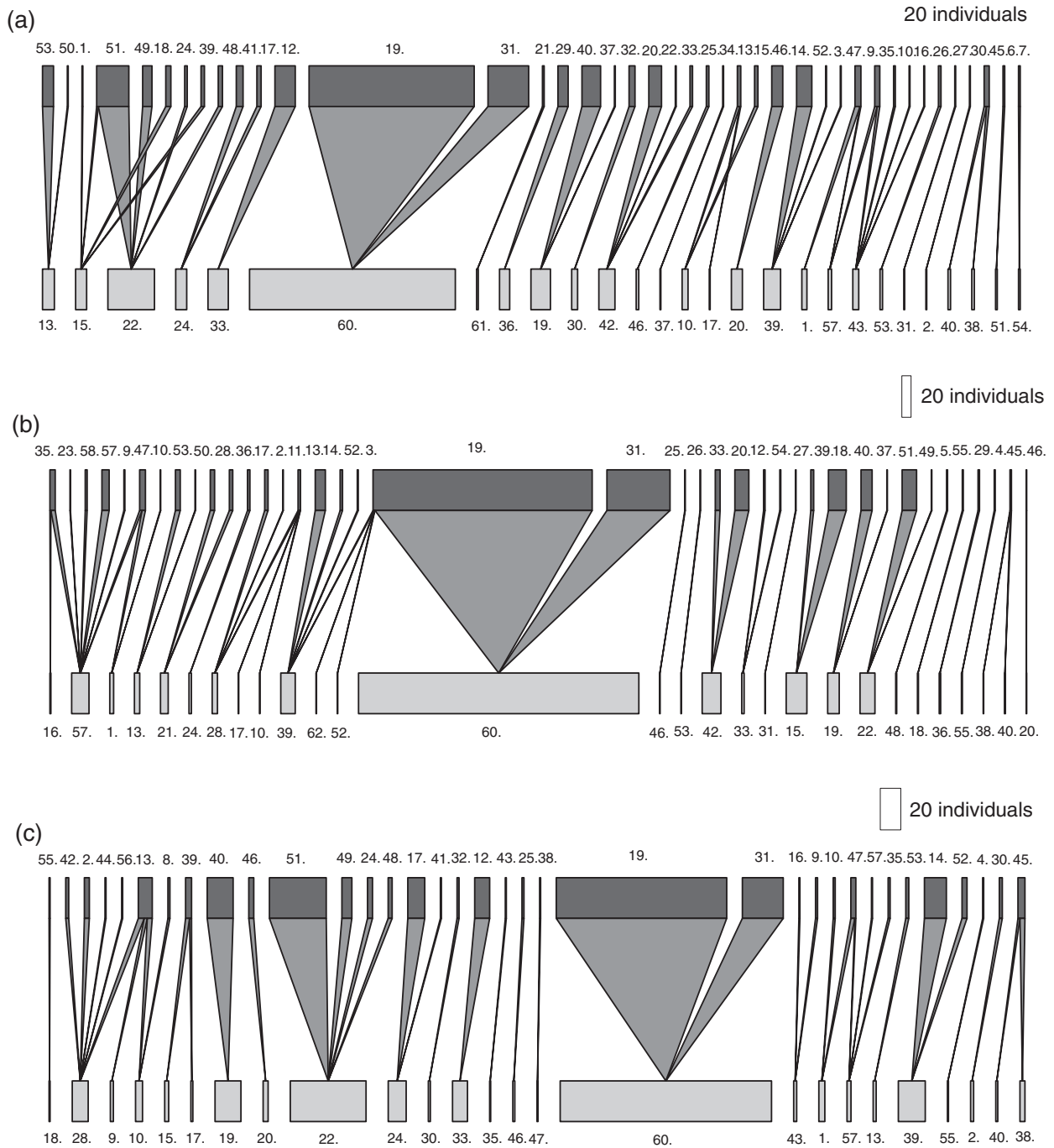
**Fig. 4.** Quantitative plant–leafminer food webs in the studied locations: (a) north-facing edges (NE), (b) interior (I), and (c) south-facing edges (SE) in fragmented Chaco Serrano. The rectangles above represent the leafminer species and the rectangles below, the host plant species. Species codes are given in the Supporting infoprmation, Table S1 (plants) and Table S2 (leafminers).The rectangle size is proportional to the abundance of the species (indicated by the empty rectangle on the right). The triangles indicate bitrophic interactions, and their width is proportional to the interaction strength.

the effects (or lack of them) of edge habitats and their geographical orientation on food web parameters.

In summary, the present study provides the first evidence of microclimatic influences on plant–leafminer–parasitoid food webs in a fragmented forest, suggesting that potential trade-offs

between direct and indirect effects of microclimatic conditions could influence plant and insect local responses. Our results also suggest that microclimatic variables could interact with each other and modify species responses, whereas intrinsic traits of each trophic level could determine differential
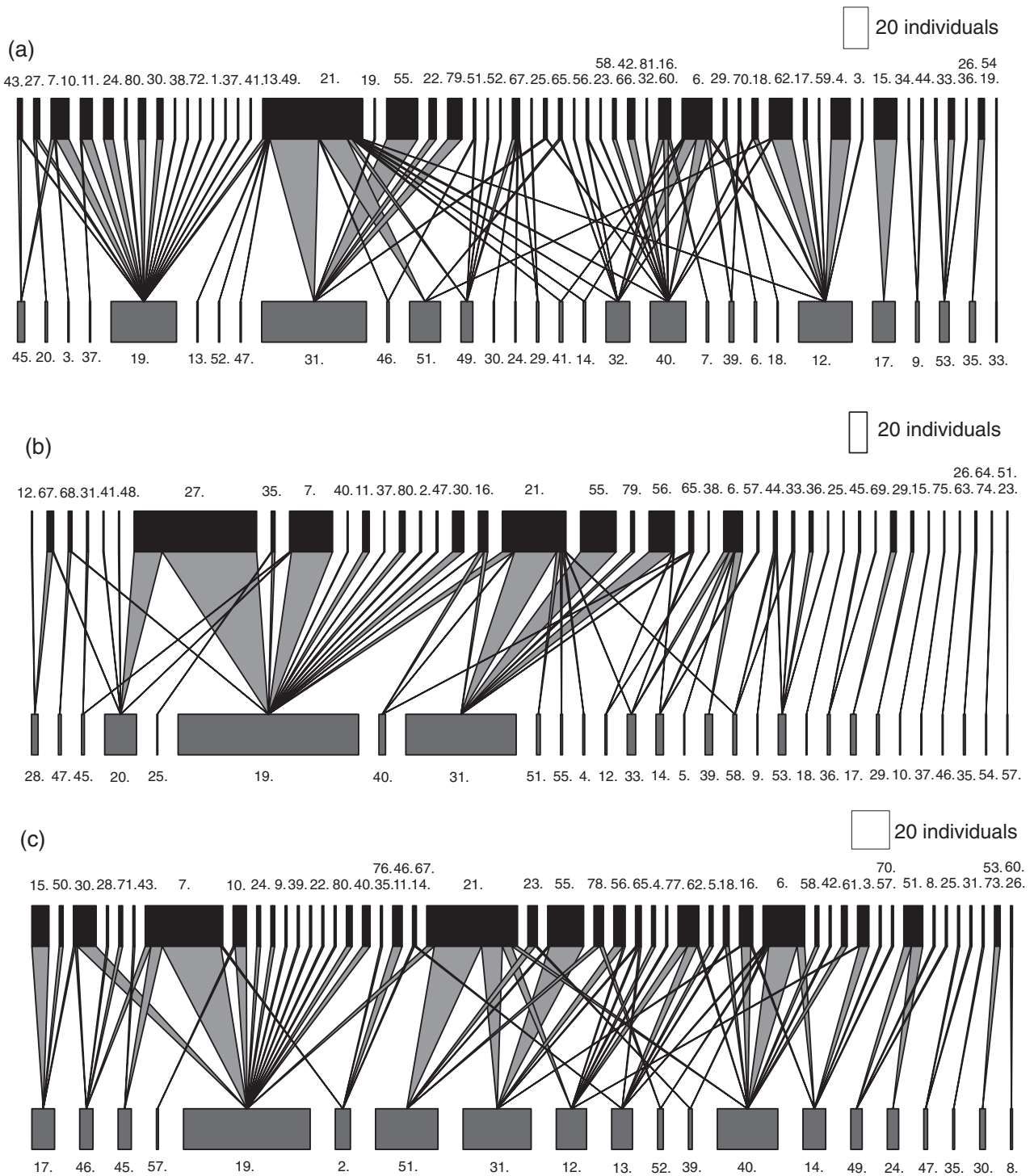
**Fig. 5.** Quantitative leafminer-parasitoid food webs in the studied locations: (a) north-facing edges (NE), (b) interior (I), and (c) south-facing edges (SE) in fragmented Chaco Serrano. The rectangles above represent the parasitoid species and the rectangles below the leafminer species. Species codes are given in the Supporting infoprmation, Table S2 (leafminers) and Table S3 (parasitoids).The rectangle size is proportional to the abundance of the species (indicated by the empty rectangle on the right). The triangles indicate bitrophic interactions, and their width is proportional to the interaction strength.

**Table 4.** Results of indicator species analysis of mined plants, leafminers, and parasitoids among locations (NE, I, and SE).

| Species | Location | Indicator value | $P$ |
|---|---|---|---|
| Mined plants | | | |
| *Gomphrena pulchella* | NE | 0.79 | 0.009 |
| *Malvastrum coromandelianum* | NE | 0.66 | 0.049 |
| *Janusia guaranitica* | NE | 0.63 | 0.025 |
| *Fleischmannia prasiifolia* | SE | 0.86 | 0.042 |
| *Bidens subalternans* | SE | 0.70 | 0.008 |
| *Iresine diffusa* | SE | 0.60 | 0.020 |
| *Anredera cordifolia* | SE | 0.60 | 0.022 |
| *Setaria oblongata* | I | 0.88 | 0.006 |
| *Sida dyctiocarpa* | I | 0.72 | 0.005 |
| Leafminers | | | |
| *Tischeria* sp2 | I | 0.62 | 0.025 |
| *Haplopeodes* near *tigrensis* | I | 0.60 | 0.030 |
| Parasitoids | | | |
| *Phaedrotoma* sp1 | I | 0.75 | 0.012 |
| *Copidosoma* sp1 | I | 0.64 | 0.022 |
| *Mirax* sp1 | SE | 0.64 | 0.021 |

Only significant indicator values ($P < 0.05$) are shown.

responses to microclimatic conditions. Our findings highlight the need for further simultaneous analyses of microclimatic effects on different trophic levels and their interactions, including other food web parameters and study systems. Understanding how ecological networks respond to small scale but significant changes in their environment, as represented by microclimatic conditions, could help us to envisage how they will respond to larger scale variations predicted by global climate change.

## Supporting Information

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

**Figure S1**. Detail of the sites and locations (of one of the sites) where the study was performed.

**Table S1.** List of plant species consumed by leafminers in the studied locations.

**Table S2.** List of leafminer species in the studied locations.

**Table S3.** List of parasitoid species in the studied locations.

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