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Research

Population and Community Ecology

Calliphoridae (Diptera) in Human-Transformed and Wild Habitats: Diversity and Seasonal Fluctuations in the Humid Chaco Ecoregion of South America

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Abstract

A temporal study of the Calliphoridae fauna was conducted in five different types of habitats in the Humid Chaco ecoregion: an urban settlement, a cattle farm, an alfalfa crop, a savanna, and a forest. Research was carried out to analyze 1) how the species composition of blow fly communities changes across different types of human-modified and wild environments, 2) their seasonal fluctuations, and 3) the influence of climatic factors (relative humidity, temperature, and precipitations) on the temporal dynamics of these communities. In each habitat, five sites were selected for the collection of blow flies using bait traps, and flies were collected for 1 yr. In total, 32,100 blow flies were collected, distributed in five genera and 11 species. The native species *Cochliomyia macellaria* (Fabricius) (Diptera: Calliphoridae) was the most abundant, followed by the exotic *Chrysomya putoria* (Wiedemann) (Diptera: Calliphoridae). The abundance of exotic species represented 59.9% of the total sample, showing a reduction toward less disturbed sites. The Calliphorid communities were compared in terms of species richness, composition, and abundance between habitats and seasons. Our results showed that the habitat type and season affect the composition of blow fly communities. The alfalfa crop and the forest showed the highest diversity of species. In general, there was a decrease in blow fly activity during winter in all habitats. The climatic factors did not greatly affect the diversity of these flies. This study provides a first understanding of several ecological aspects of the Calliphoridae assemblages of the previously unsurveyed Humid Chaco ecoregion of South America.

Key words: anthropogenic impact, biodiversity, blow fly, community composition, temporal fluctuation

Because of their abundance and variety of roles in the ecosystem, insects are excellent models to study the effects of highly anthropized ecosystems on diversity patterns and ecosystem functioning. Because insects display remarkable species–habitat associations, the assessment of different insect species and their differential responses to several types of habitats along gradients of human intervention can provide valuable information.

Typically, modifications of natural environments by human action generate drastic changes in landscapes that create new resources for the development of many invasive organisms (McKinney 2002) and lead to habitat loss for native species (Blair 2001). The urbanization process typically promotes an increase in the number of impervious surfaces and artificial structures, and a reduction of the native vegetation coverage. Indeed, built habitats (walls, buildings, and paved areas) and transformed green areas (parks, cemeteries, roadsides, lawns, and gardens) effectively define urban areas. Hence, the transformation of natural habitats into human settlements is responsible for habitat homogenization and often facilitates the introduction of exotic and synanthropic species, which are well adapted to intensely modified and built habitats, and thus act as 'global homogenizers' (Gilbert 1989, McKinney 2005). On the other hand, the transformation of pristine areas into lands for agricultural crops and cattle farming constitutes an important amount of habitat transformation by human action. The expansion of cultivated areas, the agricultural intensification, and the effect of cattle on landscape transformation are among the main global threats to wildlife. The current model of agricultural intensification, which produces high yields, has also resulted in a loss of biodiversity, ecological function, and critical ecosystem services in agricultural landscapes (Power 2010, Sarthou et al. 2014, Landis 2016). Indeed, the simplification of agroecosystems, as a result of the use of a smaller number of species during the production process, has caused a significant decline in farmland biodiversity.

Among Diptera, Calliphoridae species (commonly known as blow flies), whose larvae are scavengers, are usually the main carrion-associated flies due to their ubiquity and abundance. Ecological studies have indicated that blow flies respond rapidly to changes in ecosystems and that different species exhibit markedly differentiated spatial and temporal patterns of occurrence (Ferraz et al. 2009; Sousa et al. 2010, 2011; Patitucci et al. 2011). In agreement with this, several studies have demonstrated that some species are common in human-disturbed habitats, whereas others are strongly associated with undisturbed or better-preserved habitats (Mariluis et al. 2008, Patitucci et al. 2011, Beltran et al. 2012, De Souza and Zuben 2012, Dufek et al. 2016).

Species–habitat associations of Calliphoridae along anthropization gradients are relevant not only from an ecological point of view but also from medical and veterinary points of view because these flies are mechanical vectors of pathogens (Greenberg 1971, Paraluppi et al. 1996, Graczyk et al. 2001), agents of myiasis in humans and domestic animals (Guimarães et al. 1983, Mariluis et al. 1995, Olea et al. 2014), and valuable tools to predict the time and circumstances of death in forensic entomological research, being adults, and larvae obtained on human corpses (Oliva 1997, Mariluis 2002, Horenstein et al. 2005, Alves et al. 2014).

Several studies on Calliphoridae ecology have compared the abundance and occurrence of blow fly between seasons as well as between habitat categories. These studies are useful to detect forensically relevant species, providing information to support inference for applied research on criminal cases (Carvalho and Linhares 2001, Wolff et al. 2001, Gruner et al. 2007, Horenstein et al. 2010). However, these studies are usually restricted biogeographically, and the ecological requirements of species (e.g., habitat–species associations, diversity or spatial segregation) for most blow fly assemblages are still poorly understood.

The forest and savannas of the Chaco ecoregion have been subjected to widespread changes associated with increasing human population and deforestation due to agricultural expansion and grazing activities (Grau et al. 2005). The Chaco ecoregion extends from southern Bolivia, to west Paraguay, southern Brazil, and central-north Argentina (Cabrera and Willink 1973). Rainfalls in this ecoregion define an east-west decreasing gradient of humidity, dividing this ecoregion into two sectors: the eastern sector, belonging to the Humid Chaco, and the western sector, belonging to the Dry Chaco (Cabrera and Willink 1973). Particularly, the Humid Chaco presents numerous rivers and wetlands of high biodiversity, as well as a great variety of landscapes (e.g., gallery forests, flood forests, palm groves; Prado 1991, Oakley et al. 2005).

Although some studies have partially analyzed the faunal composition and abundance of blow fly along anthropization gradients in northeast Argentina (Mariluis et al. 1990, Dufek et al. 2016), no studies have evaluated how the blow fly assemblage changes spatially and temporally within the Humid Chaco landscape. Therefore, in the present study, we conducted a field survey of blow flies in the Humid Chaco aimed to determine how different natural and human-transformed habitats affect Calliphoridae in terms of abundance, richness, and species composition. We also aimed to assess temporal fluctuations and climatic factors associated with fly diversity. Based on patterns reported in the literature, we expected to find differences in blow fly species assemblages through the seasons. According to the process of biotic homogenization driven by human activities, we hypothesized that habitats with increasing anthropization should contain higher proportional abundance of exotic species and lower diversity of native blow flies.

Materials and Methods

Study Area

This study was performed in different habitats located in San Lorenzo Department, Chaco Province, Argentina (27° 17′ 00″ S, 60° 25′ 00″ W). This Department has a population of 14,702 inhabitants (Indec 2010) and an area of 2,135 km^2. It is characterized by intense human activities as livestock and wood exploitation for firewood and coal (Ginzburg and Moli 2005, Giraudo et al. 2013) and is located in the Humid Chaco ecoregion (Cabrera 1971; Fig. 1a). The climate is subtropical with a mean annual temperature of 18–23°C and a mean annual precipitation of 1,300 mm.

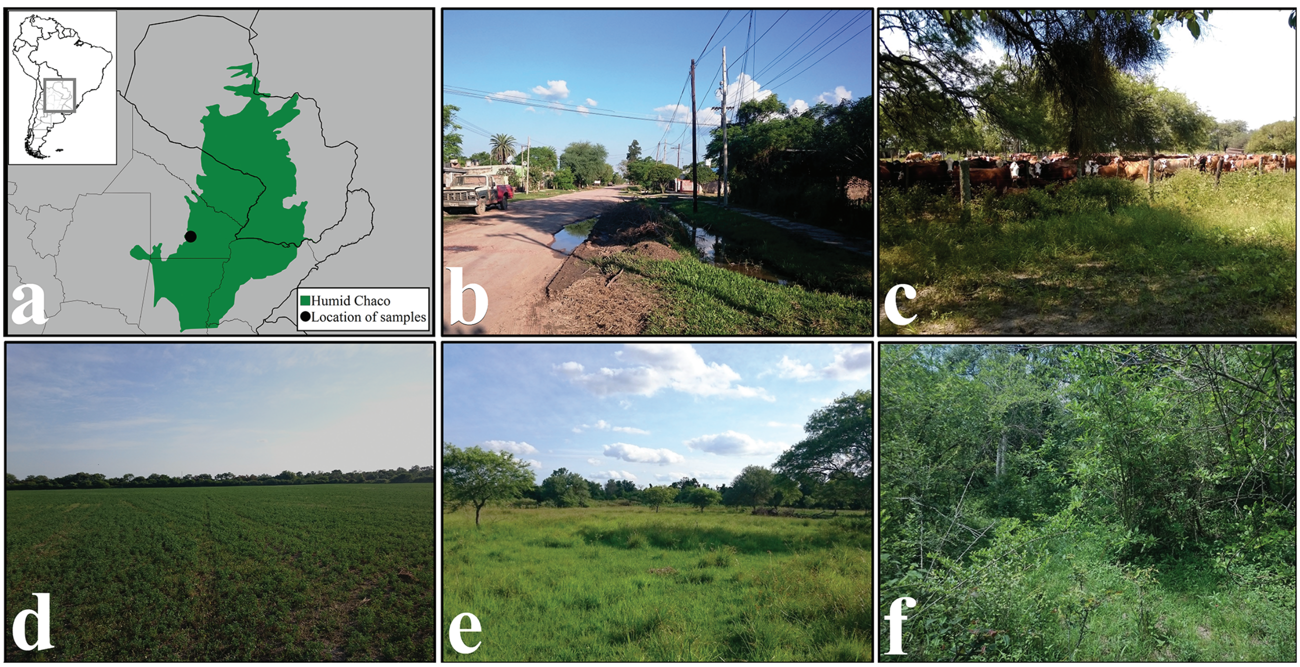

Fig. 1. (a) Location of study area in the Humid Chaco ecoregion. Chaco Province; Argentina; (b) urban; (c) cattle farm; (d) alfalfa crop; (e) savanna; (f) forest.

To evaluate the community composition of blow flies in different natural and human-transformed habitats, we selected five types of characteristic habitats of this ecoregion, separated for at least 4 km from each other to guarantee independence among each one. We defined 'habitat' as an area with similar environmental characteristics. These five habitat types were arranged into two subgroups: habitats modified by human action 1) and native wild habitats 2), as follows:

1) Urban (U): Villa Berthet (27° 17′ 09″ S, 60° 24′ 22″ W), capital city of San Lorenzo Department, with a population of 12,029 inhabitants (Indec 2010). Sample points within this habitat were placed in residential gardens (Fig. 1b).
1) Cattle farm (C): located at 9 km of Villa Berthet (27° 12′ 52″ S, 60° 23′ 14″ W), with production of livestock in an extension of 300 ha. It houses around 350 farm animals (Fig. 1c).
1) Alfalfa crop (A): a crop field located at 6 km of Villa Berthet (27° 18′ 42″ S, 60° 21′ 36″ W), with an extension of 5 ha (Fig. 1d).
2) Savanna (S): located at 6 km of Villa Berthet (27° 14′ 59″ S, 60° 23′ 06″ W), mainly with grasses and some trees (Fig. 1e).
2) Forest (F): located at 10 km of Villa Berthet (27° 13′ 34″ S, 60° 21′ 02″ W). This forest is mainly a xeric deciduous forest, with wild animals, Cactaceae, and terrestrial Bromeliaceae characteristic of the Humid Chaco ecoregion (Cabrera 1971; Fig. 1f).

Trapping Methodology and Identification

To evaluate the temporal fluctuations and climatic factors, samplings were carried out monthly from March 2015 to February 2016. Flies were collected using van Someren–Rydon canopy traps baited with 250 g of rotten squid (Fig. 2). The bait was exposed to room temperature for 72 h before samplings. The use of squid as bait is very effective in ecological studies because it maintains a moist state of decay for much longer than other baits (e.g., chicken or liver; Newton and Peck 1975, Baz et al. 2007, Martin-Vega and Baz 2013, Dufek et al. 2016). In each habitat, five sites were chosen at least 75–100 m from each other to avoid spatial pseudoreplication (Yepes-Gaurisas et al. 2013, Carvalho et al. 2017). Each trap was hung at 2 m above the ground from available trees or by using metal poles staked into the ground. Traps were exposed for 48 h. The bait traps were always placed in the same location in each habitat every month. Twelve sampling events (one per month) were conducted in each habitat. In total, 300 independent samples were collected throughout the study period, 60 in each habitat. Specimens were killed in glass vials with ethyl acetate and then stored in the field in labeled envelopes for further study in the laboratory.

The identification of blow flies was based on taxonomic keys and descriptions (Whitworth 2014, Mulieri et al. 2014, Grella et al. 2015). The identification was also supported by comparison with reference specimens deposited at the Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia' (MACN), Buenos Aires, Argentina. Voucher specimens are housed at the Universidad Nacional del Nordeste, Corrientes, Argentina (CARTROUNNE), and MACN.

Data Analysis

From each trap, the number of individuals per species was recorded. If the data were transformed during data analysis, we specified so in each analysis description. The community composition of blow flies in each habitat and season was analyzed in terms of abundance, species richness, and diversity.

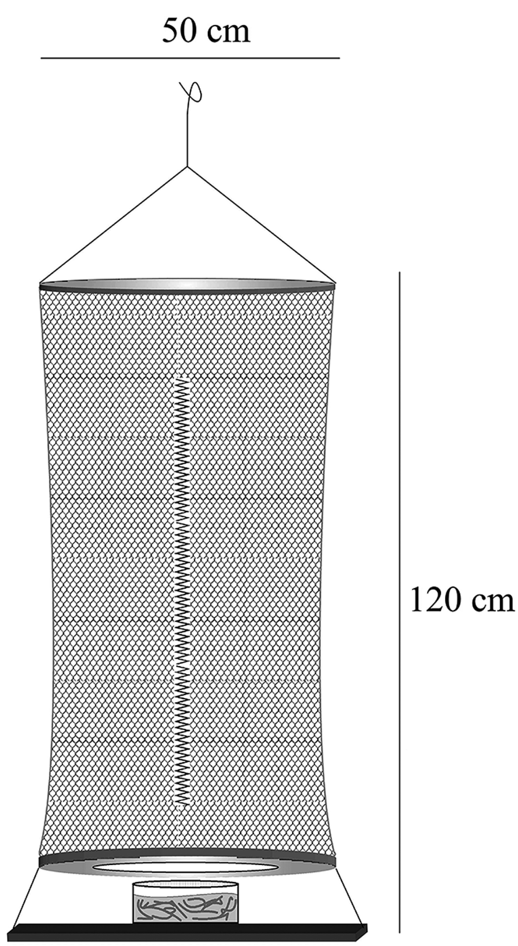

Fig. 2. Schematic illustration of van Someren–Rydon canopy trap used in this work.

The α diversity was calculated for each sample point and analyzed using different indices, including the Shannon-Wiener, equitability, and Simpson's dominance (Magurran 2004).

Analysis of variance, followed by multiple comparisons performed according to the Tukey test, was used to compare the Shannon–Wiener diversity and abundance of the total blow flies captured and at specific level between the different habitats, with the abundance data being log (n + 1) transformed to reduce the effect of discrepant values. Only the species whose abundances represented more than 5% of total catches were analyzed. This analysis was performed by using the program PAST version 3.0 (Hammer et al. 2001), with $P < 0.05$ as the significance level. In addition, indicator species analyses (followed by a Monte Carlo permutation test with 1,000 permutations) were performed in PC-ORD version 6.0 to determine whether there were species characteristic of a particular habitat or a group of habitats with presence or absence of anthropic intervention (Dufrêne and Legendre 1997).

The abundance transformed as log (n + 1), species richness and diversity (Shannon–Wiener index) in each habitat throughout the study period were evaluated. Multiple regression analyses with Bonferroni correction to P values were used to alternatively assess whether the abundance, species richness, and diversity of blow flies (Shannon–Wiener index) of each habitat were related to the following environmental variables: relative humidity, temperature, and precipitation (mean values calculated from 7 to 14 d before the sampling date; Supp. Table 1 [Online only]). Multiple regression analyses were performed using SPSS software version 25 considering $P < 0.012$ significance level (Bonferroni correction: 0.05/4 = 0.012). In addition, fluctuations in abundance every month of species whose represented more than 5% of total catches were analyzed.

Abundance of each species was used to test whether differences in the blow fly community assemblages result from differential community composition between habitats and seasons. A non-metric multidimensional scaling (NMDS) analysis was performed based on the Bray–Curtis index as a measure of similarity with the data transformed as log (n + 1) (Legendre and Legendre 1998). The distortion of the resolution of the two-dimensional arrangement is represented by a stress value. This analysis was performed using the program PRIMER version 6 (Clarke and Gorley 2001).

Finally, analyses of similarities (ANOSIM) were used to determine whether season or habitat affected the structure of blow fly assemblages. Similarity matrices were constructed using the Bray-Curtis similarity coefficient on square-root-transformed data. Moreover, similarity percentages (SIMPER) were used to explore the relative contributions of individual species to the similarity within habitats and the dissimilarity among habitats (Clarke and Warwick 2001). These analyses were conducted using PRIMER version 6 (Clarke and Gorley 2001).

Results

Diversity of Calliphoridae Communities Between Habitats

In total, 32,100 blow flies, belonging to 11 species, were captured (Table 1). The largest percentage of individuals was collected in habitats modified by human action (71.15%, Table 1).

Among all habitats, U had the highest abundance (44.51% of the total sample), followed by S (18.73%) and C (18.70%). The U habitat had the highest species richness (11 species), followed by A, C, and S (10 species each). F had the lowest species richness (nine species). The most abundant species were the native *Cochliomyia macellaria* (Fabricius) (Diptera: Calliphoridae) (33.13%), followed by the non-native (exotic species) *Ch. putoria* (Wiedemann) (Diptera: Calliphoridae) (29.87%), *Chrysomya megacephala* (Fabricius) (Diptera: Calliphoridae) (14.81%), and *Chrysomya albiceps* (Wiedemann) (Diptera: Calliphoridae) (14.79%). These four species accounted for 92.6% of all individuals collected considering all the habitats surveyed (Table 1).

Significant differences were found in the abundance of blow flies among habitats ($F_{4,20}$ = 79.07, P < 0.001). Five dominant species, whose abundances represented more than 5% of total catches, were individually analyzed. *Chrysomya albiceps* ($F_{4,20}$ = 20.49, P < 0.001) was common in all habitats. *Chrysomya megacephala* ($F_{4,20}$ = 171.4, P < 0.001) and *Ch. putoria* ($F_{4,20}$ = 170.3, P < 0.001) were most abundant in U. *Cochliomyia macellaria* ($F_{4,20}$ = 134.6, P < 0.001) was captured in all habitats, but was most abundant in S. *Lucilia ochricornis* (Wiedemann) (Diptera: Calliphoridae) ($F_{4,20}$ = 50.2, P < 0.001) was more abundant in F and U (Fig. 3).

The highest diversity was estimated for A and F (Table 2). The results obtained indicated significant differences in diversity (Shannon–Wiener index) between habitats ($F_{4,20}$ = 30.17, P < 0.001; Fig. 3).

The indicator species analysis detected only two species as indicators for the U habitat: *Ch. megacephala* (Indicator value = 86.3, P < 0.001) and *Ch. putoria* (Indicator value = 90.4, P < 0.001). Few species were identified as characteristic of habitats modified by human action and wild habitats (Table 3).

The ordination analysis (NMDS) showed that U and A were well separated from the assemblage formed by C, S, and F (Fig. 4). The low stress value (0.07) indicates a great representation of the overall variance.

Temporal Fluctuation and Relationships With Environmental Variables

The abundance and species richness per month are summarized in Table 4. The abundance of blow flies peaked in September (early spring) in all habitats, whereas the lowest numbers of flies were obtained in August (winter; Fig. 5a).

Low variation in species richness was recorded throughout the study period (Fig. 5b). The general pattern of species richness showed the highest values between September and May (autumn, spring, and summer) and the lowest values in August (winter; Fig. 5b). Multiple regression analysis only showed a relationship between richness and precipitation 14 d before samplings for S (overall regression model: $F_{7,4}$ = 24.2, R^2 = 0.93, P = 0.001; coefficient$_{\text{precip}\cdot 14}$ = 0.034, P = 0.001).

Table 1. Abundance of Calliphoridae species captured in the habitats surveyed in the Humid Chaco ecoregion, Chaco Province, Argentina, between March 2015 and February 2016

Species	U	C	A	S	F	Total	%
Chloroprocta idioidea (Robineau-Desvoidy) N	2	33	5	30	99	169	0.52
Chrysomya albiceps (Wiedemann) E	410	1,211	**975**	1,458	694	4,748	14.79
Chrysomya megacephala (Fabricius) E	4,104	30	582	20	20	4,756	14.81
Chrysomya putoria (Wiedemann) E	**8,670**	690	129	72	29	9,590	29.87
Cochliomyia hominivorax (Coquerel) N	1	9	1	9	13	33	0.10
Cochliomyia macellaria (Fabricius) N	422	**3,789**	758	**4,235**	**1,431**	10,635	33.13
Lucilia cuprina (Wiedemann) E	70	25	37	2	0	134	0.41
Lucilia eximia (Wiedemann) N	54	32	3	17	83	189	0.58
Lucilia ochricornis (Wiedemann) N	547	174	15	164	878	1,778	5.53
Lucilia sericata (Meigen) E	1	0	0	0	0	1	< 0.01
Sarconesia chlorogaster (Wiedemann) N	7	10	43	6	1	67	0.21
Abundance	14,288	6,003	2,548	6,013	3,248	32,100	100
Abundance (%)	44.51	18.70	7.94	18.73	10.12	100	
Richness	11	10	10	10	9	11	

Blow flies were captured for 1 yr in 25 sampling points (five per habitat) using van Someren–Rydon canopy traps baited with rotten squid. The traps were exposed for 48 h in each habitat per month. References: U, urban; C, cattle farm; A, alfalfa crop; S, savanna; F, forest. E (exotic species); N (native species).

Richness: total number of species.

Bold entries show the most abundant species in each habitat.

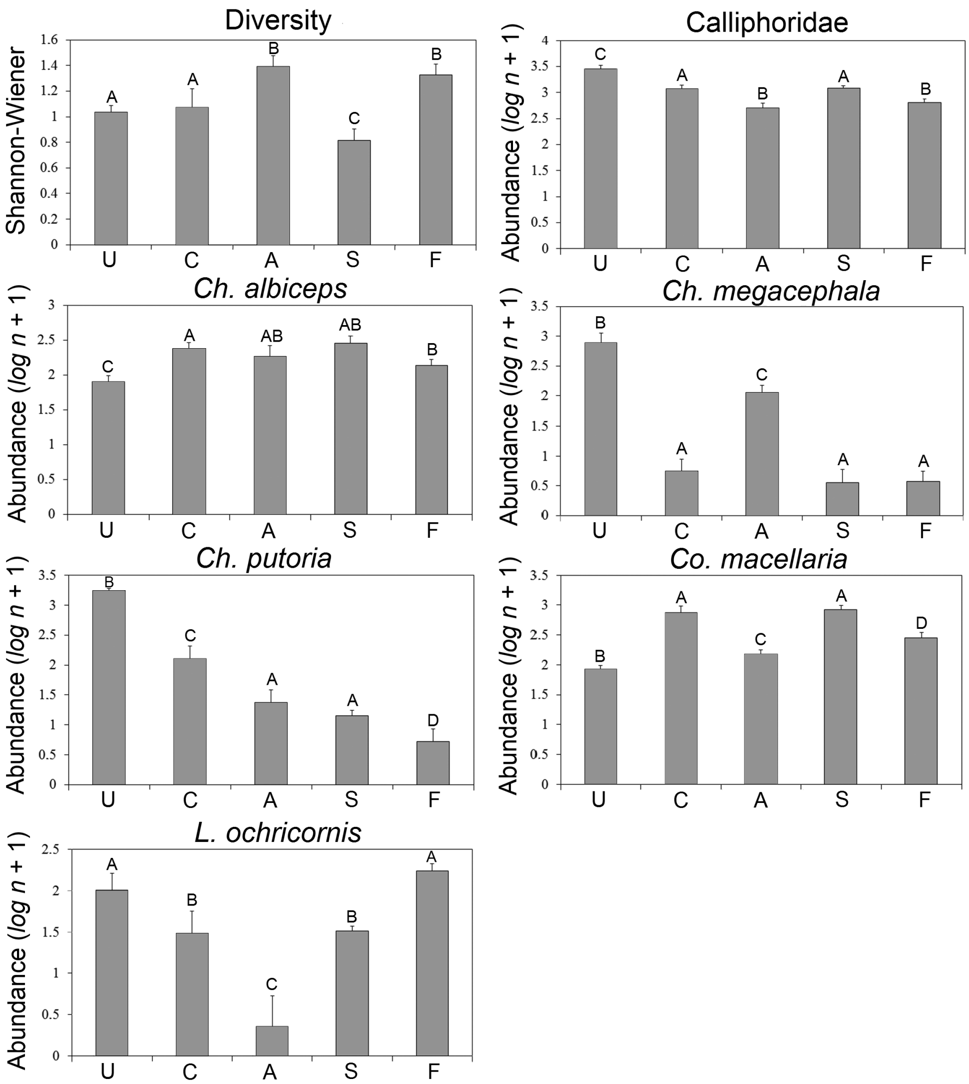

Fig. 3. Species diversity and proportional abundance of Calliphoridae and dominant species in the habitats surveyed in the Humid Chaco ecoregion, Chaco Province, Argentina, between March 2015 and February 2016. Different letters above the bars indicate significant differences (Tukey test, α = 0.05). References: U, urban; C, cattle farm; A, alfalfa crop; S, savanna; F, forest.

Table 2. Diversity indices and SD of Calliphoridae species captured in the habitats surveyed in the Humid Chaco ecoregion, Chaco Province, Argentina, between March 2015 and February 2016

Sites	Simpson	Shannon	Equitability
U	0.539 (± 0.025)	1.035 (± 0.052)	0.489 (± 0.034)
C	0.542 (± 0.079)	1.074 (± 0.142)	0.466 (± 0.061)
A	0.708 (± 0.018)	1.392 (± 0.081)	0.669 (± 0.039)
S	0.440 (± 0.053)	0.814 (± 0.089)	0.382 (± 0.026)
F	0.680 (± 0.028)	1.326 (± 0.086)	0.638 (± 0.035)

References: U, urban; C, cattle farm; A, alfalfa crop; S, savanna; F, forest.

The lowest diversity (Shannon–Wiener index) was recorded from August to September (winter and early spring), whereas the highest diversity was recorded from December to February (summer) in all habitats (Fig. 5c).

Monthly abundance (in numbers) of the five dominant species is summarized in Fig. 6. In general, the abundance of each species here studied peaked in spring season (September–November). *Chrysomya albiceps*, *Ch. megacephala*, and *Co. macellaria* markedly increased their abundance after the cold season. On the other hand, *Ch. putoria* and *L. ochricornis* occurred in relatively high abundance throughout the year, being *L. ochricornis* more abundant before winter.

Table 3. Significant indicator species identified for habitats modified by human action (H) and wild habitats (W) in the Humid Chaco ecoregion, Chaco Province, Argentina, between March 2015 and February 2016 (Monte Carlo test, α = 0.05)

Indicator site	Species	Indicator value	Mean	SD	*P*
W	*Chloroprocta idioidea*	74.6	45.6	8.05	0.004
H	*Chrysomya megacephala*	98.7	64.9	10.96	0.001
H	*Chrysomya putoria*	98.4	64.1	11.45	0.001
W	*Cochliomyia hominivorax*	60	39.5	7.91	0.022
H	*Lucilia cuprina*	97.8	41.3	7.54	0.001
H	*Sarconesia chlorogaster*	79.4	47.1	8.84	0.001

Variability in Calliphoridae Assemblages per Season

When comparing species composition among seasons (Supp. Table 2 [Online only]), NMDS analysis showed that species assemblages

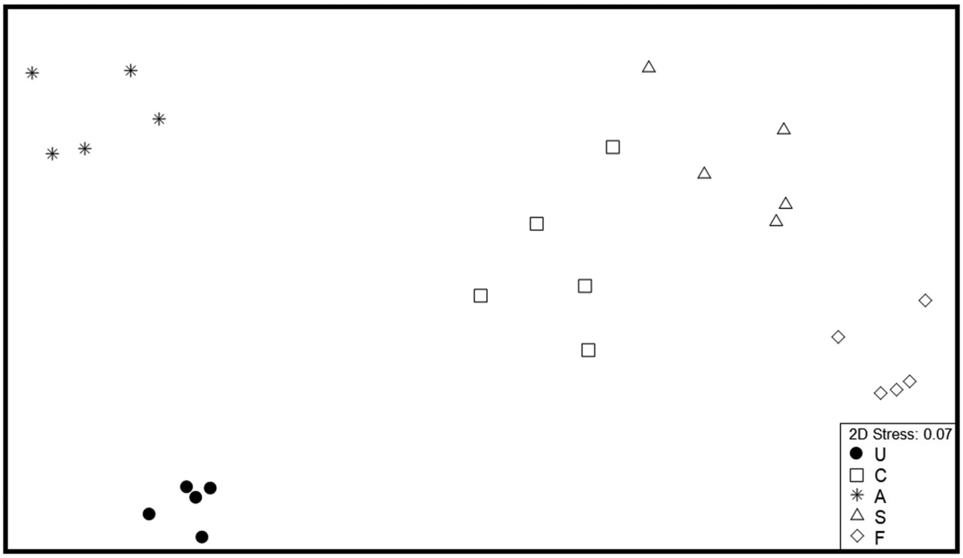

Fig. 4. Non-metric multidimensional scaling (NMDS) of Calliphoridae species at 25 sampling points in the five types of habitats surveyed in the Humid Chaco ecoregion, Chaco Province, Argentina, between March 2015 and February 2016. References: U, urban; C, cattle farm; A, alfalfa crop; S, savanna; F, forest.

Table 4. Abundance of Calliphoridae species captured between March 2015 and February 2016 in different habitats surveyed in the Humid Chaco ecoregion, Chaco Province, Argentina

Species	M	A	M	J	J	A	S	O	N	D	J	F	Total	%
Chloroprocta idioidea	17	2	20	5	1	2	3	6	2	4	3	104	169	0.52
Chrysomya albiceps	405	44	254	5	13	58	993	1,076	698	**505**	**531**	166	4,748	14.79
Chrysomya megacephala	**410**	**308**	139	35	89	26	37	544	2,345	421	336	66	4,756	14.81
Chrysomya putoria	158	108	809	53	**556**	40	1,846	**2,433**	**2,616**	342	498	131	9,590	29.87
Cochliomyia hominivorax	4	0	10	1	0	0	6	1	4	3	3	1	33	0.1
Cochliomyia macellaria	365	133	**873**	138	350	**324**	**6,038**	726	769	227	506	**186**	10,635	33.13
Lucilia cuprina	1	3	5	4	47	8	33	18	12	1	2	0	134	0.41
Lucilia eximia	14	52	44	3	50	0	22	1	0	2	1	0	189	0.58
Lucilia ochricornis	93	114	446	**353**	373	18	251	80	21	22	3	4	1,778	5.53
Lucilia sericata	0	0	0	0	1	0	0	0	0	0	0	0	1	<0.01
Sarconesia chlorogaster	0	3	3	9	22	5	25	0	0	0	0	0	67	0.21
Abundance	1,467	767	2,603	606	1,502	481	9,254	4,885	6,467	1,527	1,883	658	32,100	100
Abundance (%)	4.57	2.38	8.11	1.89	4.68	1.50	28.83	15.22	20.15	4.76	5.88	2.05	100	
Richness	9	9	10	10	10	8	10	9	8	9	9	7	11	

Blow flies were captured for 1 yr in five different types of habitats using van Someren–Rydon canopy traps baited with rotten squid. The traps were exposed for 48 h in each habitat per month.

Richness: total number of species.

Bold entries show the most abundant species in each month.

recorded in spring and winter differed from those sampled in autumn and summer (Fig. 7). This recorded pattern was confirmed by an analysis of similarities (ANOSIM), which indicated that blow fly assemblages varied significantly between seasons (R = 0.346, P = 0.001) and showed that the lowest similarity was found between winter and spring (R = 0.642, P = 0.001; Table 5).

ANOSIM test showed global significant differences in community composition for each season (autumn R = 0.818, P = 0.001; winter R = 0.784, P = 0.0001; spring R = 0.894, P = 0.001; and summer R = 0.634, P = 0.001). The habitats C and S did not differ in community composition during winter, spring, or summer. In contrast, the other habitats showed significant differences in each season (Table 6).

The mean similarity percentage (SIMPER) of samples between sites within the same habitat varied from 81 to 59% in autumn, from 80 to 49% in winter, from 84 to 79% in spring, and from 75 to 68% in summer (Table 7). The species that most contributed to the similarity between sites were *Co. macellaria*, *Ch. putoria*, *Ch. megacephala*, *Ch. albiceps*, and *L. ochricornis*.

Species responsible for dissimilarities between habitats were identified using SIMPER analysis. Lowest values of dissimilarity were obtained between C and S. In the U habitat, *Ch. putoria* and *Ch. megacephala* were the key species for the highest dissimilarity with the other habitats in all seasons. *Lucilia ochricornis* contributed most to the dissimilarity between F and the other habitats (Table 8).

Discussion

The diversity of Calliphoridae in the Humid Chaco had not yet been explored. In this work, we recorded 11 species, equivalent to 42% of the total Calliphorid fauna recorded in Argentina.

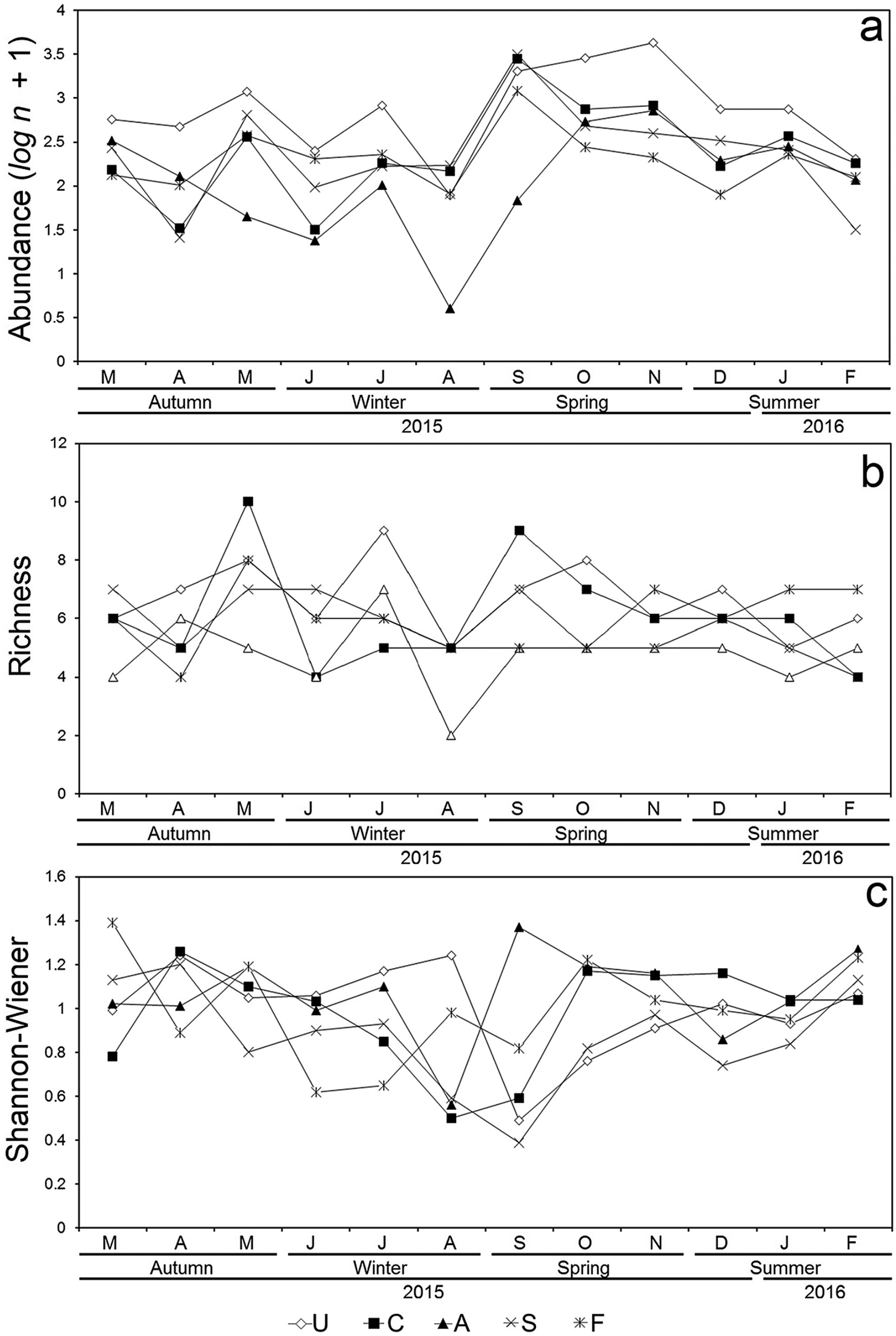

Fig. 5. Annual variation of Calliphoridae community structure in the habitats surveyed in the Humid Chaco ecoregion, Chaco Province, Argentina, between March 2015 and February 2016. References: U, urban; C, cattle farm; A, alfalfa crop; S, savanna; F, forest. (a) Abundance (log [*n* + 1]); (b) species richness; (c) Shannon–Wiener index.

Our results support the hypothesis of biotic homogenization, which predicts higher proportional abundance of exotic species and lower diversity of native blow flies in environments modified by human action. This pattern may rely on the ability of exotic species to adapt and compete in these types of environments, a phenomenon possibly attributed to the ecological disorder caused by urbanization, such as the accumulation of garbage and organic matter (Nuorteva 1963). In our study, we found five non-native species: *Ch. albiceps*, *Ch. megacephala*, *Ch. putoria*, *Lucilia cuprina* (Wiedemann) (Diptera: Calliphoridae), and *Lucilia sericata* (Meigen) (Diptera: Calliphoridae). The abundance of exotic species represented 59.9% of the total blow flies captured, surpassing the native ones. Most of these blow flies were captured in the urban habitat (69% of the total exotic species captured), which is a strong indication that urbanization has negative effects on native communities by promoting the persistence of exotic species (Kavazos and

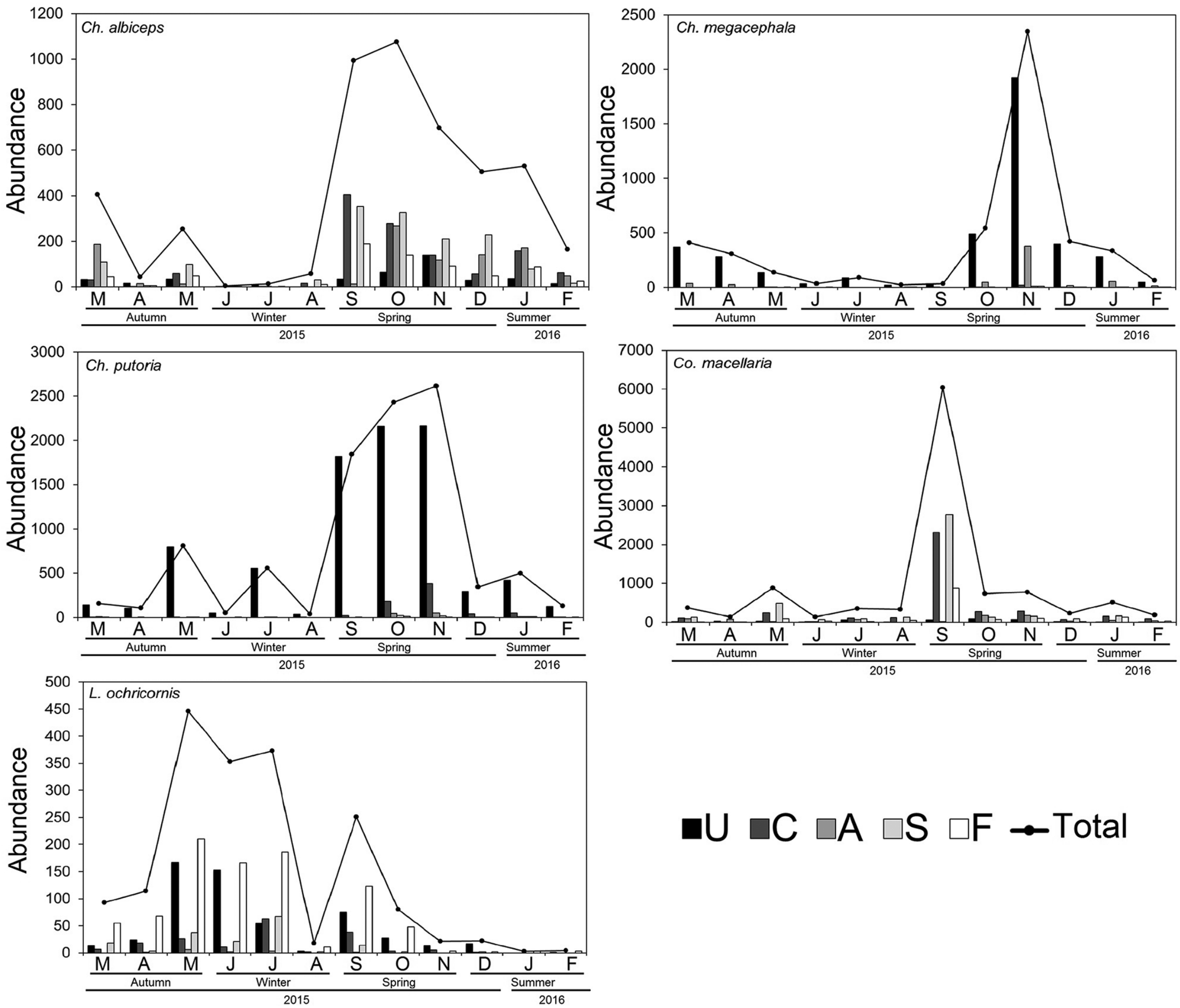

Fig. 6. Abundance of the five dominant Calliphoridae species collected in the habitats surveyed in the Humid Chaco ecoregion, Chaco Province, Argentina, between March 2015 and February 2016. References: U, urban; C, cattle farm; A, alfalfa crop; S, savanna; F, forest.

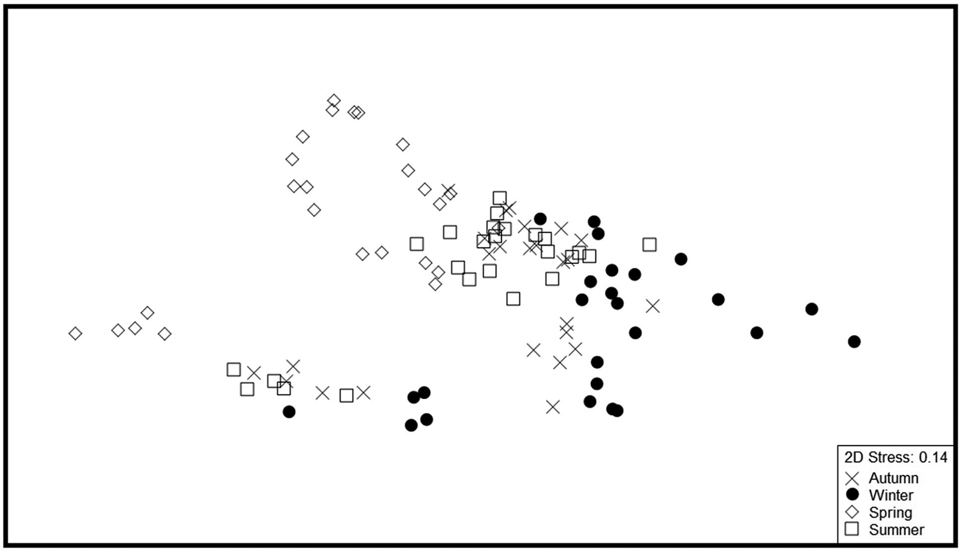

Fig. 7. Non-metric multidimensional scaling (NMDS) of Calliphoridae species grouping the 25 sampling points of all habitats per season (n = 100) surveyed in the Humid Chaco ecoregion, Chaco Province, Argentina, between March 2015 and February 2016.

Wallman 2012). The rest of the exotic species (31% of the total exotic species captured) represented a low percentage in the other habitats (10% in the cattle farm, 9% in the alfalfa crop, 8% in the savanna, and 4% in the forest). We have previously obtained similar results in the Iberá Wetlands, Corrientes, Argentina, where >65% of the blow flies captured were exotic species and >90% of these were captured in the anthropized habitat (Dufek et al. 2016). In addition, in the present study, the total abundance of blow flies was considerably higher in the urban habitat.

Two main hypotheses have been proposed to explain differences in species diversity along gradients of ecological disturbance: the niche diversification hypothesis, which predicts that more stable ecosystems such as forests contain higher species diversity, and the intermediate disturbance hypothesis, which states that diversity is maximized when the ecological disturbance is not very drastic, allowing both competitive and opportunistic species to coexist (Connell 1978). In the present study, we found that the diversity of blow flies in the Humid Chaco ecoregion depended greatly on the habitat type and that (α) diversity was highest in the alfalfa crop and forest habitats. The high diversity in the Humid Chaco may be strongly linked to the presence of forest environments. The alfalfa crop studied was close to native forest areas, which would indicate that species migrate from regions with complex vegetation structure (e.g., native forest) to open areas, such as a crop, being attracted by the bait used for the capture. The highest diversity recorded in the forest may correspond to the premise that a more complex environment will provide a greater abundance of potential niches, enabling the coexistence of a larger number of species. Environmental heterogeneity may provide a greater diversity of potential feeding resources, such as feces and animal carcasses, for both adults and larvae, as well as more shaded and stable environments (Pereira de Sousa et al. 2016). In contrast to this, the Savanna habitat, where we registered the lowest diversity, has little shade and fewer microclimates available than an area with cover. The availability of shade and variable microclimates increases with vegetation complexity, which has been shown to correlate with invertebrate diversity, including Diptera (Reid and Hochuli 2007).

There is relatively little information on Calliphorid habitat preferences along anthropization gradients. In the present study, we detected two indicator species for the urban condition: *Ch. megacephala* and *Ch. putoria*. The abundances of both species represented 89% of the total of blow flies captured in the urban habitat, which agrees with previous works where these species have been referred to as highly synanthropic (Prado and Guimarães 1982, Schnack et al. 1989, Vianna et al. 1998, Carmo and Vasconcelos 2016, Dufek et al. 2016). When analyzing the habitats taking into account anthropic intervention sensu lato (urban + cattle farm + alfalfa crop) in comparison to well-preserved habitats (savanna + forest), *Ch. megacephala*, *Ch. putoria*, *L. cuprina*, and *Sarconesia chlorogaster* (Wiedemann) (Diptera: Calliphoridae) were identified as indicator species of anthropized environments, whereas *Chloroprocta idioidea* (Robineau-Desvoidy) (Diptera: Calliphoridae) and *Cochliomyia hominivorax* (Coquerel) (Diptera: Calliphoridae) were identified as indicators of wild environments.

In general, blow fly captures were higher during spring and lower during winter, suggesting a decrease in their abundance in the cold season. Also, richness and diversity were lower in winter. A similar fluctuation pattern in terms of abundance, species richness, and diversity (Shannon–Wiener index) was found among the five environments studied. In general, the different seasons of the year did not influence differentially in each of the environments studied. This was corroborated by the low correlation between these parameters (abundance, species richness, and diversity) and the environmental variables studied.

Blow fly assemblage similarity was higher in farmlands, savannas, and fields with the presence of cattle. The presence of small forested patches, isolated trees in savannas, and cattle fields provides similar patchiness and microhabitat structure to these areas. In addition, field margins in agroecosystems are key factors to maintain landscape diversity, providing refuge and corridors to native species in these mostly open and sunny landscapes. These similar characteristics may be the cause of the dominance of *Ch. albiceps* and the native *Co. macellaria* (the most captured species in this work) in open areas of the Humid Chaco ecoregion (Marshall

Table 5. ANOSIM test for community similarities of Calliphoridae in the seasons surveyed in the Humid Chaco ecoregion, Chaco Province, Argentina, between March 2015 and February 2016

Seasons	*R* statistic	*P* value
Autumn and winter	0.163	0.003
Autumn and spring	0.349	0.001
Autumn and summer	0.130	0.002
Winter and spring	0.642	0.001
Winter and summer	0.434	0.001
Spring and summer	0.379	0.001

ANOSIM (analyses of similarities).

Table 6. ANOSIM test for community similarities of Calliphoridae in the habitats surveyed in the Humid Chaco ecoregion, Chaco Province, Argentina, between March 2015 and February 2016

Habitats	Autumn		Winter		Spring		Summer	
	R statistic	*P* value	*R* statistic	*P* value	*R* statistic	*P* value	*R* statistic	*P* value
U and C	1	0.008	1	0.008	1	0.006	1	0.007
U and A	1	0.008	1	0.008	1	0.008	1	0.008
U and S	1	0.008	1	0.008	1	0.008	1	0.007
U and F	1	0.007	0.948	0.007	1	0.008	1	0.008
C and A	0.504	0.008	0.632	0.008	1	0.006	0.618	0.007
C and S	0.380	0.038	0.006	0.436	0.208	0.062	0.036	0.236
C and F	0.908	0.007	0.906	0.007	0.912	0.007	0.444	0.049
A and S	0.544	0.008	0.748	0.008	1	0.008	0.38	0.026
A and F	0.872	0.007	0.960	0.007	1	0.009	0.764	0.006
S and F	0.992	0.007	0.969	0.007	0.812	0.008	0.388	0.031

References: U, urban; C, cattle farm; A, alfalfa crop; S, savanna; F, forest. ANOSIM (analyses of similarities).

Table 7. SIMPER analysis from comparison of Calliphoridae communities within a category in the habitats surveyed in the Humid Chaco ecoregion, Chaco Province, Argentina, between March 2015 and February 2016

Habitat	Autumn			Winter		
	Species	Average abundance	Contribution %	Species	Average abundance	Contribution %
U	*Chrysomya putoria*	209.4	45.05	*Chrysomya putoria*	129	51.7
	Chrysomya megacephala	157.4	37.81	*Lucilia ochricornis*	42	21.09
	Lucilia ochricornis	40.8	7.6	*Chrysomya megacephala*	29.2	14.34
				Cochliomyia macellaria	15.4	7.56
	Within similarity	74.33		Within similarity	70.15	
C	*Cochliomyia macellaria*	71.6	70.3	*Cochliomyia macellaria*	51	79.55
	Chrysomya albiceps	18.4	17.04	*Lucilia ochricornis*	15.2	13.71
	Lucilia ochricornis	10.2	6.45			
	Within similarity	81.03		Within similarity	68.46	
A	*Cochliomyia macellaria*	39.6	45.66	*Cochliomyia macellaria*	16.8	80.88
	Chrysomya albiceps	43.2	36.17	*Lucilia cuprina*	4	8.94
	Chrysomya megacephala	13.4	14.9	*Sarconesia chlorogaster*	3	6.89
	Within similarity	59.2		Within similarity	49.83	
S	*Cochliomyia macellaria*	125.6	70.47	*Cochliomyia macellaria*	58.8	69.17
	Chrysomya albiceps	42.4	20.81	*Lucilia ochricornis*	18	25.49
	Within similarity	75.67		Within similarity	76.95	
F	*Lucilia ochricornis*	66.6	49	*Lucilia ochricornis*	72.6	70.78
	Cochliomyia macellaria	22.2	21.03	*Cochliomyia macellaria*	20.4	21.74
	Chrysomya albiceps	19.8	20.76			
	Within similarity	71.77		Within similarity	80.62	
Habitat	Spring			Summer		
	Species	Average abundance	Contribution %	Species	Average abundance	Contribution %
U	*Chrysomya putoria*	1,229.2	72.36	*Chrysomya putoria*	166.4	51.02
	Chrysomya megacephala	489	21.89	*Chrysomya megacephala*	145.2	38.83
				Chrysomya albiceps	15.8	6.67
	Within similarity	83.97		Within similarity	68.24	
C	*Cochliomyia macellaria*	572.6	64.79	*Cochliomyia macellaria*	62.6	48.6
	Chrysomya albiceps	164.2	19.49	*Chrysomya albiceps*	55.6	38.17
	Chrysomya putoria	117.6	13.79	*Chrysomya putoria*	18.8	9.42
	Within similarity	79.09		Within similarity	72.44	
A	*Chrysomya megacephala*	85.6	35.33	*Chrysomya albiceps*	72	58.89
	Cochliomyia macellaria	71.2	30.15	*Cochliomyia macellaria*	24	23.4
	Chrysomya albiceps	79.4	26.1	*Chrysomya megacephala*	17.4	14.44
	Within similarity	78		Within similarity	73.38	
S	*Cochliomyia macellaria*	610.6	77.53	*Chrysomya albiceps*	64.8	53.44
	Chrysomya albiceps	178.2	21.01	*Cochliomyia macellaria*	52	43.84
	Within similarity	82.36		Within similarity	72.94	
F	*Cochliomyia macellaria*	207.6	62.36	*Chrysomya albiceps*	32.2	40.47
	Chrysomya albiceps	83.8	26.07	*Cochliomyia macellaria*	36	39.11
	Lucilia ochricornis	34.8	10.53	*Chloroprocta idioidea*	13.8	17.19
	Within similarity	77.48		Within similarity	75.27	

References: U, urban; C, cattle farm; A, alfalfa crop; S, savanna; F, forest. Species contributing to >90% of average similarities are listed.

and Moonen 2002). The blow fly species that most contributed to the similarity of samples in the urban environment were *Ch. putoria* and *Ch. megacephala*, whereas those in the other habitats were *Co. macellaria* and *Ch. albiceps*. In the forest, *L. ochricornis* was the main species that contributed to the similarity among samples, especially in autumn and winter. This agrees with the habitat preference by these species (Prado and Guimarães 1982, Mulieri et al. 2006, Carmo and Vasconcelos 2016, Dufek et al. 2016). Finally, the urban habitat showed a greater dissimilarity than the rest of the habitats studied. This differentiation is mainly due to the differential high abundance of species that were also identified in this work as indicators of this type of habitat.

Our results highlight the importance of habitat configuration and transformation (e.g., livestock farms, large-scale agriculture, urban settlements) in shaping the associated Calliphoridae fauna and supporting the hypotheses that anthropized habitats contain higher proportional abundance of exotic species and lower diversity of native blow flies. In addition, this study provides a first understanding of several ecological aspects of the blow fly assemblages of the previously unsurveyed Humid Chaco ecoregion and allows having a valuable insight into their patterns of resource use and temporal fluctuation. Moreover, this information should help to facilitate the wider use of blow flies in forensic and medical-veterinary investigations in this region of South America.

Table 8. Percentage contribution of each species to dissimilarities in the habitats surveyed in the Humid Chaco ecoregion, Chaco Province, Argentina, between March 2015 and February 2016

Season	Species	U vs. C	U vs. A	U vs. S	U vs. F	C vs. A	C vs. S	C vs. F	A vs. S	A vs. F	S vs. F
Autumn	*Chrysomya albiceps*		6.8			28.99	25.3	4.55	20.21	20.49	11.62
	Chrysomya megacephala	33.57	31.52	28.94	36.92	14.13			9.41	9.75	
	Chrysomya putoria	43.49	44.54	37.52	48.21						
	Cochliomyia macellaria	12.62		20.42		38.41	55.4	41.87	57.46	13.81	53.22
	Lucilia eximia						4.87			6.33	
	Lucilia ochricornis	7.82	9.64	6.42	8.78	8.97	6.72	43.88	6.78	44.23	27.83
	Between habitats dissimilarity	83.4	82.9	85.54	74.26	46.43	31.17	51.4	52.6	63.64	61.5
Winter	*Chrysomya albiceps*					5.94	10.48		6.27		4.43
	Chrysomya megacephala	12.75	13.74	12.39	14.01						
	Chrysomya putoria	51	54.1	50.09	57.73						
	Cochliomyia macellaria	16.43	4.6	18.94	3.5	58.42	50.94	30.78	55.88	10.38	35.83
	Lucilia cuprina					6.01			5.22	4	
	Lucilia eximia						3.91	4.62		4.3	
	Lucilia ochricornis	13.35	21.22	11.29	16.9	24.02	27.81	57.82	23.35	73.34	52.89
	Between habitats dissimilarity	76.57	85.46	74.8	61.56	61.54	27.61	56.18	65.29	75.39	53.94
Spring	*Chrysomya albiceps*					11.55	16.1	13.63	13.49	11.53	17.26
	Chrysomya megacephala	20.87	22.64	19.52	24.28	10.21			11.4	26.27	
	Chrysomya putoria	49.46	71.51	50.65	63.65	13.48	28.89	20.25			
	Cochliomyia macellaria	23.42		23.35	8.42	62.5	49.81	59.49	71.8	41.73	74.05
	Lucilia ochricornis									11.13	
	Between habitats dissimilarity	82.89	81.07	91.68	89.15	68.94	22.72	49.48	69.44	53.33	46.83
Summer	*Chloroprocta idioidea*							10.43		15.83	18.05
	Chrysomya albiceps	10.86	16.74	13.2	5.14	29.42	38.27	31.36	37.95	42.51	43.29
	Chrysomya megacephala	34.93	32.96	33.73	37.1	15.66			19.91	18.15	
	Chrysomya putoria	36.47	44.08	39.62	43.82	13.6	21.13	18.6			
	Cochliomyia macellaria	15.03		11.8	8.45	35.62	31.89	35.87	35.03	17.98	31.03
	Between habitats dissimilarity	80.82	78.18	86.79	85.46	41.49	27.74	36.27	33.52	42.73	34.52

References: U, urban; C, cattle farm; A, alfalfa crop; S, savanna; F, forest. Species contributing to >90% of average similarities are listed.

Supplementary Data

Supplementary data are available at *Journal of Medical Entomology* online.

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