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The role of the landscape in structuring immature mosquito assemblages in wetlands

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Abstract The distribution of mosquito populations is spatially heterogeneous and influenced by factors acting at a wide range of scales. The aim of this study was to assess the role of environmental heterogeneity at the landscape level in shaping the composition of immature mosquito communities inhabiting surface water habitats. The Paraná Lower Delta (Argentina) is a temperate wetland that extends along a 1° north–south gradient and presents high landscape heterogeneity, due to the combined action of geomorphology, hydrology and human intervention. Immature mosquitoes were collected every 2 weeks (Nov 2011–April 2012) from surface water habitats within 11 peridomestic areas interspersed along a 75 km north–south transect. The environment was quantified by 24 variables regarding the geomorphology, geography, economic use, climate, landcover and topography of each site and its surroundings at three radii. The association between the mosquito assemblage and the environment was tested by two multivariate approaches, the community-based outlying mean index and by-species generalized linear models. The former explained 93.6 % of the marginality of all taxa as a function of the type and diversity of landcover, precipitation, presence of cattle and altitude. The niche of six species, most of which were floodwater mosquitoes of the genera *Ochlerotatus* and *Psorophora*, deviated significantly from uniformity. The by-species approach rendered significant models for four species as a function of landcover type and precipitation. Both methodologies were broadly consistent in pointing that landscape elements affect the distribution of immature mosquitoes, thereby shaping the composition of the mosquito assemblage in peridomestic environments within wetlands.

Keywords Freshwater mosquitoes · Oviposition strategy · Environmental heterogeneity · Human settlements · Delta of Paraná River

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Introduction

Species live in a world ruled by heterogeneity and are therefore subjected to variability in environmental conditions, which partly determine their distribution patterns and population dynamics. The effects of the environment are particularly strong for insects due to their high dependence on climatic conditions and landscape organization (Cailly et al. 2011). Mosquitoes (Diptera: Culicidae) are holometabolous insects that occupy two distinct environments within their life cycle. Flying adults are highly mobile and tend to be widely dispersed (Rey et al. 2012). In contrast, larvae and pupae are confined to their aquatic breeding habitat, the type of which may be highly specific or not depending mainly on species requirements and oviposition strategy. The latter can be classified into four broad categories (Bentley and Day 1989; Silver 2008): (A) those that attach their eggs to vegetation, usually associated with permanent habitats (e.g. *Mansonia*, *Aedeomyia*); (B) those that lay eggs individually at or above the water line on a substrate that is subject to intermittent flooding, termed "floodwater mosquitoes" and found only in temporary habitats (e.g. *Ochlerotatus*, *Psorophora*); (C) those that deposit individual eggs on the water surface (e.g. *Anopheles*, *Toxorhynchites*) and (D) those that lay floating egg-rafts on the water surface (e.g. *Culex*, *Coquillettidia*), both of which harbor in temporary and permanent habitats. The location of breeding sites, resting places, blood and nectar sources, coupled with various landscape components such as landcover, hydrologic networks and vegetation height and density may influence mosquito patterns of movement and behavior, ultimately affecting their spatial distribution (Bidlingmayer 1985; Wekesa et al. 1996; Overgaard et al. 2003; Cailly et al. 2011). Numerous studies have linked different landscape features with the distribution of one or a few key mosquito species, usually of medical importance (e.g. Overgaard et al. 2003; Trawinski and Mackay 2010; Chuang et al. 2012). Less attention has been paid to entire mosquito assemblages (but see Alfonzo et al. 2005, DeGroote et al. 2007 and Steiger et al. 2012 for some examples) and the extent of species replacement along environmental gradients.

Although freshwater wetlands provide abundant and diverse habitats for aquatic insects including pest and disease vector species (Grillet et al. 2002), they have traditionally been a neglected area of ecological research, particularly regarding mosquitoes (Dale and Knight 2008). The Lower Delta of the Paraná River is part of the main wetland system in Argentina; its unique mixing of temperate and tropical elements coupled with its proximity to the second largest megalopolis in South America makes it a keystone for both ecological studies and health concern issues. Despite that half of its extent is affected by human activities, population density is low (<1/ha) and human settlements are small and immersed in a natural matrix (Kandus et al. 2006). In this context, many mosquitoes breeding in close contact with people are native species that disperse from the surrounding areas to take advantage of human-created habitats, as was pointed for other taxa (McKinney 2006).

Recent studies in the Paraná Lower Delta revealed that species composition, richness and α-diversity of the mosquito community of surface water habitats (in previous publications referred to as ground-water habitats) depend on the environment at the micro and meso scale (Cardo et al. 2011, 2012a). The aim of this study was to address whether one of such attributes, the species composition, is also affected by the characteristics of the environment at the landscape level. For that, the mosquito assemblage of peridomestic areas was studied along an environmental gradient intersecting a heterogeneous landscape, which is hypothesized to influence the identity of the species inhabiting surface water habitats at each site. A community-wide approach was complemented with by-species models for the identification and quantification of landscape correlates for species turnover.

Methods

Study area

The Paraná River Delta is a wetland macrosystem stretching through the final 300 km of the Paraná basin and covering 17,500 km^2 (Neiff et al. 1994). The Paraná River flows from tropical to temperate latitudes, carrying species of subtropical lineage, and converges with the Uruguay River into the de la Plata River estuary (Fig. 1). Mean temperature and annual rainfall are 16.7 °C (min. = 6 °C, max. = 30 °C) and 1,073 mm, with mild conditions resulting from the modulating effect of huge water masses (Kandus et al. 1999). The high landscape heterogeneity derived from the combination of the geomorphologic setting plus the hydrological regime favors a higher ecological diversity than expected on other areas at similar latitudes (Malvárez 1997).

The study focused on a north–south transect of approximately 0.7° (~75 km) located at the Paraná

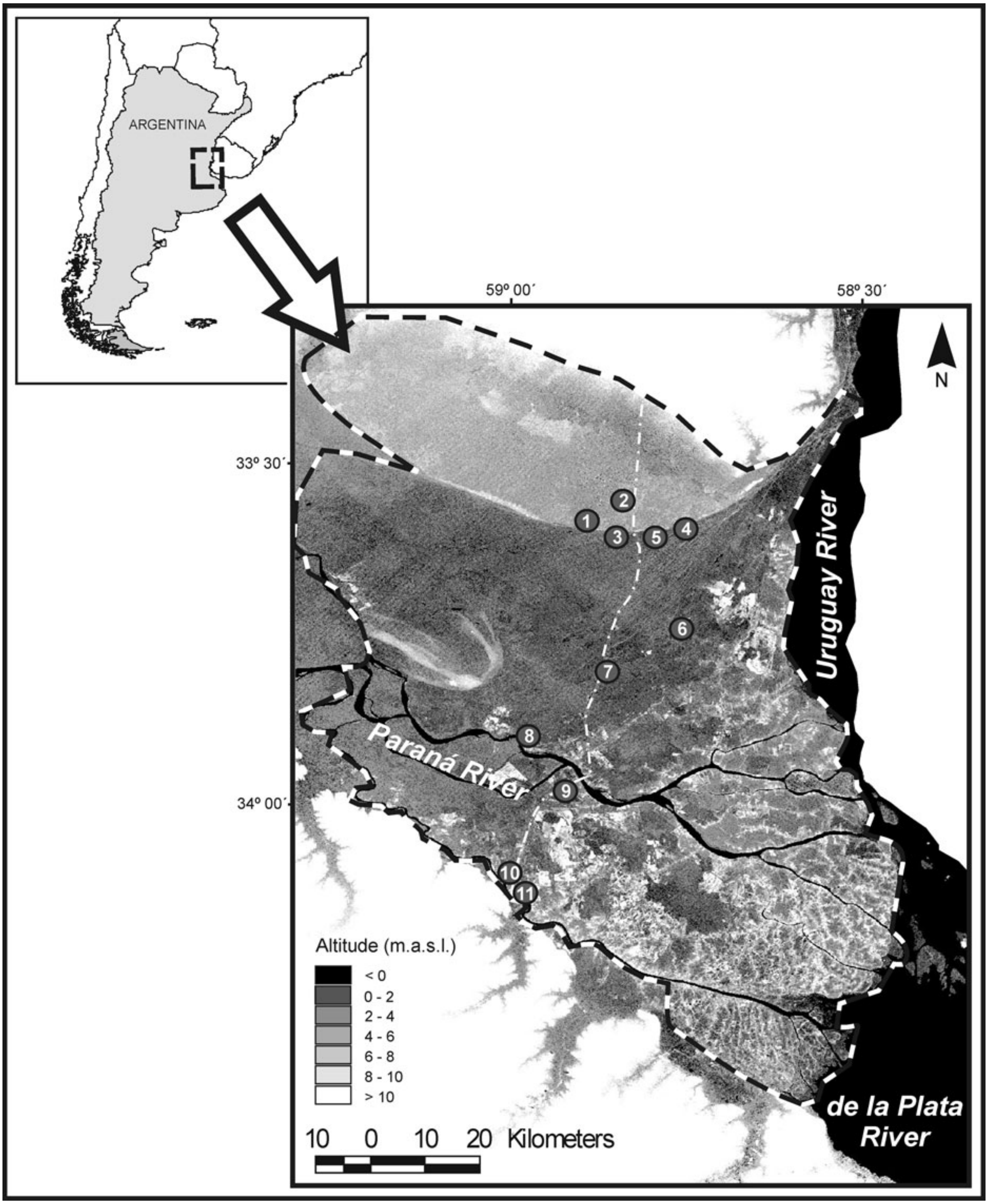

Fig. 1 Study area. The underlying *gray scale* indicates altitude. The *thin dashed white line* is the only road intersecting the study area from north to south, whereas the *thick white* and *black dashed line* circumscribes the Paraná Lower Delta. Sampling sites are indicated with *gray dots* and are numbered for text and figure references

Lower Delta (Fig. 1). Landscape patterns are greatly determined by littoral deposits derived from Mid-Holocene marine ingression and regression processes, plus recent fluvial and deltaic phases (Iriondo and Scotta 1978). The Paraná and Uruguay rivers present different seasonal patterns; the former shows maximum and minimum flow values in March and September, respectively, whereas the latter presents a defined lower phase ending in January and two increasing phases with maximum flow values in July and October (Jaime and Menéndez 2002). Such seasonal patterns, combined with local rainfall and moon and wind tides of the de la Plata River estuary, determine a highly heterogeneous hydrologic regime in the region. Water retention also varies depending on soil characteristics. Vegetation patterns vary latitudinally; the northern portion of the transect consists of a grassland matrix crossed by non functional tidal channels covered by floating vegetation, interspersed with open forest islets of *Acacia caven* and *Prosopis* spp. (Zoffoli et al. 2008). Moving south, there is an area characterized by gently undulated terrains formed by a series of paleo beach ridges dominated by low grasses separated by depressions in-between with patches of woody plants. The southernmost portion of the transect presents lowlands temporarily or permanently flooded and dominated by bulrush marshes crossed by blind creeks, i.e. streams and channels that are closed in one or the two ends, characterized by standing water and presenting diverse aquatic plant communities. Levees and meander spires have been cleared and secondary plant formations are frequent.

Dominant economic activities northwards are extensive cattle raising and logging of native species. Recreational fishing and local tourism along with Salicaceae plantations dominate the southern end. Water availability is maintained either naturally by rain or artificially by filling of watering holes for animals. In terms of the length of the period in which the water is present (hydroperiod), in the study area aquatic habitats for the development of mosquito immatures can be assigned to two broad categories: temporary rain-filled pools and flooded ground which are formed and dry periodically (herein temporary habitats), and ditches, old tide-channels and watering holes that present water all year round and are maintained either naturally or artificially (permanent habitats).

Sampling design, field work and taxonomic identification

Eleven peridomestic sites interspersed along the transect and located close to the only road crossing the region from north to south were selected for this study (Fig. 1). Peridomestic environments provide abundant natural and artificial habitats for mosquito immatures that are occupied by the surrounding species pool. By being structurally similar over large distances, the use of peridomestic areas as sampling units allows for the study of the influence of landscape patterns on mosquito communities. Working exclusively in peridomestic areas also rules out the meso environment and tidal regime effects, excluding these sources of variability from the study (Cardo et al. 2011, 2012b).

Mosquito sampling was undertaken from November 2011 to April 2012. This period includes the late spring, summer and early autumn, covering the main mosquito breeding season in the region, when mosquito densities and richness are generally at their peak (Ronderos et al. 1992; Cardo et al. 2012a). Sampling campaigns were performed once every 2 weeks, on two consecutive days.

All surface water habitats (excluding running water as in streams) encountered in the field were inspected, except when habitats were very abundant, in which a random representative sample was taken without regard for presence or absence of mosquitoes. Habitats were searched for immatures with a fine mesh strainer in case of small or shallow water bodies and by dipping with a white pan in larger water bodies. Time sampling effort was standardized between 1 min (for water bodies of 1 m^2) and 20 min ($\geq$100 m^2). Pupae were separated for rearing and the remaining content of the sample was fixed in situ to avoid predation. At the lab, morphological identification to species of third and fourth instar larvae and emerged adults was conducted under binocular microscope using dichotomical keys and specific descriptions (Darsie 1985; Forattini 2002; Rossi et al. 2002, 2008; Stein et al. 2009). Considering that larval specimens of *Culex dolosus* Lynch Arribálzaga and *Cx. eduardoi* Casal and García have been largely misidentified (Almirón and Brewer 1995; Rossi 2000) and that both taxa may belong to a species complex (Senise and Sallum 2008), all immatures collected were grouped as *Cx. dolosus s.l.*. As regards the genus *Anopheles*, very few specimens were collected and identification to species level was not successful.

Data analysis

As abundance data is highly skewed and often erratic (Rochlin et al. 2009), the proportion of occupied habitat was chosen as a more stable measure of relative abundance. The breeding site index was defined as BSI = number of habitats harboring mosquitoes/number of habitats inspected, following the reasoning used for dengue vectors in manmade container habitats (CI = container index) (Silver 2008). To test if temporary and permanent habitats were occupied by mosquitoes in equal proportions, an independent proportion test comparing the BSI between both habitat types for all sites pooled together was performed with WINPEPI software version 11.24 (Abramson 2011).

Environmental variables

Each sampling site was typified by 24 variables representing different features of the environment (Table 1). Soil drainage affects the availability of surface water habitats and their hydroperiod, whereas the distance to the nearest permanent river serves as an indicator of site-specific wetness. Because mosquito larvae are mainly filter feeders, the presence of cattle can substantially increase food availability due to livestock waste products (Leisnham et al. 2004). The climatic gradient was described in terms of mean temperature and cumulative precipitation values. Landscape pattern descriptors, which provide quantitative links between community and species patterns and the ecological condition of the landscape (Miller et al. 1997), were calculated at different radii around each site. Within a 0.5 km radius buffer, Google Earth images were processed in Arcview 3.2 by visually identifying landcover types, drawing each patch and calculating its area and perimeter. This information was used to calculate area/perimeter ratios for each landcover category (indicative of the shape of the patches) and total landcover diversity (quantifies landcover heterogeneity around each site) estimated with the Shannon-Wienner index (Magurran 2004). At the 1.5 and 3 km scale, moving windows were run for altitude and three landcover layers (trees, herbs and broad-leaved vegetation) and the mean value at each site was extracted.

Before the analyses, environmental variables within the same variable type were examined for colinearity. One variable of each pair presenting a Pearson's correlation coefficient $|r| \geq 0.8$ was removed. Between TEM and PRE ($r = 0.96$), the latter was selected due to higher reliability on the information and higher spatial accuracy. RIV was removed due to its high correlation with several other variables. Between $WAT_{0.5}$ and $HER_{0.5}$ ($r = -0.94$), the former was removed because it consisted of a mixture of several water categories while the latter was calculated straight-forward. All area/perimeter ratios for each coverage class within the 0.5 km buffer were highly correlated with their corresponding proportion of coverage ($r > 0.85$) and were omitted from further analysis. As each pair of landcover variables at 1.5 and 3 km were highly correlated ($r > 0.88$), all 3 km layers were kept to cover as much environmental heterogeneity as possible. Also, TRE_3 was highly correlated with BRO_3 (+) and HER_3 (−) and it was removed. Colinearity still remained between pairs of variables from different types (Table 2). These were retained to ensure that the various variable types were represented and were carefully handled in the by-species modeling (see below).

Community-based approach

The niche concept, as defined by Hutchinson (1957), considers the ecological niche of a species as an n-dimensional hyperspace within which the populations of a species can persist. It is defined by the combination of coexisting environmental gradients and further shaped by functional relationships among species (Whittaker et al. 1973). The outlying mean index (OMI) is a niche analysis designed for gradient studies in which the variance in species occurrence is maximized along ordination axes derived from the input of environmental data (Dolédec et al. 2000). It outperforms canonical correspondence analysis (CCA) or redundancy analysis (RDA) in that it gives a more even weight to sampling units even if they are species poor or individual poor, and does not imply any a priori shape of the species responses to the environment (as do CCA and RDA with unimodal and linear responses, respectively). It also allows for the combined use of quantitative, ordered factors and

Table 1 Environmental variables characterizing each sampling site along a 75 km N–S transect across the Paraná Lower Delta

Variable type	Variable code	Description	Source
Geomorphologic	DRA	Drainage, described categorically as water retention capability of the soil (1 < 2 < 3)	INTA 1990
Geographic	**RIV**	**Distance to the nearest permanent river**	**IGN** 2012
Economic	CAT	Presence of cattle (yes/no)	Field data
Climatic	**TEM**	**Mean annual temperature, in °C**	**New et al.** 2002
	PRE	Cumulative precipitation registered during the breeding season (Oct.-Apr.), in cm.	Meteorological stations at both ends of latitudinal gradient + linear interpolation
General landscape descriptor at 0.5 km	DIV	Shannon index describing patches richness and evenness	Google Earth images + Arcview processing
Cover-type landscape descriptors at 0.5 km	**$WAT_{0.5}$**	**Proportion of surface covered by water (rivers + artificial canals and ponds + temporary channels)**	**Google Earth images + Arcview processing**
	$FOD_{0.5}$	Proportion of surface covered by dense forest	Google Earth images + Arcview processing
	$FOS_{0.5}$	Proportion of surface covered by sparse forest	Google Earth images + Arcview processing
	$HER_{0.5}$	Proportion of surface covered by herbaceous vegetation	Google Earth images + Arcview processing
	$ROA_{0.5}$	Proportion of surface covered by roads	Google Earth images + Arcview processing
	WATap	**Area/perimeter relation for water patches**	**Google Earth images + Arcview processing**
	FODap	**Area/perimeter relation for sparse forest patches**	**Google Earth images + Arcview processing**
	FOSap	**Area/perimeter relation for dense forest patches**	**Google Earth images + Arcview processing**
	HERap	**Area/perimeter relation for herbaceous patches**	**Google Earth images + Arcview processing**
	ROAap	**Area/perimeter relation for road patches**	**Google Earth images + Arcview processing**
Cover-type landscape descriptors at 1.5 km	**$TRE_{1.5}$**	**Percentage of tree coverage around each site, 1.5 km moving window mean value**	**MODIS (Hansen et al.** 2003**)**
	$HER_{1.5}$	**Percentage of herbaceous coverage around each site, 1.5 km moving window mean value**	**MODIS**
	$BRO_{1.5}$	**Percentage of broad-leaved coverage around each site, 1.5 km moving window mean value**	**MODIS**
Cover-type landscape descriptors at 3 km	**TRE_3**	**Percentage of tree coverage around each site, 3 km moving window mean value**	**MODIS**
	HER_3	Percentage of herbaceous coverage around each site, 3 km moving window mean value	MODIS
	BRO_3	Percentage of broad-leaved coverage around each site, 3 km moving window mean value	MODIS
Topographic	**$ALT_{1.5}$**	**Mean altitude around each site, 1.5 km moving window (in m.a.s.l.)**	**USGS** 2005
	ALT_3	Mean altitude around each site, 3 km moving window (in m.a.s.l.)	USGS 2005

Variables that were removed from the analysis due to colinearity are shown in *bold* (see text for a detailed description)

Table 2 Pearson's correlation coefficients (r) between pairs of explanatory variables

	PRE	DIV	$FOS_{0.5}$
$FOD_{0.5}$	−0.93		
$HER_{0.5}$		−0.90	
HER_3			0.82
BRO_3	−0.80		−0.91

Only values of $|r| \geq 0.8$ are shown. Variables are coded as: PRE (cumulative precipitation), DIV (Shannon diversity index for landcover patches in a 0.5 km radius buffer), $FOS_{0.5}$ (% of sparse forest in a 0.5 km radius buffer), $FOD_{0.5}$ (% of dense forest in a 0.5 km radius buffer), $HER_{0.5}$ (% of herbaceous vegetation in a 0.5 km radius buffer), HER_3 (% of herbaceous coverage 3 km around each site) and BRO_3 (% of broad-leaved coverage 3 km around each site). See Table 1 for a full description of the explanatory variables

dummy environmental variables, and is robust to multicollinearity among the explanatory variables (Dolédec et al. 2000; Randa and Yuger 2006).

The species matrix contained the number of positive samples of each species per site, while the environment matrix included all selected environmental variables plus the availability of temporary and permanent aquatic habitats per site. To describe the response of the assemblage and the species in it to the environment, the following niche parameters were computed and tested. The marginality or OMI value represents the deviation of the average position of species *i* from the origin; i.e. it is a measure of the distance between the average habitat conditions used by species *i* and the average habitat conditions of the sampling area. A high OMI thus indicates a species with specific habitat requirements and a narrow niche. Total inertia is proportional to the average marginality and represents a quantification of the influence of the environmental variables on the niche separation of species. The tolerance of species *i* is a measurement of its niche breadth associated with the environmental variables, as a function of the number of sites with which a species is associated and the location of those sites along the environmental gradient. Accordingly, the residual tolerance is the variance in species niche not taken into account by the marginality axis. The statistical significance of the marginality was evaluated with a Monte-Carlo permutation test ($N = 1{,}000$), under the null hypothesis that each species and the whole community are unrelated to their environment. Rejecting it therefore means that niche segregation of a given species or the whole community is effective along the environmental gradient studied. OMI analysis was performed in R (R Core Team 2012), with the package ade4 (Dray and Dufour 2007).

By-species approach

As the identification of associations between the environment and the distribution of each species by the OMI analysis is essentially graphical and qualitative, generalized linear models (GLM) and generalized linear mixed models (GLMM) were used to further quantify these associations. Briefly, these models consist of three elements: a probability distribution from the exponential family, a linear predictor (LP) that relates the response variables to the explanatory variables, and a link function that provides the relationship between the linear predictor and the mean of the distribution function μ (McCullagh and Nelder 1989). As temporary habitats were encountered in all sites, whereas permanent habitats occurred in eight sites (Table 3), only the subset of species present at least in two sites (for species with oviposition strategy A) and in three sites (for species with oviposition strategies B, C and D), and presenting a total number of samples ≥10 was modeled individually.

For species collected in either type of aquatic habitat (*Aedeomyia*, *Mansonia*, *Ochlerotatus* and *Psorophora* spp.), the response variable was the number of positive samples (ps) of species *i* per site, modeled with a Poisson error distribution and log link, so that $\mu = \exp(\mathrm{LP})$. As the number of inspected habitats (ih) in each site differed, an offset was applied adding the log (ih) to the linear predictor. This procedure makes a weighted regression equivalent to model the BSI (ps/ih) with a binomial error. Alternatively, if the response variable as defined above was highly skewed with one very influential observation biasing the whole model, the BSI was modeled with binomial error distribution, ih as weight and logit link so that $\mu = \exp(\mathrm{LP})/(1 + \exp(\mathrm{LP})$.

For species harboring in both habitat types (*Culex* and *Uranotaenia* spp.), the modeling procedure was as follows. First, to evaluate differences in BSI between habitat types a preliminary GLMM was run using the number of positive samples of species *i* per habitat type per site as response variable, the remaining specifications as above and "site" as random factor to

Table 3 Characterization of each sampling site according to selected environmental variables

Site	Use	Prop. of temporary Habitats	Variable code										
			DRA	CAT	PRE	DIV	$FOD_{0.5}$	$FOS_{0.5}$	$HER_{0.5}$	$ROA_{0.5}$	HER_3	BRO_3	ALT_3
1	Stockbreeding	0.74	1	Yes	75	0.38	0	19.8	68.8	2.2	81.6	24.7	4.36
2	Stockbreeding	0.67	2	Yes	75	0.34	0	13.6	77.2	4.4	91.4	24.2	5.79
3	Stockbreeding	0.69	1	Yes	75	0.38	0	21.3	70.4	3.8	79.3	17.9	4.26
4	Stockbreeding	0.52	2	Yes	75	0.30	0	13.4	79.6	2.3	68.6	43.1	4.44
5	Residential	0.52	2	Yes	75	0.34	0	11.0	77.0	4.4	77.1	44.3	3.92
6	Fishing/tourism	0.44	3	No	71.8	0.31	3.9	0	81.0	5.0	56.0	56.8	2.30
7	Fishing/tourism	1	3	No	69.7	0.42	8.2	0.9	74.7	7.3	45.6	57.8	2.18
8	Fishing/tourism	1	3	No	66.4	0.52	20.3	0	35.8	0.4	55.8	46.9	2.65
9	Residential	0.5	3	No	64.9	0.30	11.9	0	79.5	8.6	53.0	58.5	4.17
10	Fishing/tourism	1	3	No	60.8	0.45	14.8	0	67.2	8.0	59.1	70.6	5.31
11	Fishing/tourism	0.76	3	No	60.2	0.54	21.0	0	49.2	4.9	66.7	62.9	9.50

The use given to the peridomestic land and the proportion of temporary habitats (of the total of temporary and permanent habitats inspected) is informed for each site. Variable codes and units are as follows: DRA (drainage, water retention $1 < 2 < 3$), CAT (presence of cattle), PRE (cumulative precipitation, cm), DIV (Shannon diversity index for landcover patches in a 0.5 km radius buffer), $FOD_{0.5}$ (% of dense forest in a 0.5 km radius buffer), $FOS_{0.5}$ (% of sparse forest in a 0.5 km radius buffer), $HER_{0.5}$ (% of herbaceous vegetation in a 0.5 km radius buffer), $ROA_{0.5}$ (% of roads in a 0.5 km radius buffer), HER_3 (% of herbaceous coverage 3 km around each site), BRO_3 (% of broad-leaved coverage 3 km around each site) and ALT_3 (mean altitude in 3 km around each site, m.a.s.l.). See Table 1 for a full description of the explanatory variables

account for potential dependence between BSI values for each habitat type within the same site. The habitat type was evaluated as a fixed factor; if not significant, all habitats were pooled and modeling proceeded as above. If significant, separate models were run for each habitat type.

A manual upward stepwise multiple regression procedure was performed to find the best models. First, explanatory variables were centered, squared and fitted individually. Significance was evaluated for each term addition with a χ^2 on the change in deviance and a significant reduction (>2) in the Akaike's information criterion (Zuur et al. 2007). The three variables that explained the higher deviance were used in turn as start up. Subsequent variables were added one at a time provided they had not a correlation coefficient $|r| \geq 0.8$ with any variable already included. Quadratic terms and interactions were also tested. Additional checking for potential colinearity was performed by restricting terms to have variance inflation factors ≤ 4 (Zuur et al. 2010). The final model parameters were bootstrapped to discard the effect of very influential observations and further compensate for the different ih in each site. If the 95 % confidence interval of a parameter included the zero value, the term was deleted from the model. Model validity was verified with residuals plots, whereas semivariograms (Bailey and Gatrell 1995) were inspected to discard any spatial correlation in the residuals. The explanatory power of the model was estimated with the ratio of the residual to null deviance (equivalent to R^2 in least-square models). Modeling was performed in R (R Core Team 2012) with the package Design (Harrell Jr 2009), and residuals plots and semivariograms were peformed in S-plus 8.0 with S + SpatialStats.

Results

The characterization of the study sites as a function of the 11 selected environmental variables showed the following general trends. Sites located at the northern end of the transect (1–5) were mostly dedicated to stockbreeding, in areas characterized by high precipitation (PRE) but low water retention of the soil (DRA) and high coverage of herbaceous plants ($HER_{0.5}$ and HER_3) and sparse forest ($FOS_{0.5}$) (Table 3). On the contrary, at the opposite end of the transect, sites were mainly used for recreational fishing and local tourism, the soil was easily flooded, no cattle was present (CAT), and vegetation was dominated by dense forests ($FOD_{0.5}$). Landcover diversity (DIV) presented no defined pattern, whereas mean altitude (ALT_3) was higher at both ends of the environmental gradient and lower in the middle (sites 6–8, Fig. 1), as a reflection of past marine ingressions.

Mosquito immatures were collected in 53.3 % of the surface water habitats. The Breeding Site Index did not differ significantly between temporary and permanent habitats ($BSI_{temp} = 0.51$; $BSI_{perm} = 0.58$; $\chi^2_{(1)} = 1.58$, $p = 0.2$). A total of 2,612 mosquito immatures of 24 species corresponding to seven genera were collected (Table 4). The most frequently collected species were *Cx. maxi* and *Ochlerotatus crinifer* (21.2 % and 20.8 % of all catches, respectively), followed by *Cx. dolosus s.l.* (13.5 %), *Psorophora cyanescens* (11.1 %) and *Aedeomyia squamipennis* (8.3 %). The only species present at all sites was *Cx. dolosus s.l.*, whereas *Ad. squamipennis*, *Oc. albifasciatus*, *Cx. maxi*, *Mansonia indubitans* and *Uranotaenia pulcherrima* were collected in 6–10 sites interspersed along the transect.

Floodwater mosquitoes were represented by the genera *Ochlerotatus* and *Psorophora*. Of the former, only two species were found; *Oc. albifasciatus* was widely distributed whereas *Oc. crinifer* was restricted to sites at the southern end of the transect. As regards *Psorophora* spp., richness was markedly higher at northern latitudes with five species collected (*Ps. ciliata, Ps. cingulata, Ps. cyanescens, Ps. confinnis, Ps. pallescens* and *Ps. varinervis*) whereas at the opposite end only two species occurred (*Ps. albigenu* and *Ps. ferox*).

Raft-laying species corresponded to the genera *Culex* and *Uranotaenia*, represented by eight and two species, respectively. In general, mosquitoes with this oviposition strategy were more evenly distributed across the landscape, especially the most frequently collected species mentioned above, C*x. maxi* and *Cx. dolosus s.l.*. Other three species, i.e. *Cx. intrincatus, Ur. nataliae* and *Ur. pulcherrima,* were also widely distributed at intermediate collection values. Four *Culex* species were collected in very low frequencies (<10 immatures) (Table 4).

Community-based approach

The OMI analysis accounted for 93.6 % of the marginality of all taxa (77.2 and 16.4 % for axis 1 and 2, respectively). The first axis was characterized by higher $FOS_{0.5}$, higher PRE and presence of cattle at the northern extreme of the transect, and high BRO_3 and absence of cattle at the southern end. The second axis was mainly associated with an altitudinal gradient (ALT_3) and landscape heterogeneity (DIV) (Fig. 2). The ordination of the study sites in the hyperspace of the environmental variables was consistent with the previous characterization of the sites and resulted in the pattern presented in Fig. 3a. Axis 1 separated sites 1–5 from the rest, whereas axis 2 disaggregated sites 6–11. The value of each environmental variable characterizing each site is shown in Table 4. In general, the ordination along each axis was concordant with the position of each site in the north–south gradient; only sites 8 and 9 were inverted.

The average marginality of all taxa was highly significant ($p = 0.003$), revealing a strong association between the composition of the mosquito assemblage and the environmental variables describing the landscape, and justifying the plotting of species on an ordination diagram (Fig. 3b). Six species (*Oc. crinifer*, *Cx. dolosus s.l.*, *Cx. tatoi*, *Ps. ciliata, Ps. cyanescens* and *Ps. ferox*) departed significantly from a uniform distribution along the environmental gradient (i.e. they had a statistically significant marginality at $p < 0.05$), two of which exhibited an OMI index >10 indicating high habitat specialization (Table 4). On the other hand, four species (*Ma. titillans*, *Ps. albigenu, Ps. pallescens* and *Ps. varinervis*) were collected in only one site each; therefore they showed the highest OMI values, and no tolerance nor residual tolerance. Even though the analysis was successful in explaining a high percentage of the marginality as a function of the environment, high residual tolerance values for several species indicate that there is an unidentified source of heterogeneity other than the variables considered.

The location of each species on the ordination diagram reflects its association with the two main axes

Table 4 Mosquito species composition, relative abundance per habitat type and outlying mean index (OMI) analysis parameters for collected species along an environmental gradient across the Paraná Lower Delta

Species	Code	No. samples in temporary habitats (sites)	No. samples in permanent habitats (sites)	OMI value	Inertia	Tol	Res tol	*p*
Aedeomyia squamipennis	Adsquam	0 (0)	26 (6)	8.28	24.21	10.97	4.95	0.113
Anopheles sp1	Ansp1	2 (2)	3 (3)	6.06	9.70	1.01	2.63	0.213
An. sp2	Ansp2	0 (0)	2 (2)	8.36	11.73	0.24	3.13	0.381
Ochlerotatus albifasciatus	Ocalbi	28 (8)	0 (0)	1.91	18.21	4.35	11.96	0.166
Oc. crinifer	Occrini	35 (4)	0 (0)	14.06	23.46	3.67	5.73	0.006 **
Culex bastagarius	Cxbasta	3 (3)	0 (0)	1.94	16.69	4.26	10.49	0.836
Cx. bidens	Cxbide	4 (2)	2 (2)	6.69	21.34	7.78	6.88	0.247
Cx. chidesteri	Cxchide	4 (4)	1 (1)	3.40	19.96	8.22	8.34	0.360
Cx. dolosus s.l.	Cxdolo	37 (7)	15 (5)	5.42	20.73	9.18	6.13	0.037 *
Cx. intrincatus	Cxintri	3 (1)	6 (3)	7.34	22.21	9.27	5.60	0.216
Cx. lahillei	Cxlahi	3 (3)	0 (0)	4.52	20.59	5.95	10.12	0.276
Cx. maxi	Cxmaxi	30 (8)	10 (4)	1.01	17.55	2.34	14.20	0.193
Cx. tatoi	Cxtato	8 (4)	0 (0)	9.32	21.43	3.46	8.64	0.014 *
Mansonia indubitans	Maindu	0 (0)	15 (6)	1.43	16.51	1.10	13.98	0.460
Ma. titillans	Matiti	0 (0)	1 (1)	8.90	8.90	0	0	1
Psorophora albigenu	Psalbi	5 (1)	0 (0)	32.00	32.00	0	0	0.086
Ps. ciliata	Pscili	14 (6)	0 (0)	4.75	13.12	3.57	4.81	0.041 *
Ps. cingulata	Pscingu	12 (2)	0 (0)	12.88	13.83	0.12	0.83	0.316
Ps. cyanescens	Pscyan	26 (5)	0 (0)	10.25	13.69	0.27	3.16	0.001 **
Ps. ferox	Psfero	16 (2)	0 (0)	22.97	27.66	1.82	2.87	0.019 *
Ps. pallescens	Pspalle	1 (1)	0 (0)	13.71	13.71	0	0	0.538
Ps. varinervis	Psvari	1 (1)	0 (0)	15.14	15.14	0	0	0.276
Uranotaenia nataliae	Urnata	8 (4)	5 (1)	1.75	15.84	4.74	9.34	0.721
Ur. pulcherrima	Urpulch	4 (3)	14 (6)	4.18	20.66	5.60	10.88	0.297
OMI mean	–			8.59				0.003 **

Tol tolerance, *Res tol* residual tolerance, *p* *p* value of Monte-Carlo permutation test

**p* < 0.05; ***p* < 0.01

of environmental variation described above. For instance, the spatial replacement of *Psorophora* spp. is evident along axis 1, with five species at the extreme of the transect characterized by higher $FOS_{0.5}$, higher PRE and presence of cattle, and the remaining two species located at the opposite end. Species closer to the origin, which represents the most general habitat conditions covered by all sampling sites, correspond to the ubiquitous or generalist species (e.g., *Oc. albifasciatus*, *Cx. maxi*, *Ma. indubitans* and *Ur. nataliae*).

Niche plots (Fig. 4) represent not only the centre of gravity for each species (as in Fig. 3b) but also the shape and breadth of the niche along with its location on the coordinate axes, which are indicative of each species distribution and environmental restrictions. Species with a similar plot such as *Cx. tatoi* and *Oc. crinifer* were collected in temporary habitats (Table 4) under the same environmental conditions and had common habitat requirements. In contrast, species collected in the same number of sites may have

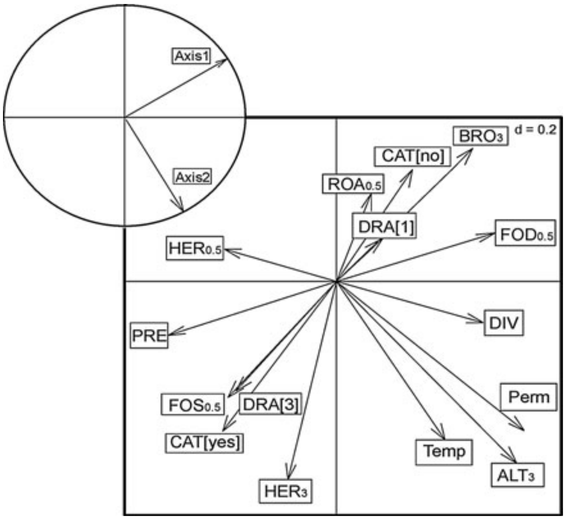

Fig. 2 First two axes of the OMI analysis (*upper left corner*) and canonical weights of the environmental variables considered (*centre*). The availability of temporary and permanent habitats is indicated by Temp and Perm, respectively. Explanatory variables are coded as: *CAT* presence of cattle, *DRA* drainage, *PRE* cumulative precipitation, *DIV* Shannon diversity index for landcover patches in a 0.5 km radius buffer, $FOD_{0.5}$ % of dense forest in a 0.5 km radius buffer, $FOS_{0.5}$ % of sparse forest in 0.5 km radius buffer, $HER_{0.5}$ % of herbaceous vegetation in a 0.5 km radius buffer, $ROA_{0.5}$ % of roads in a 0.5 km radius buffer, HER_3 % of herbaceous coverage 3 km around each site, BRO_3 % of broad-leaved coverage 3 km around each site and ALT_3 altitude 3 km around each site. For factors (CAT and DRA), levels are indicated between *square brackets*. See Table 1 for a full description of the environmental variables

presented very dissimilar niche diagrams. For example, *Ps. cyanenscens* and *Ur. nataliae* were collected in five sites each, however the former was restricted to the northernmost five sites under a narrow range of environmental conditions whereas the latter occurred throughout the environmental gradient. For some species such as *Cx. chidesteri*, *Cx. lahillei* and *Ur. nataliae*, certain negative sampling sites were located inside the polygon delimited as their niche plot. Therefore, the environmental conditions of such sites were suitable for these species, which either remained undetected or were not breeding there due to stochastic reasons.

By-species approach

Following the established criteria, the by-species analysis could be performed for 10 species (Table 5). A satisfactory model was obtained for four of them; the remaining six showed no significant association with any of the environmental variables considered. The relative abundance of *Oc. crinifer* was positively associated with BRO_3, while the opposite was verified for *Ps. cyanescens,* at equivalent percentages of explained deviance. These results reflect a niche partitioning of temporary habitats between both species, with the former breeding in plantations and dense secondary forests and the latter in sparse xerophilous forests. Moreover, the percentage of habitats harboring *Cx. dolosus s.l.* was negatively associated with $FOS_{0.5}$, which correlates highly and negatively with BRO_3 (Table 2). Therefore, this species was more abundant towards the southern end of the transect like *Oc. crinifer*. On the other hand, *Ps. ciliata* was positively associated with PRE, which is also

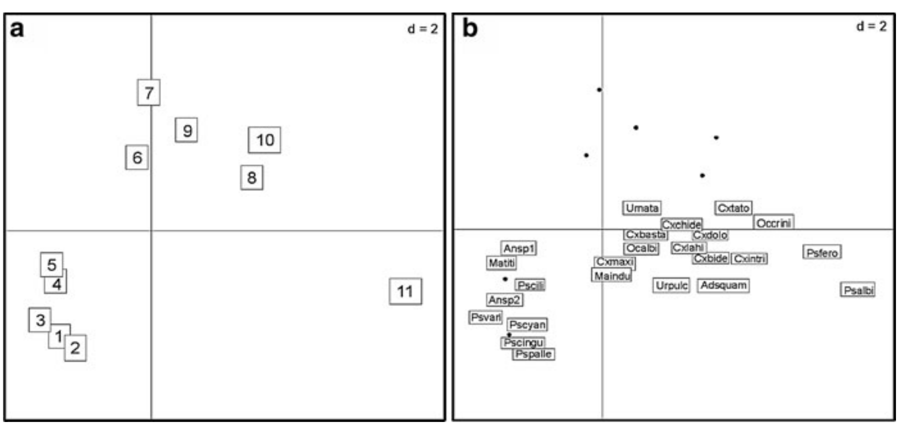

Fig. 3 Ordination of the 11 sampling sites (**a**) and the 24 species (**b**) in the 2-dimensional space defined by the OMI analysis. Sites in **a** are numbered as in Fig. 1. In **b**, the weighted averages of species (*boxes*, see Table 4 for species codes) and sites (*dots*) are superimposed

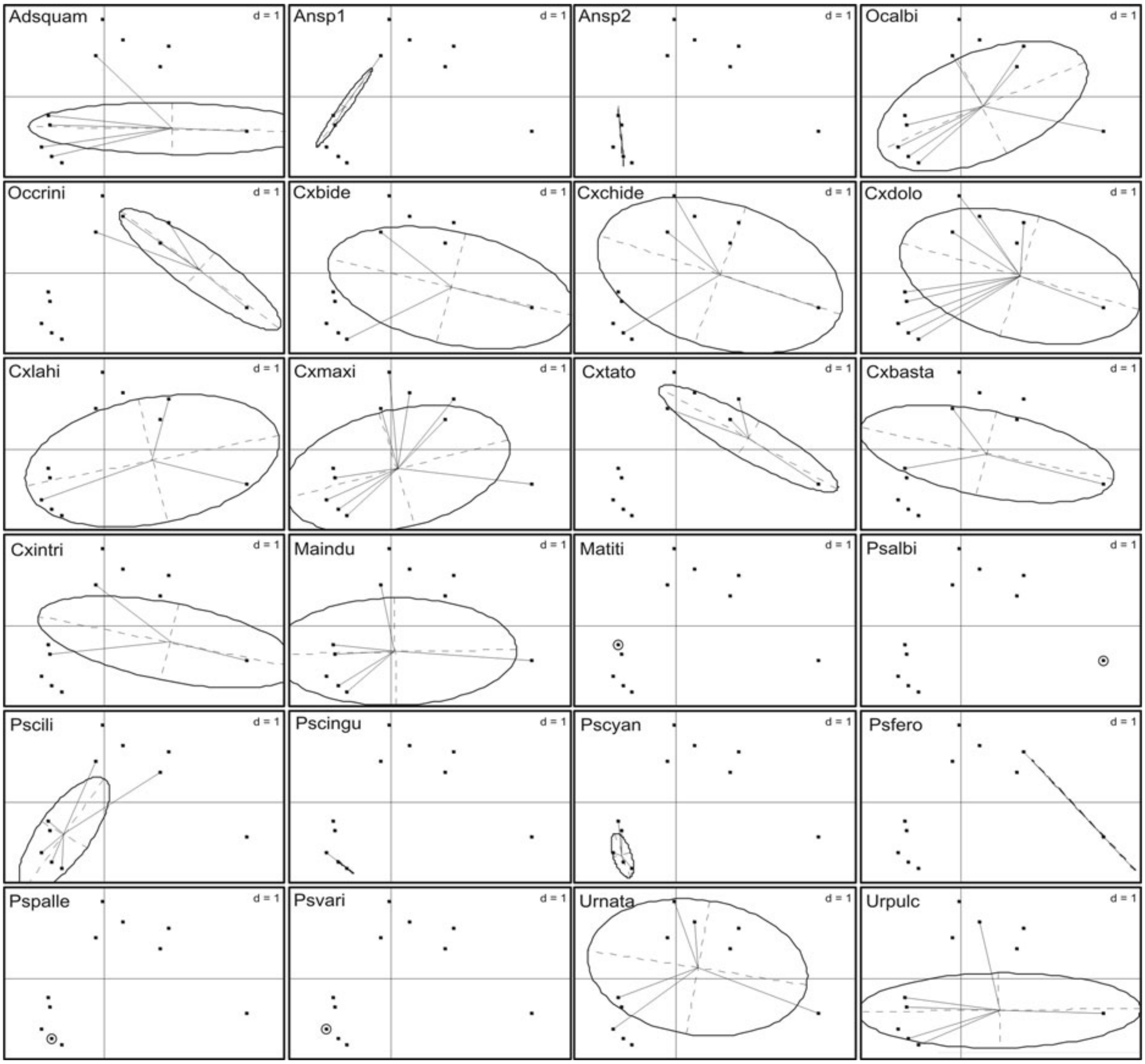

Fig. 4 Niche plots for each of the 24 species according to the OMI analysis. Sites are represented as *dots*. *Lines* link the centre of gravity of each species to each site where the species occurred. See Table 4 for species codes

negatively associated with BRO_3, being more abundant towards the northern extreme and sharing habitat with *Ps. cyanescens*.

Discussion

In the temperate wetland under study, surface water habitats within human settlements support a diverse mosquito assemblage. Representatives of the four oviposition strategies were collected, three of which were present throughout the environmental gradient. However, the majority of the species showing a significant association with the environment were floodwater mosquitoes. Within this group, a species turnover presumably related to the variation of the suitable environmental features for each species was registered. For *Ochlerotatus* spp., *Oc. albifasciatus* was widely distributed whereas *Oc. crinifer* was restricted to the southern extreme of the transect. Analyzing the occurrence of these species under the same climatic regime (<100 km), *Oc. albifasciatus* was the predominant species in temporary pools formed in parks of highly urbanized areas

Table 5 Best Generalized Linear Model for the relative abundance of 10 selected species

Species	% explained by best model	Explanatory variables included in best model	OMI result
Ad. squamipennis	–	–	n.s.
Oc. albifasciatus	–	–	n.s.
Oc. crinifer	76.5	BRO_3 (+)	**
Cx. dolosus s.l.	79.0	$FOS_{0.5}$ (−), $ROA_{0.5}$ (−)	*
Cx. maxi	–	–	n.s.
Ma. indubitans	–	–	n.s.
Ps. ciliata	65.5	PRE (+)	*
Ps. cyanescens	78.8	BRO_3 (−)	***
Ur. nataliae	–	–	n.s.
Ur. pulcherrima	–	–	n.s.

The sign between brackets next to each explanatory variable indicates the sign of the association. Variables are coded as: BRO_3 (% of broad-leaved coverage 3 km around each site), $FOS_{0.5}$ (% of sparse forest in 0.5 km radius buffer), $ROA_{0.5}$ (% of roads in a 0.5 km radius buffer) and PRE (cumulative precipitation). See Table 1 for a full description of the explanatory variables. The result of the outlying mean index (OMI) analysis for each species is shown for comparative purposes

n.s. not significant, — no significant model was obtained

*$p < 0.05$; **$p < 0.01$; ***$p < 0.001$

(Fontanarrosa et al. 2000, 2009). In contrast, in areas characterized by high relative humidity and canopy cover *Oc. crinifer* was highest in abundance and *Oc. albifasciatus* appeared only occasionally (Maciá et al. 1995; Loetti et al. 2007; Cardo et al. 2011, 2012b). This could be due to a requirement of several wet/dry cycles for *Oc. albifasciatus* eggs to hatch (Campos and Sy 2006) and/or a preference of the adults of *Oc. crinifer* for more humid and densely forested areas (Maciá et al. 1995). In this regard, even though rainfall increases towards the northern end of the gradient, higher soil drainage there favors drier soil periods between consecutive precipitation events and the development of xerophilous vegetation.

Concerning *Psorophora* spp., towards the northern end of the transect the assemblage was richer and more complex in terms of food webs and interspecific interactions, including three detritivorous species and two predators. The most abundant species in the north, *Ps. cyanescens* and *Ps. ciliata*, were significantly associated with the environment, breeding at sites characterized by low vegetation coverage. This matches previous findings that these species prefer open habitats and lay their eggs in temporary rain pools located in sunlit open fields (Snow et al. 1960; Wallis and Whitman 1970). On the contrary, the most abundant species in the southern end, *Ps. ferox*, oviposits in shaded pools inside woods and forests (Wallis and Whitman 1970; Campos et al. 1995).

An association with the environment could not be verified for the species with a non-significant result in the community-based analysis. This could be due to high ubiquity and a generalist behavior (e.g., for *Ad. squamipennis*, *Cx. maxi*, *Ma. indubitans*, *Ur. nataliae* and *Ur. pulcherrima*) or, on the contrary, due to very low abundance, in which case the analysis could not distinguish between a true environmental restriction and very low detection. That was the case for *Anopheles* spp., *Cx. bidens*, *Cx. chidesteri*, *Cx. lahillei* and for the species collected exclusively at one site.

Habitat hydroperiod category was a determinant factor in the response of the mosquito assemblages to environmental heterogeneity. Whereas several species of temporary habitats presented an association with the environment, all species of permanent habitats did not, and the behavior of the mosquitoes exploiting both types of habitats was species-specific. Two alternative explanations are proposed for such pattern. On the one hand, temporary habitats may present microenvironmental heterogeneity along the transect, in terms of hydroperiod, alkalinity, organic matter content or other characteristics influenced by variables at the landscape scale which, in the end, act as proxy for such microhabitat differences (Vanwambeke et al. 2007). Landcover type affects water temperature and debris inputs (Williams 2005), whereas livestock waste products can substantially increase the food available for larval mosquitoes (Leisnham et al. 2004). On the contrary, larger and deeper permanent habitats presumably present more uniform microenvironmental conditions across the study region. In other words, the ditches located in the south and the old-tide channels and watering holes from the north apparently play a similar functional role by providing a stable habitat with floating vegetation (*Pistia, Lemna, Azolla* and *Salvinia* spp.) that harbors the same pool of species throughout the transect, mainly *Ma. indubitans* and *Ad. squamipennis*. This adds to the notion that environmental heterogeneity is frequently perceived in a different way by researchers and their study objects, as was note by Haslett (2001) for dipterans. It also warns about the fact that common activities in the region such as field draining or polding may impact the distribution of mosquitoes (Vanwambeke et al. 2007; Zeilhofer et al. 2007), by changing the availability of breeding sites in space and time (Cailly et al. 2011; Cardo et al. 2011).

The second plausible explanation is that the observed pattern is a reflection of a differential plasticity of adult mosquitoes with each oviposition strategy. In other words, the spatial distribution of floodwater mosquitoes is restricted to certain sections of the transect as a function of the suitable characteristics for the adults whereas mosquitoes with the remaining oviposition strategies tolerate a wider range of environmental conditions and are therefore found throughout the study region. Most probably, the observed pattern is a consequence of the combination of both processes, i.e. there are differences both at the microhabitat level that affect the ecology of the immature stages as well as environmental heterogeneity that affects the distribution of the adults.

The selection of an appropriate distance that reflects environmental heterogeneity for the mosquito species under study was hampered by the lack of information on dispersion ranges in our country. Even though in laboratory conditions some species were able to travel up to 30 km (Clements 1999) and a field research recorded more than 45 km flight distance under optimal wind conditions (Harden and Chubb 1960), more recent field studies considered mosquito flight ranges within the radius considered herein (Russell et al. 2005; LaPointe 2008; Estep et al. 2010). Although distance selection is crucial in modeling the distribution of a given species, in community level studies a radius representing a compromise among meaningful distances for all species must be adopted. Such studies (e.g. Schäfer et al. 1997, 2006; Alfonzo et al. 2005; Cailly et al. 2011) have considered distances between 1 and 3 km as appropriate radii. In our setting, an adult could eventually disperse from one site to a neighboring one violating the assumption of independence between sites. However, we believe that the probability of this happening is negligible.

In conclusion, our findings state that the composition of the mosquito assemblage of surface water habitats in wetlands is strongly influenced by the environment at the landscape level. Species composition patterns were mainly driven by floodwater mosquitoes, which replaced themselves across the landscape as a function of landcover type, precipitation and presence of cattle. Both methodological approaches used were broadly consistent, rendering by-species models for four of the six species significantly associated with the environment in the community-based approach. This paper adds to the power of geomatic tools to quantify the spatial organization of mosquito communities (Cailly et al. 2011), which may allow to predict how the mosquito fauna will respond to landscape changes and provide clues as to how landscapes could eventually be managed to suppress populations of disease vectors (Overgaard et al. 2003). This information will contribute in managing the negative risks associated with wetlands in order to preserve wetland values as well as human wellbeing (Dale and Connelly 2012).

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