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SPECIES COMPOSITION AND TEMPORAL VARIATION OF ODONATE ASSEMBLAGES IN THE SUBTROPICAL-PAMPASIC ECOTONE, BUENOS AIRES, ARGENTINA

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Odonata assemblages present in the ecotone between subtropical forest and pampasic grassland in Punta Lara were characterized and compared. Four pools, one in the forest, 2 in grassland (one within a protected area) and one at the limit of both environments, were sampled during July 1996-June 1998. For each sampling station species richness and diversity were calculated, and were compared through 2 similarity coefficients (Jaccard and Winer). The highest species richness and diversity were registered in the forest, and the lowest in the protected grassland. Cluster analysis showed different schemes according to the similarity coefficient considered; a greater similarity between the forest and intermediate pools (Jaccard coefficient), or a greater similarity between grassland areas (Winer coefficient). Some biogeographical implications are discussed.

INTRODUCTION

From a biogeographical point of view Argentina is included in the Neotropical and Antarctic regions (CABRERA & WILLINK, 1980; WILLINK, 1991), the former represented by the Guyano-Brazilian and Andean-Patagonic subregions. The Subtropical and Pampasic biogeographical domains (RINGUELET, 1961, 1981) are in the southern range of the Guyano-Brazilian subregion. The marginal forest of the Paraná River and margin of the Río de La Plata in Buenos Aires province is considered as the southern limit of the Subtropical domain (Fig. 1), forming an evident ecotone with the pampasic grasslands.

Several studies regarding Odonata systematics (RODRIGUES CAPITULO, 1983, 1988, 1996; RODRIGUES CAPITULO & MUZÓN, 1990) and ecology (MUZÓN et al., 1990; RODRIGUES CAPITULO & MUZÓN, 1987) have been carried out in this area, but none concerning the dynamics of the whole odonate assemblage.

Odonata communities are poorly known in South America, although studies concerning them were recently developed in Venezuela (DE MARMELS, 1998) and Brazil (DE MARCO, 1998). The aim of the present study was to establish the species composition of odonate assemblages associated with pools in subtropical forest and adjacent grasslands, and compare their temporal changes, as well as species richness and diversity.

STUDY AREA

The study area, situated near Punta Lara (Ensenada, Buenos Aires province), comprises a band of approximately 1500 m of marginal forest between the shore of the Río de La Plata estuary and the pampasic grasslands (Fig. 1). The weather conditions of this area during sampling period are shown in Figure 2. Four sampling stations were selected (A-D). A-C are situated along a transect perpendicular to the Río de La Plata coast, parallel to a road; A is located within the marginal forest, C in the neighbouring grasslands, and B in the limit of both vegetation associations. Station D is located within grasslands of a protected area (Reserva Integral de Punta Lara):

(A) Permanent water body located five m away from the road, and around 500 m away from the shore of the Río de La Plata (34° 47,05' S; 58° 00,49' W), with a great quantity of sedimented organic matter; water level strongly influenced by the tidal cycle of this estuary. It is usually covered by *Hydromystria laevigata, Salvinia herzogii, Pistia stratiotes, Spirodella* sp., *Lemna* sp., and occasionally *Azolla filliculoides*, surrounded by *Scirpus giganteus* and shaded by a dense forest, mainly of *Salix humboldtiana, Pouteria salicifolia, Ocotea acutifolia, Sebastiania brasiliensis* and the exotic *Ligustrum lucidum*.

(B) Semipermanent pool, 1400 m away from the estuary (34° 47,25' S; 58° 01,21' W). Surrounded by *Iris pseudacorus* and covered by *Spirodella* sp., *Lemna* sp., *Wolfiella* sp., *Hydrocotile ranunculoides, Hydromystria*

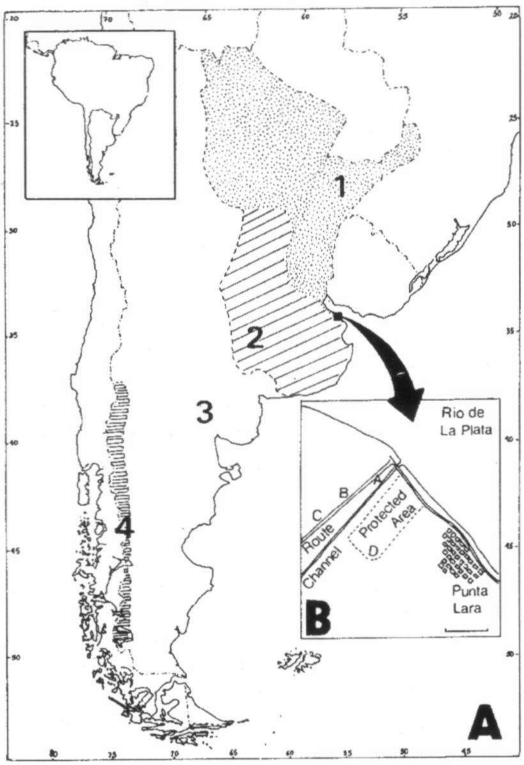


Fig. 1. (A): Map of Argentina, showing main biogeographical divisions: (1-3) Neotropical region; — (1-2) Guyano-Brazilian subregion. — 1: Subtropical domain; — 2: Pampasic domain; — 3: Andino-Patagonian subregion; — 4: Antarctic region. — (B): Location of the study area (bar = 1 km), and sampling stations; A: forest; — B: intermediate pool; — C: grassland pool; — D: protected grassland pools.

laevigata and *Azolla filliculoides*, partially shaded by trees.

(C) Temporary pool, 3000 m away from the Río de La Plata (34° 47,59' S; 58° 01,55' W). Sometimes covered by *Azolla filliculoides* and *Lemna* sp. The proliferation of *Alternanthera* sp. (rooted Amaranthaceae) left no open water.

(D) Series of natural temporary shallow pools situated within the grassland in the protected area (34° 47,53' S; 58° 00,23' W), 2400 m south from the other grassland station and almost at the same distance from the estuary. Surrounded by *Scirpus giganteus* and covered mainly by *Azolla filliculoides*; sometimes *Lemna* sp. and *Wolfiella* sp.

In the two sampling years, rainfall patterns were highly variable. Due to the heavier rainfalls during the second year (Fig. 2), pools located in the grasslands (C-D) and in the limit of both vegetation associations (B) kept their water.

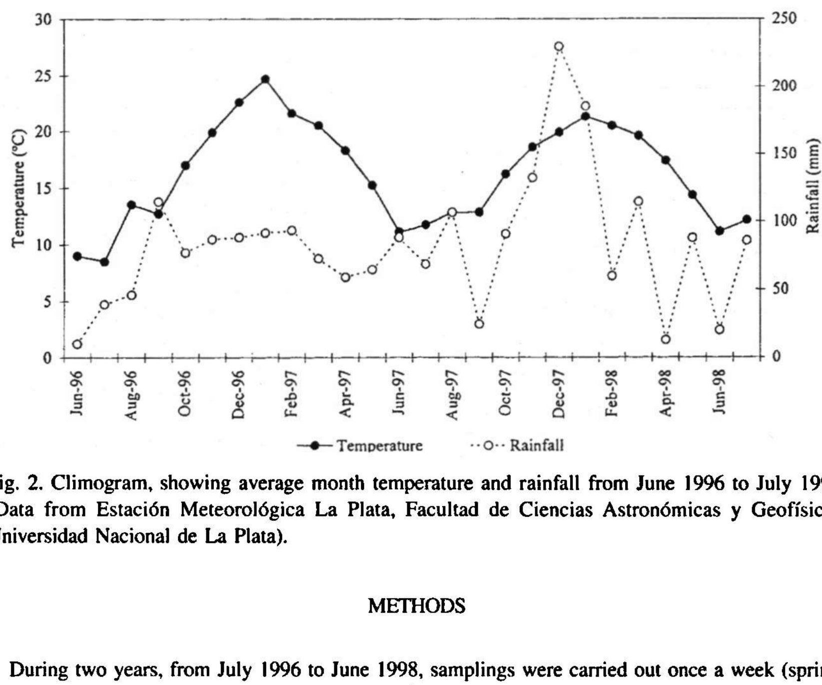


Fig. 2. Climogram, showing average month temperature and rainfall from June 1996 to July 1998. (Data from Estación Meteorológica La Plata, Facultad de Ciencias Astronómicas y Geofísicas, Universidad Nacional de La Plata).

METHODS

During two years, from July 1996 to June 1998, samplings were carried out once a week (spring--summer) or twice a month (autumn-winter) in the four described stations. In every sampling the relative quantity of water, and presence and relative density of floating vegetation were recorded. Adults were collected with a net and larvae with a round sieve; samples were quantified using a definite unit of time (one hour/worker). Besides, in each sampling station four samples of 25 cm diameter area of floating vegetation were extracted and placed in a Berlese-Tullgren funnel for 48 hours. Specimens are deposited in the Museo de La Plata Collection.

Data analysis: For each sampling station, sample intensity (individuals/species ratio) and inventory completeness (percentage of species represented by singletons) were calculated (CODDINGTON et al., 1996); presence frequency was calculated for each species, as well as richness (S) and diversity (H'). Shannon and Weaver index with the correction of Lloyd, Zar and Karr (SCHNACK et al., 1978) was used to obtain the specific diversity values.

Spearman rank correlation test was performed between species richness and diversity monthly averages with temperature and rainfall monthly averages.

Sampling areas were compared through two similarity coefficients: (1) Jaccard association coefficient: paired analyses between all sampling stations based on presence/absence of species (taxonomic similarity), and (2) Winer coefficient (SAIZ, 1980): paired analyses between all sampling stations based on presence frequency of species (temporal constancy). Cluster analyses were performed through average linkage algorithm.

RESULTS

Sixteen genera and 28 species of Odonata were recorded, belonging to four families (Tab. I); Libellulidae (57.1% of the species), Coenagrionidae (25%), Aeshnidae (10.7%) and Lestidae (7.2%).

The highest numbers of species were observed in the forest station (24), and in the intermediate and grassland stations (21), whereas in the protected grassland only 11 species were found. Maximum and average species richness and diversity values were highest in the forest station (the intermediate station shared the same diversity values), and lowest in the protected grassland station (Tab. II, Figs 8-11).

Many species were represented by few individuals and few species by many individuals, approaching a skewed frequency distribution. The most abundant species were generally also the most frequent (Figs 4-7).

From the species recorded in the forest, intermediate, and grasslands stations, *Ischnura fluviatilis, Erythrodiplax nigricans, Miathyria marcella, Micrathyria longifasciata, Orthemis nodiplaga, Tauriphila risi, Tramea cophysa* and *Aeshna confusa* were more frequent and abundant in the intermediate station; *Acanthagrion* sp., *Ischnura capreola, Oxyagrion terminale* and *Micrathyria hypodidyma* in the forest station, and *Homeoura ambigua, H. chelifera* and *Aeshna bonariensis* in the grassland stations.

Species richness and diversity were significantly correlated only with monthly mean temperature in the forest (Richness $r = 0.78$, $P < 0.0001$; Diversity $r = 0.813$, $P < 0.0001$) and intermediate stations (Richness $r = 0.78$, $P < 0.0001$; Diversity $r = 0.79$, $P < 0.0001$).

MARGINAL FOREST

Libellulidae accounted for almost 60% of the species recorded, Coenagrionidae 30% and Aeshnidae 10% (Fig. 3).

Adults were observed between September and May (spring–autumn), the longest flight period that of *Oxyagrion terminale.*

Telebasis willinki and *Erythrodiplax melanorubra* were recorded exclusively at this sampling station.

Frequency and abundance values for each species were similar in both sampling years (Fig. 4). *Oxyagrion terminale, Acanthagrion* sp., *Telebasis willinki* and *Erythemis attala* showed the highest frequency values. *Oxyagrion terminale, Acanthagrion* sp. and *Perithemis icteroptera* exhibited the highest adult abundance

Table I

Checklist of the Odonata species recorded during the sampling period (July 1996-June 1998), A = forest; B = Intermediate water body; C = Grassland; D = Protected grassland; Ad = record of adults; L = record of larvae; Ø = New record for Buenos Aires province; 1-2 = Guyano-Brazilian subregion; 1= Subtropical domain; 2 = Pampasic domain; 3 = Andino-Patagonian subregion

Family	Species recorded	A	B	C	D	Known distribution in Argentina (after MUZÓN & VON ELLENRIEDER (1998)
Coenagrionidae	*Acanthagrion* sp.	Ad-L	Ad-L	Ad-L		
	Homeoura ambigua (Ris)	Ad-L	Ad-L	Ad-L	Ad-L	1-2
	Homeoura chelifera (Selys)	Ad-L	Ad-L	Ad-L	Ad-L	1-2
	Ischnura capreolus (Hagen)	Ad-L	Ad-L	Ad-L	Ad-L	1-2
	Ischnura fluviatilis Selys	Ad-L	Ad-L	Ad-L	Ad-L	1-2-3
	Oxyagrion terminale Selys	Ad-L	Ad-L		Ad	1-2
	Telebasis willinki Fraser	Ad-L				1
Lestidae	*Lestes spatula* Fraser			L		1
	Lestes undulatus Say			Ad-L	Ad-L	1-2-3
Libellulidae	*Erythemis attala* (Selys)	Ad-L	Ad-L	Ad		1-2
	Erythemis plebeja (Burmeister)		Ad	Ad		1-2
	Erythrodiplax melanorubra Borror	Ad-L				1
	Erythrodiplax nigricans (Rambur)	Ad-L	Ad-L	Ad-L	Ad-L	1-2-3
	Miathyria marcella (Selys)	Ad	Ad	Ad		1-2
	Micrathyria hypodidyma Calvert	Ad-L	Ad-L	Ad	Ad-L	1-2
	Micrathyria longifasciata Calvert	Ad	Ad	Ad		1-2-3
	Micrathyria ringueleti Rodrigues Capítulo	Ad		Ad		1-2
	Micrathyria sp.			Ad		
	Orthemis ambinigra Calvert	Ad	Ad			1
	Orthemis nodiplaga Karsch	Ad-L	Ad-L	Ad-L	Ad-L	1-2-3
	Pantala flavescens (Fabricius)	Ad		Ad		1-2-3
	Perithemis icteroptera (Selys)	Ad-L	Ad-L			1
	Perithemis mooma Kirby	Ad-L	Ad			1
	Tauriphila risi Martin	Ad-L	Ad	Ad		1-2
	Tramea cophysa Hagen	Ad	Ad	Ad		1-2
Aeshnidae	*Aeshna bonariensis* Rambur	Ad-L	Ad-L	Ad-L	Ad-L	1-2-3
	Aeshna confusa Rambur	Ad-L	Ad-L	Ad-L	Ad-L	1-2-3
	Aeshna cornigera planaltica Calvert Ø	Ad	Ad			1

Table II
Summary values per sampling station

	Forest	Intermediate	Grassland	Protected grassland
Average species richness	7.2 ± 2.83	5.88 ± 2.23	2.95 ± 2.23	2.5 ± 1.57
Average species diversity	2.16 ± 0.74	2.16 ± 0.56	0.99 ± 0.83	0.9 ± 0.68
Maximum species richness1st year	12	11	8	6
Maximum species richness 2nd year	11	10	7	5
Maximum species diversity 1st year	3.07	3.1	2.59	2.28
Maximum species diversity 2nd year	3.12	3.64	2.31	1.94
N° of adults	609	540	446	251
N° of larvae	1683	270	364	269
Sampling intensity	95.5	38.6	38.6	47.3
N° of singletons	3	2	6	0
Inventory completeness	12.5 %	9.5 %	28.5 %	0 %
Drought period during first sampling year (duration months)	-	summer (1)	summer -autumn (5)	summer (3)

values, whereas the larvae of *Telebasis willinki* and *Erythemis attala* were the most abundant.

Several species recorded in the first sampling year were not found during the second (Fig. 4); this situation is reflected in the lower summer richness values of the second year (Fig. 8).

INTERMEDIATE POOL

The families, and percentages of species in them, were the same as in the forest station.

Erythrodiplax nigricans and *Homeoura ambigua* showed the longest flight periods, between September and May (spring-autumn).

Oxyagrion terminale and *Erythrodiplax nigricans* were the most frequent species during both years, *Orthemis nodiplaga* was also frequent during the first year and *Aeshna bonariensis* in the second (Fig. 5).

The highest abundance values were those of adult *Oxyagrion terminale, Erythrodiplax nigricans* and *Tauriphila risi*, and larvae of *O. terminale, Homeoura ambigua* and *Aeshna bonariensis.*

During the dry up of this pool (January first sampling year), species richness and diversity values did not decrease (Fig. 9), because a high number of feeding adults were recorded.

GRASSLAND

Four families were recorded in this station; Libellulidae had more than 60% of

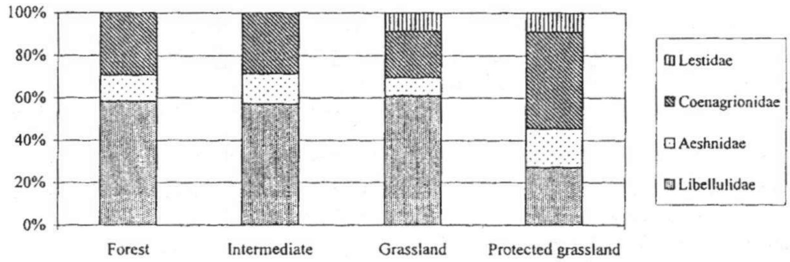


Fig. 3. Percentage of species per family in each sampling station.

the species, Coenagrionidae 20%, Lestidae and Aeshnidae each 10% (Fig. 3).

Most of the species showed a fragmentary record; *Erythrodiplax nigricans* and *Homeoura ambigua* showed the longest flight periods, between September and May (spring-autumn).

Lestes spatula and *Micrathyria* sp. were found only in this sampling station.

Several species had different frequency and abundance values between first and second years. *Erythrodiplax nigricans* was most frequent in both sampling years; *Aeshna bonariensis, Lestes undulatus, Homeoura ambigua* and *Ischnura fluviatilis* showed high frequency values only during the second year (Fig. 6). The highest abundance values were exhibited by adults and larvae of *Lestes undulatus* and adults of *Erythrodiplax nigricans.*

During the drought period observed at this pool (January-May first sampling year), species richness and diversity values decresed gradually, reaching zero in May (Fig. 10).

PROTECTED GRASSLAND

The same families as in the grassland station were recorded, but Coenagrionidae was the best represented (Fig. 3).

Adults were recorded between September and May the first year, and between November and May in the second. Flight periods of *Homeoura ambigua* and *Erythrodiplax nigricans* were the longest.

Aeshna bonariensis was the most frequent and abundant species, followed by *Homeoura ambigua, Erythrodiplax nigricans* and *Aeshna confusa.*

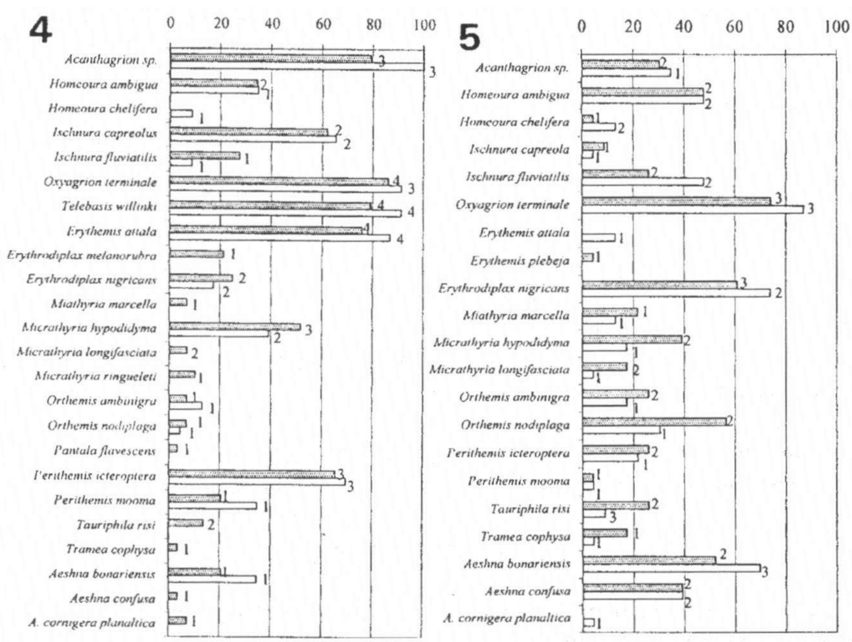
SIMILARITY ANALYSIS

According to the taxonomic similarity (by presence/absence), the forest and intermediate environments built up the highest similarity nucleus, then the grassland, with the protected grassland the least similar (Fig. 12A). When the temporal factor was considered (temporal constancy), the cluster structure inverted, with the highest similarity nucleus formed by the grasslands (protected and not protected), then the intermediate station, and finally the forest (Fig. 12B).

DISCUSSION

Singletons or “rare” species are valid indicators that an inventory is incomplete (CODDINGTON et al., 1996). Since the inventory completeness was in general low (Table II), and many singletons can be explained in the present study by edge effects (both habitat and distribution), the samples were highly probably exhaustive. Several species found only once in a sampling station were recorded in another station. So, these singletons were likely caused by an habitat edge effect, being registered at a station by chance after dispersal (i.e. *Tramea cophysa* and *Aeshna confusa* in the forest station, *Erythemis plebeja* in the intermediate station, *Erythemis attala, Miathyria marcella, Micrathyria ringueleti* and *Tramea cophysa* in the grassland station). *Pantala flavescens* and *Aeshna cornigera planaltica* found as singletons in the forest and grassland stations, and intermediate station respectively, could be caused by a distributional edge effect.

The high dispersal capacity of these insects probably biased the results of the



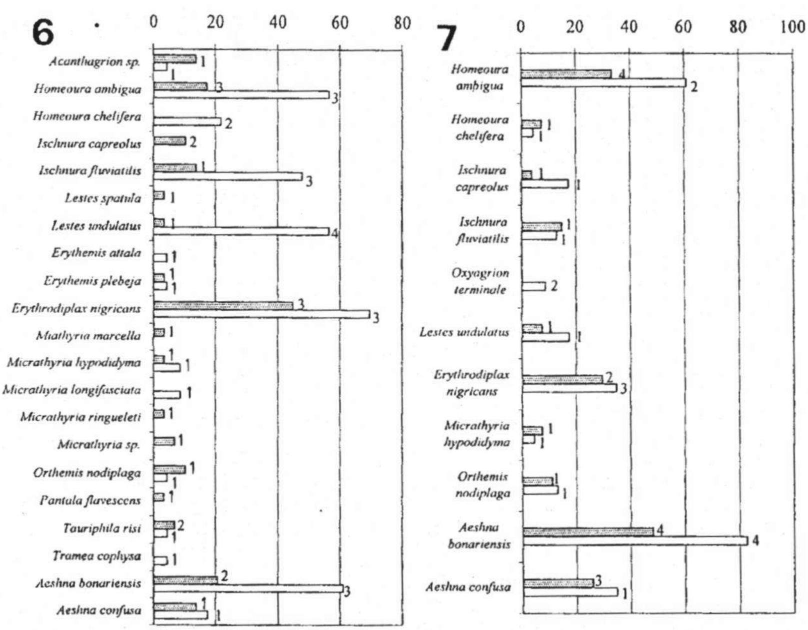
Figs 4-7. Species frequency and abundance per sampling station. Horizontal bars: frequency (stippled: first sampling year, white: second sampling year); – digit: maximum number of individuals registered in one or more samples (scale: 1 = 1-4; 2 = 5-9; 3 = 10-19; 4 = 20 or more individuals): (4) marginal forest; – (5) intermediate pool.

presence/absence analysis, due to their occasional presence in environments where they are usually not established. Because of this, I consider that the temporal analysis (Winer coefficient) reflected better the relationships between these environments than the merely taxonomic one (Jaccard coefficient).

ODONATE STRATEGIES CONCERNING STABILITY OF THE ENVIRONMENT

CORBET (1958, 1983) classified Odonata adaptive strategies according to the presence or absence of a diapause in the course of development, its position in the life cycle, and degree of synchronization in adult emergence. He recognized (1) spring species, whose emergence is synchronized by the presence of a diapause in the last larval instar, (2) summer species, without synchronization in their emergence and with a diapause in the egg stage, and (3) species without diapause or synchronization. Regarding this third type, MUZÓN et al., (1990) analyzing the cycles of some species in this area, found that in spite of the absence of a diapause, there is nevertheless some degree of synchronization in adult emergence, which is determined by climatic factors such as temperature and photoperiod, highly seasonally in this latitude.

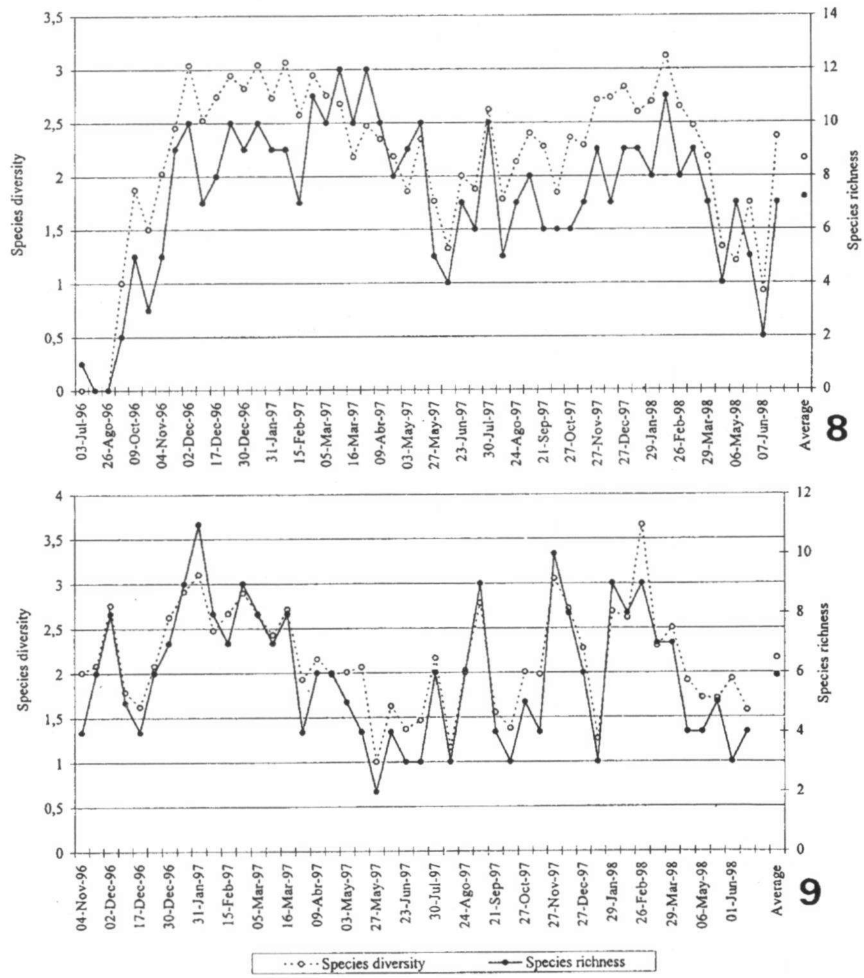
Two of these strategies were registered in the present study; type 2 in *Lestes undulatus*, and type 3 in the remaining species which could be analyzed.



Figs 4-7, continued: (6) grassland; — (7) protected grassland.

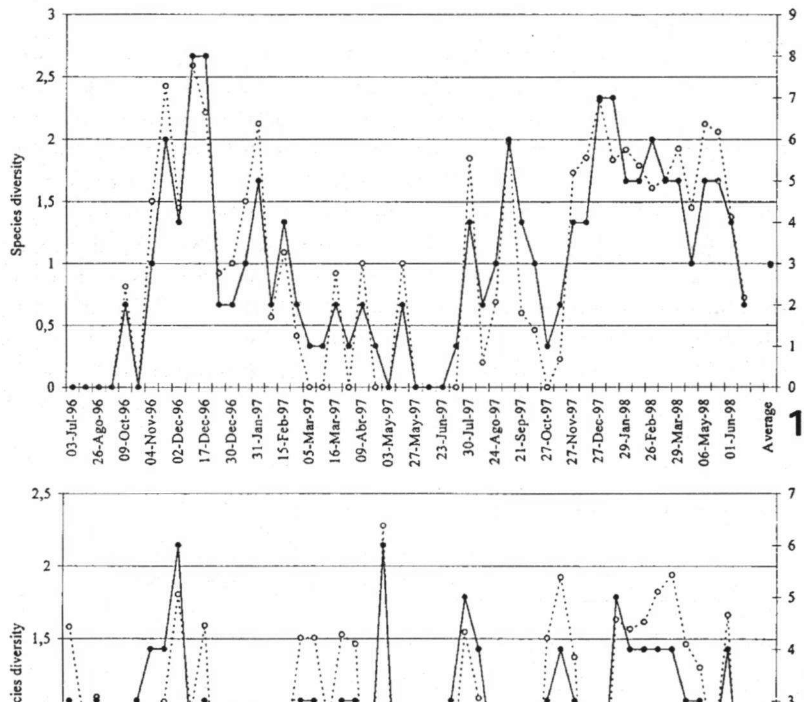
Several Lestidae species are recognized as "summer species", with univoltine life cycles, adapted to temporal environments because they can survive during the dry period as eggs (HODGKIN & WATSON, 1958; WIGGINS et al., 1980). In the grassland station, larvae of *Lestes undulatus* appeared in great numbers during winter of the second year, and since no adults of this species were registered after the drought, it was probably present as eggs.

Coenagrionidae and Aeshnidae could survive also as eggs during the drought, but no larvae of species other than *Lestes undulatus* were found in the temporary



Figs 8-11. Species richness and diversity (July 1996-June 1998): (8) marginal forest; — (9) intermediate pool.

pools after the dry period and before the record of adults. Probably the adults move to permanent pools; this could happen in the recorded species of *Aeshna, Micrathyria, Erythrodiplax, Orthemis, Acanthagrion, Homeoura* and *Ischnura*, found in the temporary pools, and recorded in the forest during the drought period. The protected grassland station, where drought ended in late summer, was recolonized by adults, the larvae of which were found during winter. In the not protected grassland station, at which the dry period was longer (summer-autumn), no odonate larvae were recorded when the drought ended in winter. Probably adults recolonized this pool in spring, when a second short generation developed, with



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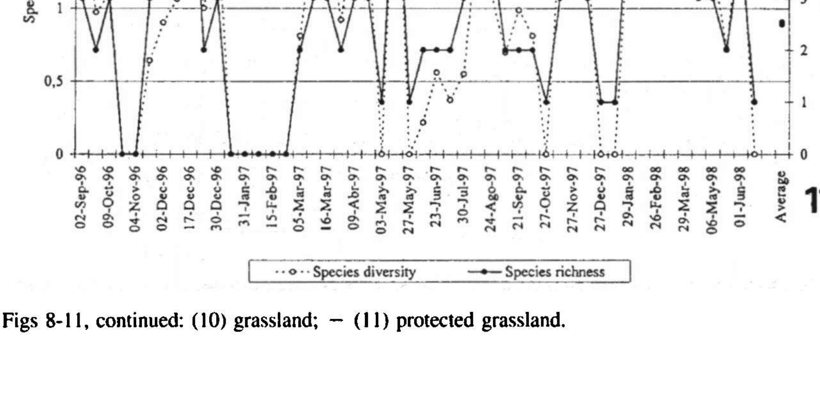

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Figs 8-11, continued: (10) grassland; — (11) protected grassland.

high growth rates. High growth thermal coefficients are usual in the species that breed in temporary environments (HODGKIN & WATSON, 1958). Thus, the species recorded in the temporary pools studied probably have two annual generations.

BIOGEOGRAPHICAL REMARKS

The species found only in the forest, or only in the forest and intermediate pools, are mainly subtropical in distribution, namely *Telebasis willinki, Erythrodiplax melanorubra, Orthemis ambinigra, Perithemis icteroptera, P. mooma* and *Aeshna cornigera planaltica.*

Several species registered also in the grassland pools have a wide distribution in Argentina, exceeding the Guyano-Brazilian subregion (Tab. I). Only *Lestes spatula* and *L. undulatus* were recorded exclusively in the grasslands stations; the former inhabits temporary pools within grasslands associated with the Subtropical forest from the Northeast of the country to Buenos Aires province (MUZÓN, 1993), and the second is widely distributed in Argentina, being found also in the Andean-Patagonic subregion (MUZÓN & VON ELLENRIEDER, 1998). Thus, there seems to be no Odonata species restricted to the Pampasic domain of the Guyano-Brazilian subregion, at least in the study area, and as was stated by RINGUELET (1955, 1961) for other Arthropoda groups, the Pampasic domain has apparently no elements of its own, being a kind of "impoverished Subtropical domain".

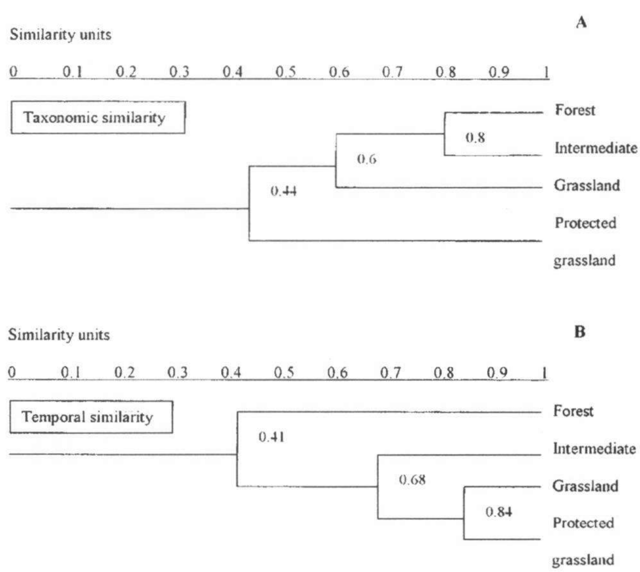

Fig. 12. Cluster analysis of sampling stations according to: (A) taxonomic similarity (Jaccard coefficient) and – (B) temporal constancy (Winer coefficient).

The pools located in the margin of the road (pools A-C) are very exposed to antropic pollution, and since they are artificial shallow depressions, will gradually fill up with sediments from the adjacent terrestrial ecosystems. Besides, this area is seriously threatened, since a highway and a bridge will be build across the Río de La Plata estuary, departing from the study area. The grassland temporary pools are represented inside the "Reserva Integral de Punta Lara", so this kind of environment would be protected someway. The absence of a pool with floating vegetation in the marginal forest within the protected area makes the situation of the forest pool assemblage particularly delicate. Several species were recorded only in this pool, and its assemblage of Odonata species is certainly different from that of the other sampled pools. Because of its permanence, it probably worked as a reservoir for many species that overcome the unfavorable period as adults at permanent pools, colonizing temporary pools by means of dispersal flights. If pools with these features are not preserved, the dynamic of this ecotone would be altered and part of its species richness will be lost.

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