



## Tardigrade diversity: an evaluation of natural and disturbed environments of the province of Salta (Argentina)

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Argentine tardigrades are relatively unknown and, in many cases, unstudied; in the province of Salta in north-western Argentina the lone record of tardigrade dates to the 1980s. Here, we evaluate and compare tardigrade diversity in natural habitats (N), urban environments (U) and rural communities (R) of Yungas. This work seeks to verify the existence of a reduction in tardigrade diversity outside their native habitats and if there is a biotic homogenization in the urban communities. Tardigrade community assemblages were compared between habitats using non-metric multidimensional scaling and a multi-response permutation procedure. Beta diversity was analysed in its component parts, species turnover and nesting, using a modified Raup–Crick test. Gamma diversity was divided into alpha and several beta levels. In total, 2080 eutardigrade and heterotardigrade specimens were registered and showed differences in tardigrade assemblages between habitats; the most diverse habitat was R. The beta diversity partition showed a nesting pattern in the U communities, highlighting faunal homogenization, while species turnover was key in the R and N communities. There was species loss from N to U communities, most markedly between R and U; various forces (both stochastic and deterministic) influence the structure of these communities.

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### INTRODUCTION

As of publication, more than 1220 tardigrade species have been described (Guidetti & Bertolani, 2005; Degma & Guidetti, 2007; Degma, Bertolani & Guidetti, 2009–2015; Vicente & Bertolani, 2013), and despite multiple studies of terrestrial tardigrades in South America (e.g. du Bois-Reymond Marcus, 1944; Ramazzotti, 1964; Nelson, Grigarick & Schuster,

1982; Grigarick, Schuster & Nelson, 1983; Nelson, Kincer & Williams, 1987; Maucci, 1988; Pilato & Binda, 1990; Nickel, Miller & Marley, 2001; Pilato *et al.*, 2002, 2004; Pilato, Binda & Lisi, 2003; Michalczyk & Kaczmarek, 2005, 2006; Pilato, 2007; Londoño *et al.*, 2015; Roszkowska, Ostrowska & Kaczmarek, 2015), Argentine tardigrades remain very poorly known. Approximately 115 tardigrade species have been described in the country; the first record in Salta province was that of Claps & Rossi (1984). These authors reported 14 species for Salta

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province: *Doryphoribius zappalai* Pilato, 1971; *Echiniscus bigranulatus* Richters, 1907; *Macrobiotus echinogenitus* Richters, 1903; *M. hibiscus* de Barros, 1942; *M. hufelandi* C.A.S. Schultze, 1834; *M. spectabilis* Thulin, 1928; *Milnesium tardigradum* Doyère, 1840; *Paramacrobiotus richtersi* (Murray, 1911); *P. areolatus* (Murray, 1907); *Pseudechiniscus bartkei* Weglarska, 1962; *Ramazzottius anomalus* (Ramazzotti, 1962); *R. baumanni* (Ramazzotti, 1962); *R. oberhaeuseri* (Doyère, 1840); and *R. saltensis* (Claps & Rossi, 1984).

Globally, very few studies have compared the composition of tardigrade communities in urban and peri-urban areas (natural or rural). Three such studies have been carried out in Nearctic regions (Meininger, Vetz & Snider, 1985; Johansson *et al.*, 2011; Meyer, Hinton & Dupré, 2013) and two in Palearctic regions (Séméria, 1981, 1982). All the aforementioned publications have described the importance of the prevailing conditions of urban and non-urban habitats on the composition and distribution of tardigrades.

Environmental disturbances caused by the presence and activities of humans impact biota and generate modifications, either by causing local extinctions or by facilitating the expansion of exotic species. This can lead to a 'biotic homogenization' (McKinney & Lockwood, 1999; Olden & Poff, 2003; Olden & Rooney, 2006; Rooney *et al.*, 2007), as urbanization is one of the most homogenizing human activities (McKinney, 2006).

The rural–urban gradient is the standard focus of studies interested in the effects of urbanization on natural systems, as it considers a linear gradient of physical changes that influence habitat availability. Furthermore, habitat fragmentation is known to generate nested patterns, because these landscapes are characterized by patches that differ in size and degree of isolation (Martínez-Morales, 2005); and these changes in diversity between landscapes can be understood as ordered variations of extinction and colonization that then lead to a nested pattern.

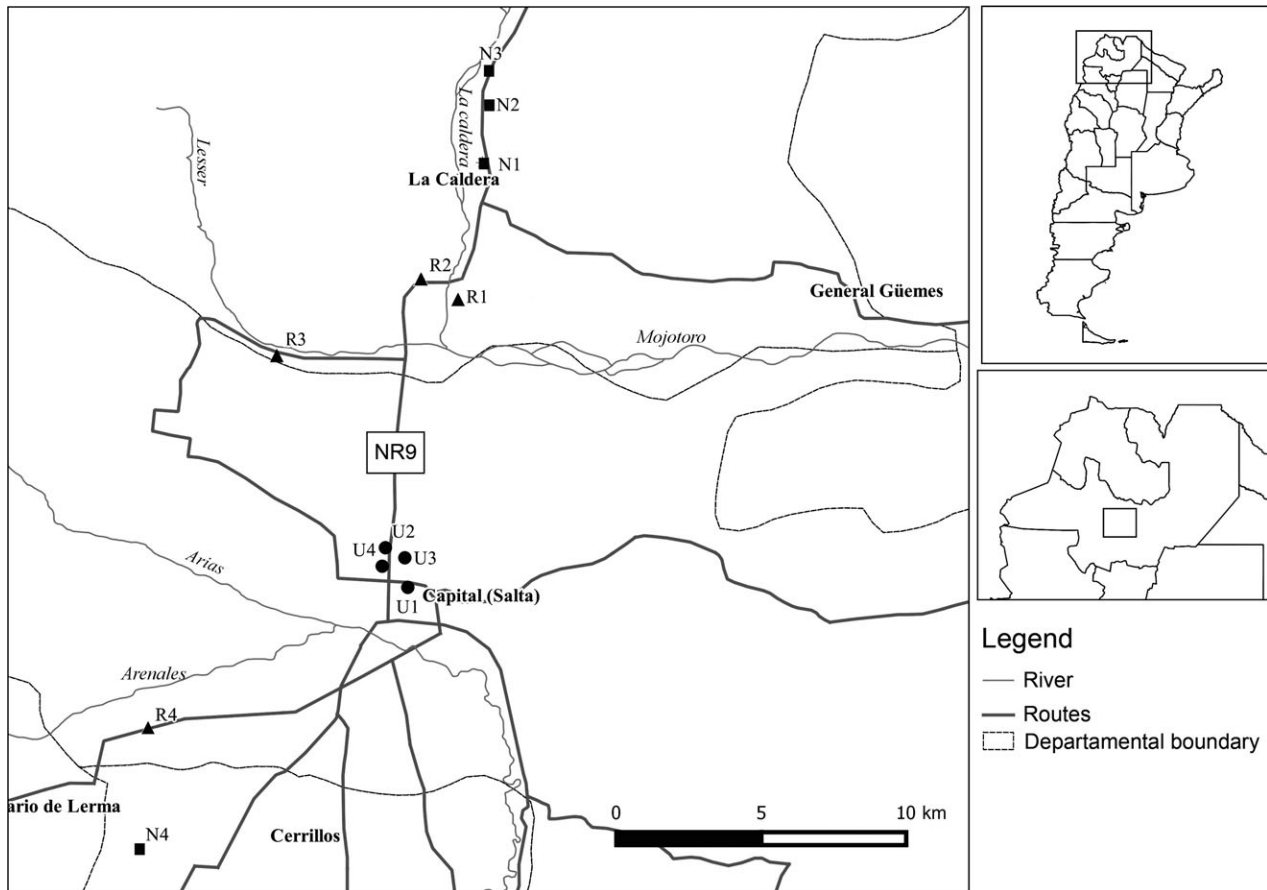
The main goal of the present work was to evaluate and to compare the diversity of tardigrades in different habitats, ranging from natural to urban environments, and including rural areas in the Selva Montana of Yungas in Salta province. This study seeks to evaluate whether urban habitats in the city of Salta, Argentina, exhibit a reduction in tardigrade diversity and a biotic homogenization compared to natural areas.

## MATERIAL AND METHODS

Tardigrades were collected from communities of lichen and moss growing on trees in the city of Salta

(24°27'–25°47'S, 64°55'–65°40'W), and surrounding areas within an area of approximately 20-km radius (Fig. 1). The native sampling area is located in the Yungas ecoregion, corresponding to the altitudinal floor of Selva Montana (700–1500 m a.s.l.), where annual rainfall is around 2000 mm (Brown *et al.*, 2006). The dominant vegetation (Brown *et al.*, 2002) is represented by: *Ficus maroma* (Moraceae), *Cinnamomum porphyrium*, *Nectandra pichurim* and *Ocotea puberula* (Lauraceae), *Inga edulis*, *I. semialata*, *I. saltensis* and *Tipuana tipu* (Leguminosae), and *Blepharocalix salicifolius* (Myrtaceae). The city of Salta has an area of 1772 km<sup>2</sup> with a population of 535 303 inhabitants. It is a regional commercial, educational and administrative centre without industries in the sampling areas. Urban habitats sampled in the city of Salta corresponded to an area with heavy vehicular use especially in main avenues and around the interurban bus station, with a transit of more than 3200 vehicles per hour (Musso *et al.*, 2002). Surrounding the city, rural areas are mainly represented by smallholder farmers cultivating vegetables and forage crops, and sometimes legumes (Pereira, IE & Nardo, 2001), following a traditional management but using different chemical pesticides for control of agricultural pests (Olivo *et al.*, 2015). The landscape is complemented by a very small number of establishments that are responsible for raising cattle and goats.

Epiphytic communities were sampled in: (1) four sites of heavy vehicular transit (urban habitat, U); (2) four sites in the surrounding rural areas (rural habitat, R); and (3) four sites in natural areas (native habitat, N). At each site, four trees were randomly selected from which nine sub-samples of lichen were taken at approximately chest height (1.3 m) with an 11-mm cork borer. Sample and sub-sample size were selected following Morgan (1977) and Steiner (1994b). The samples (48), which were collected in May 2014, were placed in paper bags and stored at room temperature. Prior to study samples were rehydrated for 42 h and adults, moults and eggs were separated with micropipettes. The individuals were placed in a stove at 60 °C to induce asphyxia and were subsequently fixed in 10% neutralized formaldehyde. A portion of the material was mounted in polyvinyl lacto-phenol for microscopy. The identification of tardigrades and their eggs was carried out using a Leica DM500 binocular microscope. The collected material was separated to the lowest possible taxonomic level (species/morphospecies), and was used to generate a database of digital photos indicating distinctive characteristics, using the web application IEBIdata (Ortega, 2011). All individuals of each species/morphospecies was quantified to generate the data sheet for analysis.



**Figure 1.** Sample site locations in urban, rural and native communities in relation to central Salta province. NR9, National Route No. 9.

#### DATA ANALYSIS

##### *Community structure, inventory and $\alpha$ -diversity in each habitat*

Whittaker curves were used to contrast tardigrade community structure in the habitats studied, and were generated using the program Biodiversity-Pro (McAlecece *et al.*, 1997). These curves represent the diversity of assemblages according to the relative abundances of species (Feinsinger, 2003). The resulting curves were fitted with theoretical models (log-normal, geometric series, log-series, broken-stick) using the program PAST 3.01 (Hammer, Harper & Ryan, 2001). The bootstrapping method (Krebs, 1999) was used to evaluate the existence of statistically significant differences in species richness and abundance by habitat, using the program PAST 3.01 (Hammer *et al.*, 2001). 'True diversity', based on species richness and the effective number of species in each community, was also used for comparison. As such, three measures of true diversity were considered:  ${}^0D$ , whose value is equivalent to species richness ( ${}^0D = S_{\text{obs}}$ ) and is not sensitive

to relative species abundance;  ${}^1D$  (Shannon exponential) and  ${}^2D$  (inverse of Simpson index). These values were calculated using the one-parameter family of Renyi's diversity index (Tóthmérész, 1995), which allows a scalable comparison of the diversity of assemblages of two or more communities (Moreno *et al.*, 2011). For this, the following equation was used:

$$H_{\alpha} = \exp\left(\frac{1}{1-\alpha} \ln \sum_{i=1}^S p_i^{\alpha}\right)$$

where  $\alpha$  represents the sensitivity of the index to the relative abundances of the species; values are 0, 1 or 2 according to diversity order zero ( ${}^0D$ ), one ( ${}^1D$ ) or two ( ${}^2D$ ), respectively. Thus, when  $\alpha = 0$ , the index is not sensitive to species abundances, being equivalent to species richness. Values of  $\alpha < 1$  overestimate rare species; by contrast,  $\alpha > 1$  overestimate common species. When  $\alpha = 1$ , all species are included with a proportional weight to its abundance in the community (Hill, 1973; Moreno *et al.*, 2011).

The estimated true diversity (Jost, 2006, 2007) was calculated using the program SPADE (Chao & Shen, 2010) using ACE (abundance coverage-based estimator) for extremely heterogeneous communities ( $CV_{\text{rare}} > 0.8$ ) (Chao & Shen, 2010), MLE\_bc (bias-corrected Shannon diversity estimator) ( ${}^1D$ ) and MVUE (minimum variance unbiased estimator) ( ${}^2D$ ) (Moreno *et al.*, 2011) as measures of zero, first- and second-order diversity, respectively. Each habitat's inventory completeness was calculated as a proportion of the estimated richness (ACE) to the observed species richness. Equations of diversity estimators used here are shown as follows; for more details see Chao & Shen (2012):

$$\text{ACE} = \hat{S} = D_{\text{abund}} + \frac{D_{\text{rare}}}{\hat{C}_{\text{rare}}} + \frac{f_1}{\hat{C}_{\text{rare}}} \hat{y}_{\text{rare}}^2$$

$$\text{MLE\_bc} = - \sum_{i=1}^s I(x_i > 0) \frac{X_i}{n} \log \left( \frac{X_i}{n} \right) + \frac{\hat{S} - 1}{2n}$$

$$\text{MVUE} = \sum_{k=1}^n f_k \frac{k(k-1)}{n(n-1)}$$

#### *Analysis of $\beta$ -diversity and its components*

Non-metric multidimensional scaling (NMS) of the sample sites, using Sorensen's index (Bray–Curtis) as a measure of distance, was carried out using the program PAST 3.01 (Hammer *et al.*, 2001) to analyse the degree of association/similarity of the species assemblages. The resulting groups were corroborated using a non-parametric multi-response permutation procedure (MRPP).

Following the methodology outlined by Chase *et al.* (2011), the Raup–Crick similarity index ( $\beta_{\text{RC}}$ ), which provides information about the degree to which the communities are more different (or similar) than would be expected by chance, was calculated using the software PAST 3.01 (Hammer *et al.*, 2001). The values obtained were standardized to values between  $-1$  to  $+1$  according to the methodology proposed by the same authors. Using this system, for values of 0 (zero) the dissimilitude between communities is equal to what would be expected by chance; positive and negative values represent greater or lesser dissimilitude than would be expected by chance, respectively.

A multiplicative partition of the gamma diversity allowed the evaluation of the differential contribution of the alpha and beta components of regional diversity. This partition was created using the program PARTITION 3.0 (Veech & Crist, 2009), and defining  $\gamma = \alpha 1$  (within the samples)  $\times \beta 1$  (between samples)  $\times \beta 2$  (between sites)  $\times \beta 3$  (between habitats). Using the same program, the resulting values were compared to the values expected assuming a

random distribution of individuals (1000 randomizations) (Crist *et al.*, 2003). To examine the effect of urbanization on the communities, the beta diversity of each habitat, and between pairs of habitats, was partitioned into its two component parts using Sorensen's dissimilitude ( $\beta_{\text{SOR}}$ ), in which:  $\beta_{\text{SIM}}$  represents the dissimilitude due to species turnover between communities and  $\beta_{\text{SNE}}$  represents nesting of the assemblages (Baselga, 2010). This analysis was carried out using the program R and the Betapart package (Baselga *et al.*, 2013). Nested assembler analysis has been used as an ecological tool to describe patterns in species presence and the causes that provoke these changes. In this system, the composition of species in small assemblages in nested systems is a sub-sample of the composition of species in larger assemblages (Ulrich, Almeida-Neto & Gotelli, 2009).

#### *Indicator species by habitat*

The indicator value (IndVal) proposed by Dufrene & Legendre (1997) was used to find indicator species/assemblages of species in each habitat. This analysis is based on the degree of specificity (exclusive to a particular habitat) and the degree of fidelity (frequency of occurrence within the same habitat). Species with a high indicator value ( $> 70\%$ ) are considered 'indicator species', while those with intermediate values ( $50\text{--}70\%$ ) are considered 'detector species' (McGeoch, Van Rensburg & Botes, 2002). The statistical significance of the indicator values was measured using the Monte Carlo test, with 4999 permutations. This test, as well as determination of IndVal, was carried out using the program PC-ORD 6 (McCune & Mefford, 2011).

## RESULTS

### ALPHA DIVERSITY AND COMMUNITY STRUCTURE

In total, 2080 specimens were collected (Table 1), and it is likely that some of the species are new to science. The U habitat had the greatest tardigrade abundance ( $N = 1256$ ), followed by R ( $N = 556$ ) and N ( $N = 268$ ); these differences in abundance were statistically significant ( $P < 0.05$ ) between all of the habitats studied. Species richness (Table 2) was significantly greater in R ( $P < 0.05$ ) than U; while N was not significantly different from either R or U.

According to Whittaker curves (Fig. 2), the community structure was different in each of the three habitats studied, particularly U, in which *Macrobiotus hufelandi* was the dominant species ( $N = 704$ , 56.05%), followed by one morphospecies of *Milnesium*. In contrast, the native community was dominated by the species *Paramacrobiotus areolatus*

**Table 1.** Recorded species richness and abundance in three habitats in Salta province

Family	Species	Urban	Rural	Native
Echiniscidae	<i>Echiniscus</i> C.A.S. Schultze, 1840			
	<i>E. manuelae</i> Da Cunha & Do Nascimento Ribeiro, 1962	0	2	3
	<i>E. rufoviridis</i> du.Bois-Reymond Marcus, 1944	146	48	73
	<i>E. sp. nov.</i>	0	12	0
Hipsibiidae	Morpho1	63	61	2
Macrobotidae	<i>Macrobotus</i> C.A.S. Schultze, 1834			
	<i>M. hufelandi</i> C.A.S. Schultze, 1834	704	269	30
	<i>M. sp1</i>	0	1	5
	<i>Minibiotus</i> R.O. Schuster, 1980			
	<i>M. sp1</i>	3	18	36
	<i>Paramacrobotus</i> Guidetti, Schill, Bertolani, Dandekar & Wolf, 2009			
Milnesiidae	<i>P. areolatus</i> (Murray, 1907)	12	77	108
	<i>Milnesium</i> Doyère, 1840			
	<i>M. sp1</i>	328	68	11
Total		1256	556	268

**Table 2.** Observed and estimated values of 'true diversity' ( ${}^0D$ ,  ${}^1D$ ,  ${}^2D$ ) (estimated diversity is accompanied by the corresponding coefficient of variation) and per cent inventory completeness by habitat in the city of Salta, Argentina

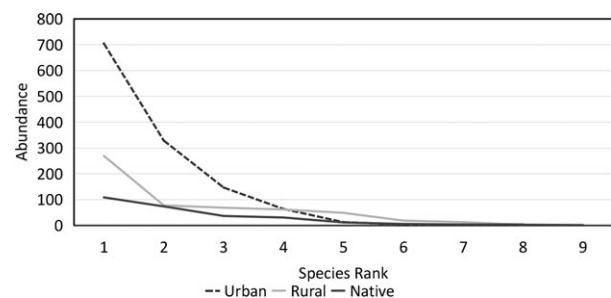
Habitats	Observed diversity			Estimated diversity			% of inventory completion
	${}^0D$ (Sobs)	${}^1D$ (Shannon exponential)	${}^2D$ (inverse of Simpson Index)	${}^0D$ (ACE)	${}^1D$ (MLE bc)	${}^2D$ (MVUE)	
Urban	6	31 088	25 095	6	1.136 ± 0.023	2.512 ± 0.340	100
Native	8	46 065	37 122	8	1.570 ± 0.391	3.750 ± 0.262	100
Rural	9	47 657	34 574	10 ± 1.9	1.541 ± 0.050	3.472 ± 0.256	90

( $N = 108$ , 40.29%) and community structure was more even. The community structure of urban and rural tardigrades was found to best fit a log-series theoretical model ( $P < 0.001$ ), where there is a small number of abundant species and a large proportion of rare species; while the community from the native habitat best fitted a broken-stick theoretical model ( $P < 0.001$ ), showing an evenness in community structure.

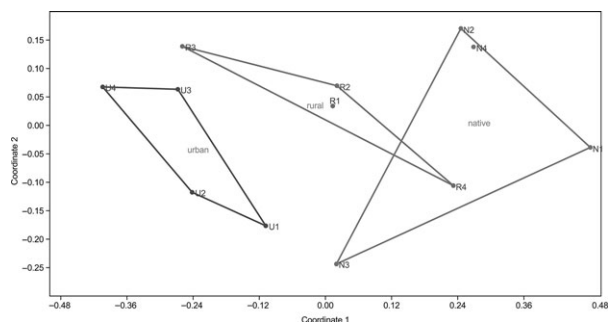
The inventory completeness obtained was very good, reaching 90% in the case of R, and was complete (100%) for both the N and the U communities (Table 2). On the other hand, taking the measure of first-order diversity ( ${}^1D =$  Shannon exponential) into account, the tardigrade community R was 1.04 and 1.53 times more diverse than N and U (Table 2).

#### BETA DIVERSITY, PARTITION AND BIOLOGICAL INFERENCE

The assemblage of urban tardigrades differed from assemblages in the other habitats studied, as was illustrated by the NMS, in which the sampling sites

**Figure 2.** Comparison of tardigrade community structure in selected habitats of Salta province (Argentina) by Whittaker curves, where the species are ordered from most to least abundant. The native community fits better to a broken-stick model showing evenness, meanwhile the log series model best describes the data of urban and rural tardigrade communities.

were ordered by habitat along the first axis, which explained 63% of the total variation (stress = 0.14) (Fig. 3). These results were corroborated by the MRPP, which showed that the assemblages from each of the three habitats were different ( $A = 0.2350$ ,

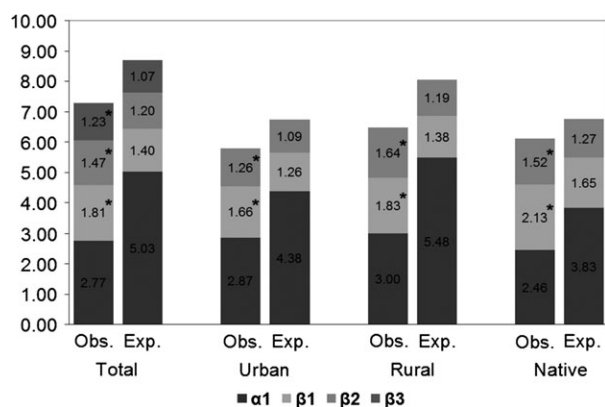


**Figure 3.** NMS showing the similitude of tardigrade assemblages from the sampled communities ordered by habitat on the first axis.

$P = 0.022$ ,  $A$  = chance-corrected within-group agreement), but when comparing paired habitats, only the N and U assemblages were significantly different ( $A = 0.3704$ ,  $P = 0.008$ ).

Regional diversity was partitioned into its alpha and beta components. Analysis of the multiplicative partition of gamma diversity showed that beta diversity was, in every case, greater than would be expected in a random distribution of individuals (Fig. 4), demonstrating that every level of beta diversity analysed is important to regional diversity. In this way, in the landscape analysis,  $\beta_1$  and  $\beta_2$  contributed more than the diversity between habitats ( $\beta_3$ ). However, the beta diversity between samples ( $\beta_1$ ) was the primary source of the diversity recorded within each habitat, except in R, in which the diversity between communities ( $\beta_2$ ) was also important.

Taking these results and the  $\beta_{RC}$  analysis into account, one can infer that deterministic factors (competition, predation, etc.) dominate the structuring of the urban communities, while the rural



**Figure 4.** Partition of gamma diversity into its alpha and beta components and the relationship between observed and expected diversity at each partition level. \*Statistically significant differences between two values.

communities are primarily influenced by stochastic factors (disturbance, dispersion, etc.). In contrast, in N habitats, the similitude of assemblages between communities can be explained by the effect of deterministic factors (biotic and abiotic) that complement stochastic factors (such as dispersion), particularly between distant communities (Table 3).

The partitioning of beta diversity ( $\beta_{SOR}$ ) into its component parts (species turnover and nesting) showed that beta diversity was greater in R and N habitats, as species turnover ( $\beta_{SIM}$ ) was the primary component determining differences in community composition in these habitats (Table 4). Conversely, in the U habitat, beta diversity between sites was due exclusively to nesting ( $\beta_{SNE}$ ). This same component explained the beta diversity between pairs of habitats, suggesting that there was a loss, rather than a turnover, of species between these habitats.

In the analysis of the potential use of tardigrade species as indicator species, two species were defined as detectors in the U habitat: *Macrobiotus hufelandi* (60.6%,  $P = 0.0040$ ) and a morphospecies of the genus *Milnesium* (69.6%,  $P = 0.0004$ ). *Paramacrotus areolatus* (53.8%,  $P = 0.0222$ ) was identified as a detector in the N habitat. No species of tardigrade was defined as an indicator species for any studied habitats.

## DISCUSSION

This is the first study of tardigrade communities in Argentina in which diversity and community structure are compared and analysed in urban, rural and native habitats. Nine species are listed, and our reported inventories appear to be very complete, except in the rural habitat, in which an additional species may be reported. The estimated completeness of our inventories is probably due to the low number of reported species as singletons (species with only one individual); this parameter is used as an estimator of species richness. Although in Argentina there are no previous ecological studies such as the present, there are reports of different species of tardigrades registered on mosses and lichens in urban and rural habitats in different localities in the province of La Pampa (Moly de Peluffo *et al.*, 2006; Peluffo, Rocha & Moly de Peluffo, 2007). While these data are not comparable to our study, because the number of samples collected here was higher than those studies, the methodology for collecting tardigrades was similar. Bearing these in mind, the number of species recorded by us exceeds those of previous studies.

Johansson *et al.* (2011) indicated that species richness is greater in rural than in urban zones, and our results corroborate this with more tardigrades in

**Table 3.** Modified Raup–Crick similitude ( $\beta_{RC}$ ) value in accordance with Chase *et al.* (2011) (light grey:  $\beta_{RC} \sim 0$ ; black:  $\beta_{RC} \sim 1$ , dark grey:  $\beta_{RC} \sim -1$ )

	U1	U2	U3	U4	R1	R2	R3	R4	N1	N2	N3	N4
U1	–	0.709	0.827	0.707	0.737	0.442	0.144	0.708	–0.630	0.404	0.151	0.848
U2		–	0.895	0.972	0.460	0.720	0.287	0.640	–0.531	0.707	0.288	0.294
U3			–	0.892	0.593	0.842	0.563	0.296	–0.856	0.846	–0.246	0.579
U4				–	0.449	0.712	0.284	0.635	–0.515	0.718	0.294	0.296
R1					–	–0.180	–0.359	0.430	–0.919	–0.170	–0.385	0.566
R2						–	0.144	–0.112	–0.668	0.440	0.151	0.092
R3							–	–0.539	–0.215	0.829	–0.842	0.632
R4								–	–0.550	–0.101	0.284	0.297
N1									–	–0.639	0.593	–0.231
N2										–	–0.677	0.137
N3											–	–0.239
N4												–

$\beta_{RC} \sim 0$ ,  $\text{Dis/Similitude}_{\text{obs}} \sim \text{Dis/Similitude}_{\text{exp}}$  (dissimilitude is equal to dissimilitude expected by chance) inferring that there is dispersion;  $\beta_{RC} \sim 1$ ,  $\text{Dis/Similitude}_{\text{obs}} > \text{Dis/Similitude}_{\text{exp}}$  (communities are more similar than expected by chance), biotic interaction acts between sites;  $\beta_{RC} \sim -1$ :  $\text{Dis/Similitude}_{\text{obs}} < \text{Dis/Similitude}_{\text{exp}}$  (communities are less similar than expected by chance), abiotic forces influence assemblage similitude between site.

**Table 4.** Values of beta diversity and nesting between sites of each habitat and between them (different letters indicate statistically significant differences,  $P < 0.05$ )

	$\beta_{SIM}$	$\beta_{SNE}$	$\beta_{SOR}$
Urban	0.000000 <sup>a</sup>	0.212121 <sup>a</sup>	0.212121 <sup>a</sup>
Rural	0.315789 <sup>ab</sup>	0.142543 <sup>b</sup>	0.458333 <sup>b</sup>
Native	0.434782 <sup>b</sup>	0.034605 <sup>c</sup>	0.469387 <sup>b</sup>
Urban-Rural	0.000000	0.200000	0.200000
Urban-Native	0.000000	0.142857	0.142857
Rural-Native	0.000000	0.588235	0.588235

$\beta_{SOR}$ , overall beta diversity;  $\beta_{SIM}$ , dissimilitude due to species turnover between communities;  $\beta_{SNE}$ , nesting of the assemblages.

rural zones than in native or urban ones. In urban environments, lower tardigrade species richness has been related to vehicular traffic and air quality (Meininger *et al.*, 1985; Steiner, 1994a; Moly de Peluffo *et al.*, 2006; Peluffo *et al.*, 2007). In our study area, a direct evaluation of these variables was not made but the observed reduction in species richness of tardigrades in urban habitats can probably be explained by them. The city of Salta is characterized by an ‘urban dome’, a layer of warm air around the city in which contaminants (mainly nitrogen oxides and ozone produced by the high vehicular traffic) are evenly distributed (Musso *et al.*, 2002). The sample sites in the city of Salta in our study are consistent with those where air quality was evaluated by Musso *et al.* (2012). These authors considered that the air

quality of this urban area is poor, given that they obtained an annual average of  $\text{NO}_2 = 49 \mu\text{g m}^{-3}$  and  $\text{O}_3 = 78 \mu\text{g m}^{-3}$  for the period 2011–2012.

Urban sites are characterized by a marked dominance by certain species: *Macrobotus hufelandi* and a morphospecies of *Milnesium*. This can be explained by the observation that in urban areas, many animal communities show an increase in the biomass and density of generalist species (Adams, Vandruuff & Luniak, 2005). The distribution of species abundances within a community is of great interest, as it can help to outline the distribution of niches within the community and explain why, at certain levels of species richness, a community can maintain itself; it therefore allows researchers to monitor the stress due to contamination (Magurran, 2004). This same author mentions that all assemblages can reflect the existence of infrequent or migratory components (species), as is the case with an *Echiniscus* species in the present study, which was recorded only in the rural habitat. The tardigrade community in the native habitat described in this study showed a better fit to a broken-stick theoretical model, which is common in assemblages in which the evenness in species abundance increases over time (Wilson *et al.*, 1996).

The results indicate that there is a high degree of nesting and species loss in the urban habitat in the city of Salta; consequently, the composition of these communities would be more homogeneous than in the other habitats studied. This nesting may be limited by species distribution, biogeographical history or physical heterogeneity (Wright & Reeves, 1992), and could just as well be explained by diverse

deterministic and stochastic phenomena (Wright & Reeves, 1992; Ulrich *et al.*, 2009). All these causes are related to variation in homogeneity, as anything that introduces heterogeneity into a system will minimize nesting to some degree. Thus, in the urban habitat, the deterministic forces that drive the community's structure steer it toward nesting; and in this way the species *Macrobiotus hufelandi* and one morphospecies of *Milnesium* seem to be the predators that organize the remainder of the trophic hierarchy (detritivores and herbivores) in the community. In contrast, species turnover drives the composition of the native and rural tardigrade communities. Consequently, in rural communities, the probability that a species will colonize new habitats depends on its regional abundance or fragmentation, which can lead to nesting in the habitat and species. Finally, both stochastic and deterministic processes play a role in the structure of native communities. It is possible that *Paramacrobiotus areolatus* plays an important role in the structure of these communities by preventing trophic overlap with other species. In our results, *Macrobiotus hufelandi* is dominant in urban environments, while *P. areolatus* dominates in rural and native environments, possibly competitively excluding the former, probably through competition for food. Results detailing the complete exclusion between *Macrobiotus hufelandi* and another *Paramacrobiotus* species are reported in Wright (1991).

We conclude that tardigrade communities show a nested pattern of diversity from native to urban environments in the city of Salta (Argentina), resulting in homogenization of the city's fauna. This pattern suggests an important loss of species in the urban habitat as compared to the rural habitat. Furthermore, the specific composition and structure of the tardigrade assemblages in each of these environments reflects the different forces (stochastic, deterministic, or both) that drive them.

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