

## Water bears in the Anthropocene: a comparison of urban and woodland tardigrade (Phylum Tardigrada) communities in Southwestern Louisiana, USA

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### ABSTRACT

Humans have had such a profound effect on global ecosystems, including biodiversity, that Anthropocene is being increasingly used as a chronological term to mark the period of greatest human impact. No areas show the effect of human impact on the environment more than cities, which often have novel combinations of species in unique communities. Tardigrades (Phylum Tardigrada) have often been collected in cities, but studies dedicated to urban tardigrade biodiversity are few, and those comparing urban diversity with nearby rural or natural sites even fewer. In this paper we compare the diversity and abundance of tardigrade species in Lake Charles with a nearby forested non-urban site, Sam Houston Jones State Park (SHJSP). Although tardigrade density did not differ significantly between Lake Charles and SHJSP, species richness and diversity were greater in SHJSP (17 species,  $H_1=3.01$ ) than in Lake Charles (8 species,  $H_1=1.30$ ). All but one species found in Lake Charles also occurred in SHJSP. The number of species found in Lake Charles lies within the range (5-10) found in previous urban surveys. All tardigrade studies comparing urban with nearby nonurban habitats have found lower species richness in cities.

Key words: Tardigrada, urban ecology, tardigrade ecology, biogeography.

### INTRODUCTION

The distribution and abundance of species in the modern world is not solely the result of natural, non-anthropogenic factors. Anthropogenic biomes (urban, village, cropland, rangeland and semi-natural forest) cover more than 75% of Earth's ice-free land (Ellis and Ramankutty, 2008). Indeed, human-caused changes to the Earth's climate, land, oceans and biosphere are now so pervasive that the establishment of a new geological epoch, the Anthropocene, defined by the actions of humans, is being seriously considered (Zalasiewicz *et al.*, 2011).

Humans generate spatial heterogeneity as they transform land, extract resources, introduce exotic species, and modify natural agents of disturbance, and nowhere is this more evident than in cities and other urbanising areas (Alberti, 2008). Human activities directly affect land cover, which controls primary productivity and biotic diversity (Sukopp, 1990). Urbanising areas often have novel combinations of species in unique communities, with diversity peaking at intermediate levels of urbanisation (Alberti *et al.*, 2003). Disparate biotas in widely-separated areas can become more homogenised with increasing urbanisation (Olden and Rooney, 2006).

Terrestrial tardigrades (Phylum Tardigrada) are microscopic panarthropods frequently found in moss, lichens, liverworts, leaf litter and soil. Although tardigrades have often been collected from urban settings (Curtin, 1948), studies designed to investigate urban tardigrade diversity are few, and those comparing urban with nearby rural or natural habitats even fewer. Grothman (2011) collected twelve

species of tardigrades from the grasslands and woods of a large urban park in Calgary, Canada, but did not collect in the city proper. Moly de Peluffo *et al.* (2006) and Peluffo *et al.* (2007) examined tardigrade distribution and diversity in two Argentine cities, but did not compare these to surrounding non-urban areas. Mitchell *et al.* (2009) investigated tardigrade diversity on an urban university campus in Philadelphia, USA. Steiner (1994a, 1994b, 1994c) collected extensively in Zürich, Switzerland, and nearby rural areas but his reported tardigrade diversity data did not distinguish between the two habitats. In a series of published abstracts, Utsugi (1985, 1986, 1987, 1988, 1990, 1992) summarised the results of a comprehensive tardigrade survey of 25 Japanese cities and surrounding areas. However, Utsugi did not publish his full results, and the abstracts do not directly contrast urban and non-urban tardigrade diversity.

Three studies have explicitly compared urban and rural or peri-urban tardigrade community composition: Séméria (1981, 1982) in Nice, France; Meininger *et al.* (1985) in Cincinnati, USA, and Johansson *et al.* (2011) in Fresno, USA. In this paper we compare the diversity of tardigrade communities in the city of Lake Charles with nearby woodland in Sam Houston Jones State Park (SHJSP). We do not address environmental or other factors that might result in differences between these communities.

### METHODS

#### Study sites

Lake Charles and SHJSP are located in Calcasieu

Parish, Louisiana, USA. The area is part of the West Gulf Coastal Plain; elevation ranges from sea level to 29 m. Summers in Calcasieu Parish are hot and humid; winters are warm but are occasionally interrupted by freezing temperatures (Hardner, 1960; Roy and Midkiff, 1988) with a normal annual range of 5.1 to 31.6°C (National Weather Service Lake Charles Office). Annual precipitation averages 135.1 cm (Roy and Midkiff, 1988). The parish is frequently impacted by hurricanes. Approximately 46% of Calcasieu Parish land is devoted to agriculture or rangeland (rice, soybeans and cattle), 23% is woodland, 11% is marsh and 4% is swamp (Roy and Midkiff, 1988). The remaining 16% is urban. Lake Charles (population 72,000 in 2010 Census) is a deep-water port connected to the Gulf of Mexico (Jones *et al.*, 1954). Large petroleum-related industries are located near Lake Charles.

Sam Houston Jones State Park consists primarily of bottomland forest along the Calcasieu river, while the area where Lake Charles now stands was originally bottomland forest, swampland and coastal prairie (Neyland *et al.*, 2000). Most of Louisiana's original forests were logged in the Nineteenth and Twentieth Centuries, including the area now incorporated in SHJSP. Vegetation structure in SHJSP can also be significantly impacted by hurricanes, most recently by Hurricane Rita in 2005. Therefore the woodland in SHJSP constitutes secondary forest as defined by Chokkalingam and de Jong (2001), *i.e.*, a forest regenerated largely through natural processes after significant human and/or natural disturbance of the original forest vegetation. In the typology of Chokkalingam and de Jong (2001) the forest in SHJSP is a combination of post-catastrophic and post-extraction secondary forest.

### Sampling and analysis

Sampling was conducted in spring, 2011. At SHJSP 52 samples (27 moss, 15 lichen, 2 mixed cryptogams and 8 leaf litter) were collected from trees and the forest floor. Sampling was distributed among the Longleaf Pine, Blue, river Walk and Yellow Trail regions of the park (13 samples per region, all substrate types collected in each region). In Lake Charles 40 samples were collected (24 lichen, 8 moss, 1 mixed cryptogam, 1 tree fern and 6 leaf litter), with eight samples from each of five urban landscape types: single family residential (all substrates), undeveloped lot (all substrates), light commercial property (no leaf litter), dense commercial property (all substrates) and industrial zone (no moss). These landscape types were chosen to represent a wide range of typical urban habitats. Samples were stored in paper envelopes or bags. The preponderance of moss samples in the forest and lichens in the city reflects their relative availability in the sites.

In the laboratory samples were air dried for 24 h and weighed to the nearest 0.01 g using an Acculab EC211 electronic balance, placed in tap water and soaked

overnight to rehydrate tardigrades. After soaking they were examined with a dissecting microscope (Nikon SMZ-U Zoom 1:10). Tardigrade specimens and eggs were extracted with an Irwin loop and mounted on slides in polyvinyl lactophenol and examined using phase microscopy (Nikon Eclipse 50i; Nikon, Tokyo, Japan). Tardigrades were identified using keys and descriptions in Nelson and McInnes (2002), Pilato and Binda (2010) and Ramazzotti and Maucci (1983), and by reference to the primary literature. Taxonomic nomenclature is based on Guidetti and Bertolani (2005), Degma and Guidetti (2007) and Degma *et al.* (2012).

The statistical program EstimateS Version 8.2.0 was used to estimate species richness (Colwell, 2006), using the seven estimators included in EstimateS (Chao 1, Chao 2, ACE, ICE, Jackknife 1, Jackknife 2, and Bootstrap). No single estimator is accurate for all tardigrade habitats (Bartels and Nelson, 2007). To eliminate biases in estimated species richness caused by the patchy distribution characteristic of tardigrades (Meyer, 2006), we used 100 randomizations and patchiness set at zero. Because of the disparate types of samples (leaf litter, moss on trunks, lichens wrapped around twigs, *etc.*) determination of tardigrade density per unit area was not feasible; density per gram substrate was used as a crude approximation. Density and diversity were compared using formulas found in Cox (2001).

### RESULTS

A total of 1470 tardigrade specimens from seventeen species and eight genera were found in moss, lichen and leaf litter samples from SHJSP and Lake Charles (Tab. 1); 1384 were identifiable. At SHJSP 63% of the samples contained tardigrades; in Lake Charles 68% of the samples were positive. Tardigrade density in samples positive for tardigrades (8.8 specimens g<sup>-1</sup> at SHJSP and 14.0 specimens g<sup>-1</sup> in Lake Charles) did not differ significantly (t-test, P=0.54). However, species richness at SHJSP (seventeen species) was more than double that in Lake Charles (eight); diversity was significantly greater at SHJSP than in Lake Charles (Shannon-Weiner Index: SHJSP, H'<sup>'</sup>=3.01; Lake Charles, H'<sup>'</sup>=1.30; t-test, P<0.05). Mean estimates of tardigrade species richness predicted by the seven estimators in EstimateS ranged from 18 to 26 at SHJSP and from 8 to 11 in Lake Charles. The maximum number of species found in a single sample was four at both sites.

The tardigrade fauna of Lake Charles was dominated by two species (nearly 80% of all specimens), *Minibiotus acadianus* Meyer and Domingue, 2011 (primarily in cryptogams) and *Paramacrobotus richtersi* (Murray, 1911) (in leaf litter). *Paramacrobotus richtersi* was only found in undeveloped lots, which was the urban landscape with the most well-developed leaf litter. *Minibiotus acadianus*

was collected in all landscapes except undeveloped lots. The number of species found in the different urban landscape types ranged from two in undeveloped lots to five in the industrial zone (species richness in other landscapes: residential 4, light commercial 3, heavy commercial 3). At SHJSP the most abundant species, *Macrobiotus cf. echinogenitus*, constituted about a third of the tardigrades. It was found in all regions of the park, as was *Milnesium sp.*

Tab. 1 shows from which substrates tardigrade species were collected. Three species (*Milnesium cf. reticulatum*, *Macrobiotus cf. echinogenitus* and *M. acadianus*) were present in all substrates.

The absence of eggs precluded specific identification of *Macrobiotus cf. echinogenitus*, *Macrobiotus cf.*

*harmsworthi*, and *Minibiotus cf. intermedius*. *Macrobiotus cf. hufelandi* and *Milnesium cf. reticulatum* are undescribed species which will be described elsewhere.

## DISCUSSION

Three species collected at SHJSP in this study – *Echiniscus perarmatus* Murray, 1907, *Hypsibius dujardini* (Doyère, 1840) and *Paramacrobiotus tonollii* (Ramazzotti, 1956) – are new to the fauna of Louisiana. Earlier papers (Meyer, 2001; Hinton *et al.*, 2010) recorded eleven species from SHJSP. Three of these species – *Diphascion (Diphascion) pingue* (Marcus, 1936), *Astatumen trinacriae* (Arcidiacono, 1962) and *Itaquascon cf. umbellinae* were not collected in this study. Only one species, *Macrobiotus occidentalis* Murray, 1910, has previously

**Tab. 1.** Tardigrade diversity in cryptogams and leaf litter from Sam Houston Jones State Park and Lake Charles, LA: number of samples positive for a species, number of specimens, and substrates.

Species	Positive samples (number of specimens; substrates)	
	SHJSP	Lake Charles
<i>Echiniscus cavagnaroi</i> Schuster and Grigarick, 1966	1 (1; lc)	0
<i>Echiniscus perarmatus</i> Murray, 1907	1 (39; m)	0
<i>Echiniscus virginicus</i> Riggan, 1962	3 (10; m)	0
<i>Pseudechiniscus brevimontanus</i> Kendall-Fite and Nelson, 1996	1 (1; m)	0
<i>Milnesium sp.</i> ([3-3]-[3-3] claw configuration)	13 (80; lc, m)	3 (27; lc)
<i>Milnesium cf. reticulatum</i>	3 (20; lc, ll)	15 (70; lc, ll, m)
<i>Hypsibius dujardini</i> (Doyère, 1840)	0	2 (4; lc, ll)
<i>Isohypsibius sp.</i>	1 (2; ll)	0
<i>Macrobiotus cf. echinogenitus</i>	12 (213; lc, ll, m)	3 (10; lc)
<i>Macrobiotus cf. harmsworthi</i>	3 (11; ll)	3 (20; lc, ll)
<i>Macrobiotus cf. hufelandi</i>	4 (57; m)	0
<i>Macrobiotus occidentalis</i> Murray, 1910	1 (1; lc)	0
<i>Minibiotus acadianus</i> Meyer and Domingue, 2011	4 (17; lc, m)	17 (334; lc, ll, m)
<i>Minibiotus cf. intermedius</i>	7 (21; lc, m)	0
<i>Paramacrobiotus areolatus</i> (Murray, 1907)	3 (21; lc, m)	2 (9; lc, m)
<i>Paramacrobiotus richtersi</i> (Murray, 1911)	6 (30; ll, m)	3 (342; lc, ll, m)
<i>Paramacrobiotus tonollii</i> (Ramazzotti, 1956)	6 (44; lc, m)	0

lc, lichen; ll, leaf litter; m, moss.

**Tab. 2.** Urban and non-urban terrestrial tardigrade species richness in and near seven cities.

City (2012 population)	Number of species		Reference
	Urban	Non-urban	
Cincinnati, USA (297,000)	5	8	Meininger <i>et al.</i> (1985)
Fresno, USA (510,000)	10	19	Johansson <i>et al.</i> (2011)
General Pico, Argentina (54,000)	5	Unknown	Moly de Peluffo <i>et al.</i> (2006)
Lake Charles, USA (72,000)	8	16	Present study
Nice, France (345,000)	4	16	Séméria (1981, 1982)
Philadelphia, USA (1.5 million)	8	Unknown	Mitchell <i>et al.</i> (2009)
Santa Rosa, Argentina (97,000)	5	Unknown	Peluffo <i>et al.</i> (2007)
Tokyo, Japan (13 million)	10	Unknown	Utsugi (1985)

been reported from Lake Charles (Meyer, 2001); it was not found there in this study. *Minibiotus acadianus* has hitherto only been recorded from its type locality in Acadia Parish, Louisiana (Meyer and Domingue, 2011).

Earlier studies have assessed tardigrade diversity in seven urban areas (Tab. 2) with human populations ranging from 54,000 (General Pico) to over 13 million (Tokyo). The number of tardigrade species found in these cities ranges from four to ten (Tab. 2); Lake Charles falls within this range. In four studies comparing urban to non-urban tardigrade diversity (Tab. 2), urban species richness is consistently lower than non-urban (from 25 to 63%). The proportion of samples containing tardigrades ranges in these studies from 38% (Fresno) to 98% (General Pico).

Johansson *et al.* (2011) noted that in Fresno very few species were common to both urban and rural sites. On the other hand, in Cincinnati, Lake Charles and Nice most species found in urban sampling were also present in urban areas. The tardigrade taxa most widely reported from cities are *Milnesium* sp. and *Ramazzottius oberhaeuseri* (Doyère, 1840); the latter was not found in Lake Charles. Several authors (Séméria, 1981, 1982; Meininger *et al.*, 1985; Steiner, 1994b) have suggested that certain tardigrades species [e.g., *Milnesium tardigradum* Doyère, 1840, *Macrobiotus hufelandi* C.A.S. Schultze, 1936, *Ramazzottius oberhaeuseri* and *Diphascion* (*Diphascion*) *scoticum* Murray, 1905] have high resistance to urban environmental conditions and may therefore be characteristic of cities worldwide. However, different urban tardigrade studies tend to find a different suite of species in their cities (Johansson *et al.*, 2011). Since some species widely reported in cities belong to species complexes, identifications in older literature need to be confirmed, and claims that individual species are characteristic of urban faunas worldwide must be treated with caution. It is worth noting that tardigrades of the class Heterotardigrada have been collected in only three of eight urban areas surveyed (General Pico, Santa Rosa and Tokyo), but were abundant in all non-urban surveys.

While this study did not attempt to determine the cause of differences in tardigrade diversity between urban and non-urban habitats, other papers have demonstrated the effects of human actions on tardigrade distribution and abundance. Tardigrade densities in lichens were lower in trees treated with DDT (Barrett and Kimmel, 1972) or downwind of a coal-burning plant (Hohl *et al.*, 2001), while proximity to road-generated dust altered tardigrade species composition (Meininger and Spatt, 1988). In urban environments, lower tardigrade species richness in urban areas has been related to vehicular traffic and air quality (Meininger *et al.*, 1985; Steiner 1994b; Moly de Peluffo *et al.*, 2006, Peluffo *et al.*, 2007). However, Johansson *et al.* (2011) found no relationship between lower urban tardigrade diversity and lower pH.

## CONCLUSIONS

Tardigrade species richness and diversity in Lake Charles were substantially less than in a nearby forest, although tardigrade density did not differ. Similar patterns have been found in other studies comparing urban and non-urban areas. The degree to which tardigrade diversity may vary within a city (*i.e.*, between urban landscapes ranging from parks to densely inhabited zones) and whether urbanisation is homogenising global tardigrade fauna remain unanswered questions worthy of further research.

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