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Ground beetles (Coleoptera: Carabidae) inhabiting anthropogenic habitats in the lower delta of the Paraná river, Argentina: geographic distribution and ecological characteristics

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Abstract The primary aims of this paper were to provide the first inventory of carabid beetles collected in five different anthropogenic habitat types of the Lower Delta of the Paraná River, to describe their main ecological characteristics and to provide information on their distribution range in ecoregions, subregions and ecosystem complexes of Argentina and across the Neotropical region. Species were grouped according to six classes of distributions in relation to their presence in the Delta of the Paraná River. In addition, rarefaction curves were built in order to compare the seasonal species richness. We collected 1486 individuals belonging to 48 species. The southernmost distribution limit of 50% of the species is located south of the Delta region. Moreover, 21% of the species are confined to the Delta and Islands of the Parana and Uruguay Rivers ecoregion and to localities within the neighbouring ecoregions of Espinal and Pampa. Most (63%) of the species were zoophagous and 25% were either omnivorous or seed eaters; 52% were hydrophilous, 44% mesophilous and one was xerophilous. The high number of species found in this ecoregion emphasising its importance as a biodiversity hotspot of South American carabids. Human activities have led to changes in the landscape of the Delta Islands which could favour the establishment of mesophilous and xerophilous species from other ecoregions. Seasonal carabid richness is higher in the warm seasons (spring and summer) compared with the cold seasons (autumn and winter). Although, the highest absolute richness was found in the most anthropised habitat types, secondary forests had exclusive species, showing the importance of preserving the ecological mosaic of the landscape.

Key words afforestation habitat, Argentinian ecoregion, assemblage, habitat use.

INTRODUCTION

Carabidae are the most thoroughly studied family of the order Coleoptera in the world (Kotze *et al.* 2011). Carabids are primarily terrestrial, and predominate in anthropised sites such as agroecosystems (Thiele 1977; Lövei & Sunderland 1996; Ulrich *et al.* 2004; Nanni *et al.* 2014). Thus, they serve as bioindicators of land-use change and of pesticide contamination (Allegro & Sciaky 2003; Callaham *et al.* 2006; Tulli *et al.* 2009; Trager *et al.* 2013). There is little information on their distribution, diversity and population dynamics in the Neotropical region. In South America about 4400 species are known, distributed in seven subfamilies, 50 tribes and 335 genera (Roig-Juñent 1998). For Argentina, 679 species have been reported (Roig-Juñent 1998), although the total is probably higher (by 2012, 844 species were documented, A.C. Cicchino, pers. Comm.). Particularly, in the ecoregion Delta and Islands of the Parana and Uruguay Rivers, in Argentina, have been scarcely investigated despite this ecoregion being considered a biodiversity hotspot (Bó 2005). The terminal portion of this ecoregion corresponds to the Paraná River Delta with a surface area of about 17 000 km^2 (Quintana & Bó 2011). Three main sectors are considered within this area: upper, middle and lower delta (*sensu* Bonfils, 1962). It is characterised by a heterogeneous biogeographic profile (Ringuelet 1961) resulting from subtropical intrusion into a temperate region. The Paraná and Uruguay Rivers act as corridors facilitating the dispersal of propagules from the north, while the De La Plata River allows access from the southeast (Quintana & Bó 2011). The presence of large water masses creates favourable environmental conditions for several taxa, as they increase environmental humidity and have a buffer effect on maximum and minimum absolute temperatures (Kandus *et al.* 2006; Quintana & Bó 2011). Consequently, species of tropical and subtropical lineage can establish and coexist with temperate species (Ringuelet 1961). Moreover, the recent and past geomorphological history of the region along with a complex hydrological regime account for a high environmental heterogeneity determining a diversity of available habitat types (Quintana & Bó 2011).

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In this context, the primary aim of this paper was to provide the first inventory of carabid species collected in an area of Lower Paraná River Delta, and to describe their main ecological characteristics. We also provide data on their distribution in the ecoregions, subregions and ecosystem complexes of Argentina, and their known geographic range for the Neotropical region, in order to provide baseline information for future faunistic, conservation or territorial planning works either for this ecoregion or Argentina.

MATERIALS AND METHODS

Study area

The study was conducted in the Lower Delta of the Paraná River (Fig. 1), which is located at the end of the Paraná River Complex (33°48′ 34°26′S, 59°00′ 58°31′ W), with the typical delta landscape morphology (Kandus & Malvárez 2004). The landscape is shaped by a peripheral levee covered by riparian forests while the interior is characterised by freshwater marshes dominated by *Scirpus giganteus* (Quintana & Bó 2011).

The principal economic activity in the Lower Delta is poplar and willow plantations (MAGyP 2011). These afforested areas are not homogeneously distributed, and the largest concentration is located in the so-called 'forest nucleus' (Fracassi *et al.* 2013). Therefore, the original landscape of the study area has been highly modified by humans, and it has now become a complex and patchy environment. Currently, these forested areas are interspersed with remnants of native riparian forest, secondary forests (dominated by exotic plant species), and occupied or abandoned homesteads (Quintana 2011). In the 1990s, the introduction of cattle to the afforestation systems represented a drastic change in the production scenario of the region, with its consequent impacts on the system (Quintana *et al.* 2014).

Our sampling was carried out at the Agricultural Experimental Station (EEA) – Delta INTA – located in the confluence between the Paraná de Las Palmas River and the Laurentino Comas Channel – 4th Island Section, Campana District, Buenos Aires province (34°10′33.95″ S; 58°51′47.54″ W). In this study, we selected the following habitat types for collecting carabids: adult (APA) and young (YPA) poplar (*Populus deltoides*) plantations, secondary forests inside and outside dykes (SFID and SFOD, respectively), and grasslands for cattle grazing (GCG) (Fig. 1, Table 1).

Collection of carabidae

Specimens were collected from 75 pitfall traps located in the five habitat types mentioned above. In each habitat type, 15 traps were placed 50 m apart. Traps were surveyed monthly between April 2008 and March 2009. The pitfall traps were made of plastic containers (9 cm in diameter and 10 cm deep), and contained 400 ml of 96% ethanol and glycerol for sample preservation. A 15-cm-diameter plastic lid was suspended above each trap to protect it from rainfall and leaf litter. Once collected, the specimens were identified to species level (by A.C.C.) using taxonomic keys (Reichardt, 1967 to tribes; Cicchino, unpublished MS to species level) when necessary. Voucher specimens were deposited in the Entomology Collection of the Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Buenos Aires, Argentina.

Species distribution

For each species, we constructed a data matrix (see Supporting Information Table S1 and Table S2) of its geographic range using records obtained from the following sources: personal

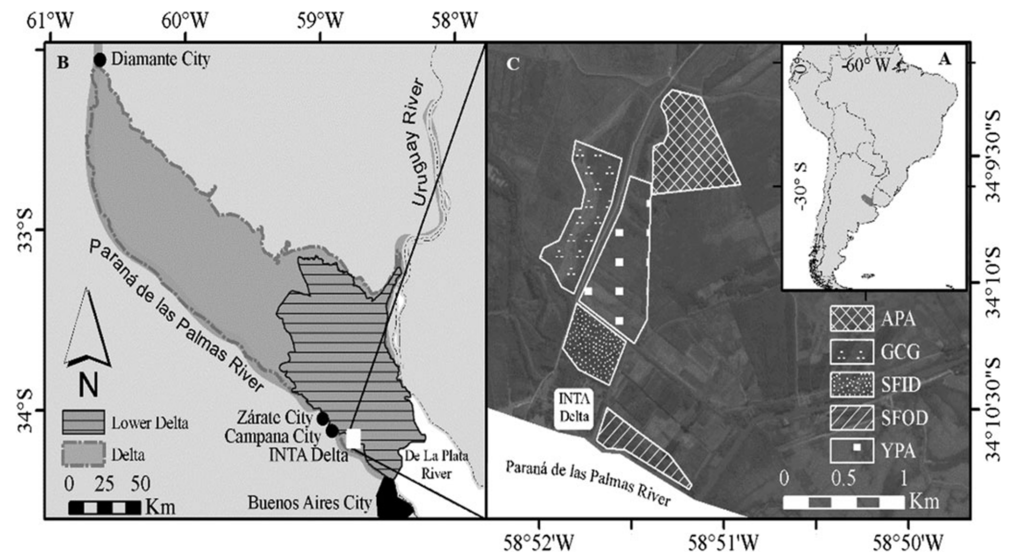

Fig. 1. Location of the study área in A) Argentina and B) the ecosystem complex 'Paraná River Delta'. C) Detail of the hábitat types in the Agricultural Experimental Station (EEA) Delta INTA. APA: Adult Poplar Afforestation, YPA: Young Poplar Afforestation, GCG: Grassland for Cattle grazing, SFID: Secondary Forests inside Dykes and SFOD: Secondary Forests outside Dykes.

Table 1 Habitat type's characteristic. APA: Adult Poplar Afforestation, YPA: Young Poplar Afforestation, GCG: Grasslands for Cattle grazing, SFID: Secondary Forests inside Dykes and SFOD: Secondary Forests outside Dykes

Habitat type	Age (year)	Type of management	Cattle grazing	Channels	Understory	Layer number
APA	11	Managed	Occasional	Yes	Scarce	HerbaceousArboreal
SFOD	18	Unmanaged since 1997	No	No	Abundant	HerbaceousArbustiveArborealVines and Creepers
GCG	–	Managed	Permanent	No	–	HerbaceousArbustive
YPA	4	Managed	Permanent	Yes	Abundant	HerbaceousArbustiveArboreal
SFID	23	Unmanaged since 1994	No	No	Abundant	ArbustiveArborealVines and Creepers

collection of A.C.C., unpublished records by Diego Carpintero and Manuel J. Viana, published articles (see citations on Tables 2 and 3), and specimens deposited in major institutional collections of Argentina (Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Buenos Aires; Fundación e Instituto Miguel Lillo, Universidad National de Tucumán, Tucumán province; Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, Buenos Aires; and Instituto Argentino de Zonas Áridas, CONICET, Mendoza Province). The resulting locations of Carabidae were superimposed on the corresponding Argentinean ecoregions and ecosystem complexes *sensu* Morello *et al.* (2012).

Collected species were classified into six distribution classes in relation to their presence in the Delta of the Paraná River Complex and in South America: (1) widely distributed, from the northern to the southern ends of the Neotropical region; (2) from the northern end of the Neotropical region to the Delta of the Paraná River Complex and surroundings; (3) from northern Argentina and southern Paraguay, Bolivia, Brazil and some localities in central-northern Chile to southern Argentina (north of Chubut Province); (4) from northern Argentina and southern Paraguay, Bolivia, Brazil and some localities in central-northern Chile to the Delta of the Paraná River Complex and surroundings; (5) mainly distributed in the Pampa ecoregion, with some species in neighbouring localities within the ecoregions of Espinal and Delta and Islands of the Paraná and Uruguay Rivers; and (6) mainly restricted to the ecoregion of Delta and Islands of the Paraná and Uruguay Rivers, with some species in neighbouring localities within the ecoregions of Espinal and Pampa.

Assemblage species description and characterisation

Carabid species were classified and characterised considering ecological criteria taken from literature (See Supporting Information Table S3). In addition, rarefaction curves were built in order to compare the seasonal species richness and to evaluate whether sampling effort ($n = 75$) was adequate. Confidence intervals for rarefaction curves (95% CI) were calculated using the Boostrap method (Colwell *et al.* 2004). Species richness was estimated using Jacknife 1's and Chao 1's indices (Moreno & Halffter 2001). Inventory completeness for each seasonal was measured as the percentage of species observed from the total number of species predicted by the estimators. These analyses were performed using the EstimateS 7.5 statistical software (Colwell 2005).

RESULTS

Species distribution

We collected a total of 1486 individuals belonging to 48 species, 28 genera and 15 tribes (Table 2). Considering the six classes of distribution in which we classified the species, the southern distribution limit of 50% of the species is located south of the ecoregion Delta and Islands of the Paraná and Uruguay Rivers, while 21% of the species are restricted to this ecoregion and to neighbouring localities within the ecoregions of Espinal and Pampa. The remaining 29% of the species are found in the other classes (Fig. 2). From the total number of species found in this study (48), 14 species were new for the northeastern quadrant of the Buenos Aires province. YPA and GCG were the habitats with the highest richness (28 species and 27 species, respectively) with the remaining habitat types with a lower number of beetle species (20, 17 and 16 species for APA, SFID and SFOD, respectively).

Assemblage species description and characterisation

In terms of habitat use, 48% of the species were ubiquitous, 46% specialists, and 21% were classified generalists. No reliable information is available for the remaining 33%. Most of the species were hemisynanthropic (42%) and 17% were synanthropic (Table 3). With regard to the feeding habits, 63% were zoophagous, 25% were omnivorous or essentially seed eaters, and there was no reliable information for the remaining 12%. Concerning soil-moisture preference, 52% species were hydrophilous, 44% mesophilous and only one (*Carbonellia platensis*) was xerophilous. Although the soil-moisture preference of *Apenes* sp.3 is unknown, the fact that it was found in the secondary forest outside dike subjected to the periodic flooding of the Paraná River suggests that this is hydrophilous species. Twenty-nine % of the species underwent adult overwintering (Table 3). The richness of mesophilous species was higher in habitat types inside dykes. In contrast, number of hydrophilic species was higher in the secondary forest outside dykes, which is under the influence of hydrological regime of the Paraná River. We recorded a large number of zoophagous species in all the studied habitat types. On the other hand, all seed eater and omnivorous species were found in the Young Poplar Afforestations and Grasslands for cattle grazing.

The greatest seasonal species richness was observed during the southern spring (October to December), followed by summer (January to March), winter (July to September) and autumn

Table 2 Distribution range and habitat's types of the carabid species from the Lower Delta of the Paraná River (Argentina). Class indicate as we grouped species in relation to their presence in the Delta of the Paraná River Complex, the associate number summarise the amount of Ecosystem Complex that each species was found. APA: Adult Poplar Afforestation, YPA: Young Poplar Afforestation, GCG: Grassland for Cattle grazing, SFID: Secondary Forests inside Dykes and SFOD: Secondary Forests outside Dykes, Pp: Present paper. For other acronyms see Annex 1 and 2

	Geographic distribution			
Species	Countries and Argentinean provinces	Argentinean ecoregions, subregions and ecosystem complexes	Class	Environment
Bembidion uruguayense (Csiki 1928)	UR, AR (*BA, ER*) Pp.	di (1 (II), 2 (I, II)) Pp.	F-3	SFID-SFOD
Paratachys bonaerensis (Steinheil 1869)	UR, AR (*BA, ME, ER*) Pp.	di (2 (I, II), pa (1 (I, III, IV), 2 (I, V, VI, VII)), mp (1 (I)) Pp.	C-10	YPA
Paratachys laevigatus (Boheman 1858)	AR (*BA*) Pp.	di (2 (I, II)), pa (1 (III, IV), 2 (VI)) Pp.	E-5	SFOD
Brachinus olidus (Reiche 1842)	CO, AR (*BA, CH, TU, SE, CO, CR, SF, ER*) Pp.	di (1 (II), 2 (I)), pa (1 (I, III), 2 (V, VII)), es (1 (II)), dc (1 (VII, X), 2 (II)), sy (1 (II)) Pp.	B-11	GCG-YPA
Brachinus fuscicornis (Dejean 1826)	BR, BO, PA, UR, AR (*BA, SF, ER, CO*) Pp.	di (1 (II), 2 (I)), pa (1 (I, III), 2 (I, VII)), dc (1 (I)) Pp.	C-7	GCG
Brachinus pallipes (Dejean 1826)	UR, AR (*BA, TU, CH, SF, ER, RN, SE*) Cicchino 2013; Pp.	di (1 (II), 2 (I, II)), pa (1 (I, III, IV), 2 (I, V, VI, VII)), dc (1 (VII, IX, X)), ps (2 (I)), mp (2 (I)) Pp.	C-15	GCG-YPA
Brachinus immarginatus (Brullé 1838)	BR, UR, AR (*BA, MI, CH, SE, SF, CR, ER, RN*) Cicchino 2013; Pp.	di (1 (II), 2 (I, II)), pa (1 (I, III, IV), 2 (I, VI, VII)), wc (1 (IV)), dc (1 (IX)), ps (2 (I)), sf (2 (I)), iw (1 (III)) Pp.	C-14	GCG
Calosoma retusum (Fabricius 1775)	BR, BO, UR, AR (*JU, TU, SA, SE, SF, CO, SL, CH, MI, ME, BA, RN*) Gidaspow 1963; Pp.	di (1 (II), 2 (I, II)), pa (1 (III, IV), 2 (I, III, V, VI, VII)), sf (2 (II)), dc (1 (VII, X), 2 (I, II)), sy (1 (I, II)), es (3 (II)), mp (1 (I), 2 (I)) Pp.	C-20	GCG
Odontocheila chrysis (Fabricius 1801)	PA, BO, BR,CO, FG, GU, PE, SU, UR, VE, AR (MI, ER, BA, JU, CH, CO, CR, FO, SA, SE, TU) Wiesner & Bandinelli 2014; Pp.	di (2 (I, II)), pa (1 (I, III)), sf (1 (I), 2 (V)), sy (1 (I, II)), dc (1 (I, II, VII), 2 (I)), wc (1 (I, II, III)), iw (1 (II)), es (1 (III), 2 (II)) Pp.	B-18	SFOD
Aspidoglossa intermedia (Dejean 1831)	BR, UR, PA, AR (*BA, ER, MI, SE, SF, FO, TU*) Cicchino 2010; Pp.	di (1 (II), 2 (I, II)), pa (1 (I, III, IV), 2 (I, VI, VII)), sf (1 (I)), wc (1 (I)), dc (1 (VIII, X)) Pp.	C-13	APA-YPA-SFID-SFOD-GCG
Clivina laeta (Putzeys 1866)	UR, AR (*MI, ER, CO, BA*) Pp.	di (2 (I, II)), pa (1 (I, III)), sf (2 (V)), dc (3 (I)) Pp.	D-6	APA
Paraclivina breviuscula (Putzeys 1866)	UR, AR (*MI, BA, CH*) Cicchino & Farina 2010; Pp.	di (2 (I, II)), pa (1 (III, IV), 2 (VI, VII)), sf (1 (I)), dc (1 (VII)) Pp.	C-8	APA-YPA-SFID
Semiclivina platensis (Putzeys 1866)	UR, AR (*BA, ER, SF*) Pp.	di (2 (I, II)), pa (1 (I, III, IV), 2 (I, VI, VII)) Pp.	E-8	SFOD-GCG-YPA-SFID
Whiteheadiana stenocephala (Brullé 1838)	AR (*BA,CR, ER*) Pp.	di (1 (II), 2 (I, II)),es (1 (III)) Pp.	F-4	YPA
Galerita collaris (Dejean, 1826)	BR, BO, PA, UR, AR (*BA, JU, SA, TU, SE, CA, LR, CO, FO, CH, SF, MI, CR, ER)* Reichardt 1967; Pp.	di (1 (I, II), 2 (I, II)), pa (1 (I, III, IV), 2 (I, VI, VII)), sf (1 (I) 2 (I)), cm (1 (I)), iw (1 (I)), es (1 (I, II, III), 2 (II)), wc (1 (I, II, III, IV, V)), dc (1(I, II, III, VIII, X), 2 (I, II), 3 (I, II)), sb (1 (I, III)) Pp.	C-34	GCG-YPA
Galerita lacordairei (Dejean 1826)	UR, BR, BO, PA, AR (*BA, ME, TU, CO, SA, ER, CR, FO)* Reichardt 1967; Pp.	di (1 (I), 2 (I, II)), pa (1 (III,IV), 2 (VI, VII)), mp (1 (I)), dc (1 (VIII, X), 2 (II), 3 (I)), cm (1 (II)) Pp.	C-13	SFOD
Anisostichus posticus (Dejean 1829)	UR, AR (*TU, BA, RN, SA, CO, SF, ER*) van Endem 1953; Pp.	di (1 (II), 2 (I, II)), pa (1 (I, III, IV), 2 (VI, VII)), es (3 (II)), dc (2 (II)), wc (1 (IV, V)), sy (1 (I, II)) Pp.	C-14	APA-SFID-SFOD
Bradycellus cfr. ruficollis (Solier 1849)	AR, CH (*MI, CO, FO, CH, CR, ER, BA*) Pp.	di (1 (II), 2 (I, II)), pa (1 (I, III, IV), 2 (I, VI, VII)), sf (1 (I)), dc (1 (VII), 2 (II)), wc (1 (I)) Pp.	C-13	YPA
Bradycellus sp. *1*	UR, AR (*TU, ME, ER, RN, LP, BA*) Pp.	di (2 (I, II), 3 (I)), pa (1(III, IV), 2 (I, V, VI, VII)), es (3 (III)), dc (2 (I)), mp (1 (I), 2 (I)) Pp.	C-13	GCG-YPA-SFID

(Continues)

Table 2 (Continued)

Species	Geographic distribution: Countries and Argentinean provinces	Geographic distribution: Argentinean ecoregions, subregions and ecosystem complexes	Class	Environment
Bradycellus sp. *2*	AR (*CO, ME, ER, BA*) Pp.	di (2(I, II)), pa (1 (I, III, IV) 2 (I, VI, VII)), dc (2 (II)) Pp.	C-9	GCG-YPA
Bradycelus sp. *5*	AR (*BA*) Pp.	di (2 (I, II)), pa (1 (III, IV), 2 (VI, VII)) Pp.	E-6	YPA
Gynandropus placidus (Putzeys 1878)	BR, AR (*SA, MI, ME, CH, CO, ER, BA*) Cicchino & Farina 2010; Pp.	di (2 (I)), pa (1 (I, III, IV), 2 (I, VI, VII)), es (3 (II)), sf (1 (I)), dc (1 (VII, XI), 2 (II), 3 (II)), sb (1 (I)), mp (1 (I)) Pp.	C-15	APA-GCG
Polpochila pueli (Négre 1963)	CH, BO, UR, PA, BR, AR (*BA, SE, SF, ER, CO, LR, TU, JU, SA, SJ*) Négre, 1963; Pp.	di (1 (II), 2 (I, II)), mp (1 (I)), pa (1 (I, III, IV), 2 (I, V, VI, VII)), ps (1 (II), 2 (II), 3 (II)), dc (1 (X), 2 (I, II), 3 (I)) Pp.	C-18	GCG-YPA-SFID
Polpochila flavipes (Dejean 1831)	UR, AR (*BA, CO, ER, ME, SF, TU, RN*) Négre, 1963; Pp.	di (2 (I, II)), pa (1 (I, III, IV), 2 (I, VI, VII)), es (1 (II), 3 (II)), dc (1 (X), 2 (II)), mp (1 (I), 2 (I)) Pp.	C-14	APA-GCG-YPA
Polpochila nigra (Gory 1833)	BR, UR, AR (*BA, ER*) Négre, 1963; Pp.	di (2 (I, II)), pa (1 (I, III, IV), 2 (VI)) Pp.	D-6	GCG-YPA
Selenophorus alternans (Dejean 1829)	BR, CU, FG, PA, MX, UR, VE, BO, AR (*BA, ME, SE, CH, CO, SA, SJ, MI, TU, SF, SL*) Pp.	di (2 (I, II)), pa (1 (I, III, IV), 2 (I, V, VI, VII)), es (2 (I), 3 (II, III)), sf (1 (I)), iw (1 (I)), wc (1 (V)), dc (1 (I, II, X), 2 (II), 3 (I, II)), mp (1 (I)), ua (2 (V)), sb (1 (III)) Pp.	A-24	GCG
Selenophorus chalcosomus (Reiche 1843)	CO, VE, BR, AR (*BA, SF, ER, MI, CO, CH, TU*) Steinheil 1869; Pp.	di (2 (I, II)), pa (1 (I, III, IV), 2 (I, V, VI, VII)), es (1 (III), 2 (I)), sf (1 (I)), dc (1 (VI, IX), 2 (II)) Pp.	A-15	GCG-YPA
Selenophorus antarctioides (Steinheil 1869)	UR, AR (*BA*) Pp.	di (2 (I)), pa (1 (III)) Pp.	F-2	GCG
Selenophorus sp.*1*	AR (*BA*) Cicchino & Farina 2010; Pp.	di (2 (I)), pa (1 (III), 2 (VI)) Pp.	E-3	GCG
Selenophorus lugubris (Putzeys 1878)	AR (*BA*) Cicchino & Farina 2010; Pp.	di (2 (I)), pa (1 (III, IV), 2 (VI, VII)) Pp.	E-5	GCG-YPA
Ega montevidensis (Tremoleras 1917)	UR, AR (*BA, FO, ER*) Pp.	di (2 (I, II)), pa (1 (I, III, IV), 2 (I, V, VI, VII)), es (3 (II)), wc (1 (I)) Pp.	C-11	GCG
Apenes seriatus (Motschulsky 1864)	CE, VE, AR (*TU, BA, SA)* Cicchino 2006; Cicchino 2010; Pp.	di (2 (I)), pa (1 (III), 2 (VI, VII)), dc (1 (II, X)) Pp.	B-6	SFID-SFOD
Apenes sp. *3*	AR (*BA*) Pp.	di (2 (I)) Pp.	F-1	SFOD
Carbonellia platensis (Berg 1883)	AR (*BA, CO, LP, ME, RN*) Pp.	di (2 (I, II)), pa (1 (III, IV), 2 (VI, VII)), es (2 (II), 3 (II, III)), mp (1 (I)) Pp.	C-10	SFID
Loxandrus audouini (Waterhouse 1841)	AR (*ER, SF, BA*) Pp.	di (2 (I, II)), pa (1 (I, III, IV), 2 (VI, VII)) Pp.	E-7	APA-YPA-SFOD-SFID
Loxandrus pseudomayor (Straneo 1991)	UR, AR (BA) Pp.	di (2 (I, II)), pa (1 (III)) Pp.	F-3	APA-YPA-SFOD
Loxandrus sp.*1*	AR (*BA, ER*) Pp.	di (2 (I, II)), pa (1 (I, III)) Pp.	F-4	APA
Aephnidius bonariensis (Chaudoir 1876)	AR (*BA*) Cicchino *et al.* 2013; Ball &Shpeley 2002; Pp.	di (2(I, II)), pa (1 (III)) Pp.	F-3	APA-GCG-YPA-SFID
Incagonum lineatopunctatum (Dejean 1831)	UR, AR (*BA, ER, SF, LP, RN*) Pp.	di (2 (I, II)), pa (1 (I, III, IV), 2 (I, III, V, VI, VII)), es (1 (I, II), 3 (II, III)) Pp.	E-14	APA-SFID
Incagonun discosulcatum (Dejean 1828)	UR, AR (*MI, CO, BA, SF, ER*) Pp.	di (1 (II), 2 (I, II)), pa (1 (I, III, IV), 2 (IV, VI, VII)) Pp.	C-8	APA-SFOD-SFID
Argutoridius abacetoides (Chaudoir 1876)	UR, AR (*ER, BA*) Cicchino *et al.* 2013; Cicchino 2013; Pp.	di (2 (I), pa (1 (I, III)), es (1 (I, III)) Pp.	F-5	APA-SFOD-GCG-YPA-SFID
Argutoridius bonariensis (Dejean 1828)	*UR, AR (LP, ER, SF, ME, NE, CU, SL, RN, CO, CR, BA)* Castro *et al.* 2012; Pp.	di (1 (II), 2 (I, II)), pa (1 (I, III, IV), 2 (I, III, V, VI, VII)), es (1 (II, III), 2 (II, III), 3 (II, III)), mp (1 (I), 2 (I, II, III)), ua (2 (VI)), dc (1 (X), 2 (II), 3 (I)) Pp.	C-25	APA-SFOD-GCG-YPA-SFID

(Continues)

Table 2 (Continued)

Species	Geographic distribution: Countries and Argentinean provinces	Argentinean ecoregions, subregions and ecosystem complexes	Class	Environment
Argutoridius chilensis (Dejean 1828)	UR, CH, AR (*ME, NE, RN, LP, BA, CU, CR, COL, ER,SF*) Straneo 1969; Pp.	di (2 (I, II)), pa (1 (III, IV), 2 (I, III, VI, VII)), es (1 (I), 3 (II)), ua (3 (I)), mp (1 (I), 2 (I)), dc (2 (II)), pf (1 (I, III, IV, V)), ps (3 (I, III)) Pp.	C-20	APA-SFOD-GCG-YPA-SFID
Meraulax alatus (Brullé 1838)	AR (*BA, CO, ER, SF*) Pp.	di(1 (II), 2 (I)) Pp.	F-2	APA-YPA-SFID
Pachymorphus striatulus (Fabricius 1792)	BR, BO, CH, PA, UR, AR (*MI, BA, LP, ME, RN, JU, SA, TU, CA, CO, SL, NE, CU, ER, SE*) Paleólogos 2012; Pp.	di (1 (I, II) 2 (I, II), 3 (I)), wc (1 (I)), sf (1 (I), 2 (II)), sy (1 (I, II)), sb (1 (I, II, III)), pu (1 (I, II, III), 2 (I)), dc (1 (VIII, IX, X, XI), 2 (I, II), 3 (I)), mp (1 (I), 2 (I)), ua (2 (V, VI), 3 (I)), ps (3 (III)), pa (1 (III, IV), 2 (I, V, VI, VII)), es (3 (III)) Pp.	C-37	APA-SFOD-GCG-YPA
Lophogenius ebeninus (Arribálzaga 1878)	BR, BO, PA, UR, AR (*BA, CO, FO, ER, SF, TU, MI*) Pp.	di (2 (I, II)), pa (1 (I, III, IV), 2 (I, VI, VII)), es (1 (I, III)), sf (2 (V)), wc (1 (I)), dc (1 (X)), sy (1 (II)) Pp.	C-14	APA-GCG-YPA
Scarites anthracinus (Dejean 1828)	BR, PA, UR, CH, AR (*BA, NE, ME, SA, LR, SE, CO, RN, CH, SF, FO, CR, ER*) Pp.	di (1 (I, II), 2 (I, II)), pa (1 (I, III, IV) 2 (I, V, VI, VII)), es (1 (I, II, III), 2 (II), 3 (II, III)), pf (1 (III)), iw (1 (I, III)), wc (1 (I, II)), dc (1 (II, VI, IX, XI), 3 (I)), mp (1 (I)), ps (2 (I)) Pp.	C-29	APA-GCG-YPA
Oxytrechus arechavaletai (Putzeys 1870)	UR, AR (*BA, SF, ER*) Cicchino 2013; Pp.	di (1 (II), 2 (I, II)) Pp.	F-3	APA-YPA

(April to June) (Table 4). Carabid seasonal richness was higher in the warm seasons (spring and summer) with respect to the cold ones (autumn and winter). According to the Jacknife 1 estimator, our sampling collected 73–82% species present (Table 4) and 71–90% according to the Chao 1 estimator (Table 4). All singleton values were lower than 10 (Table 4) which also indicates that our sampling effort, despite the assemblage is likely to be at 10–20% larger than observed, was pretty adequate. Values of rarefaction curve for spring were significantly greater than those of the other three seasons. The summer rarefaction curve crossed over the winter one, which is why its slope could not be compared with the others (Fig. 3).

DISCUSSION

Species distribution

The assemblage found in the Lower Delta was composed by beetle species with different geographic distributions and one species (*Apenes* sp.3) present only in this area. While, 21% of species has a distribution restricted to the ecoregion Delta and Islands of the Paraná and Uruguay Rivers and 15% was restricted to the Espinal and Pampa ecoregions, 64% showed a wider distribution within the Neotropical region. This shows the role of the lower delta as an area in which species with different geographical range and lineages coexist because of the presence of suitable environmental conditions (Ringuelet, 1961).

Until now, a total of 358 carabid species have been reported for Buenos Aires Province (Cicchino 2006; 2007; 2010; 2013; Cicchino & Farina 2005; Castro *et al.* 2012; Cicchino *et al.* 2013). The lower delta, located within the northeastern quadrant of the province, supports the largest number of species (292) (A.C. Cicchino, pers. comm.). This is explained by the conjunction in that quadrant of three ecoregions (Delta and Islands of the Paraná and Uruguay Rivers, Pampa and Espinal) with 16 ecosystem complexes (Morello *et al.* 2012) that enable the coexistence of species of different origin (subtropical and temperate), which makes manifest the biogeographic importance of the sector for this family. The number of carabid species mentioned above is probably underestimated because most of the recorded species were obtained from several captures but from a few systematic methods of sampling (present paper; Castro *et al.* 2014 and 2012; Porrini *et al.* 2010).

As for the richness of beetle species in the different surveyed habitat types, the highest values were related to the most anthropised ones, which is coincident with those observed in other studies (Thiele 1977; Lövei & Sunderland, 1996; Ulrich *et al.* 2004; Nanni *et al.* 2014). In contrast, habitat types with no management actions (secondary forests) showed a lower richness. Nevertheless, some carabid species found in them were not found neither in willow and poplar plantation nor in grasslands grazed by cattle. This points to the importance in maintaining secondary forests in the ecological mosaic of the afforestation landscapes of this region.

Table 3 Characterisation of the carabid species from the Lower Delta of the Paraná River (Argentina) with respect to habitat use, strategy to survive low winter temperatures, soil-moisture preference and feeding habit. Sp: Specialist, G: Generalist, S: Synanthropic, Hs: Hemisynanthropic, U: Ubiquitous, Ow: Overwintering, H: Hydrophilous, M: Mesophilous, X: Xerophilous, Z: Zoophagous, Se: Seed eater and O: Omnivorous. Pp: Present Paper

Tribu	Species	Characteristics	Bibliography
Bembidiini	*Bembidion uruguayense* (Csiki 1928)	Sp-H-Z	Nanni 2010
Bembidiini	*Paratachys bonaerensis* (Steinheil 1869)	U-H	Cicchino *et al*. 2003
Bembidiini	*Paratachys laevigatus* (Boheman 1858)	Hs-H-Z	Cicchino, 2003
Brachinini	*Brachinus fuscicornis* (Dejean 1826)	U-H-Ow-Z	Nanni 2010
Brachinini	*Brachinus immarginatus* (Brullé 1838)	Sp-H-Ow-Z	Nanni 2010
Brachinini	*Brachinus olidus* (Reiche 1842)	Hs-H-Ow-Z	Nanni, 2010
Brachinini	*Brachinus pallipes* (Dejean 1826)	Hs-U-H-Ow-Z	Nanni 2010
Carabini	*Calosoma retusum* (Fabricius 1775)	Hs-G-U-M-Ow-Z	Cicchino *et al*. 2003; Cicchino & Farina 2010; Cicchino 2006; Montero & Lietti 1998
Cicindelini	*Odontocheila chrysis* (Fabricius 1801)	Sp-U-H-Ow-Z	Nanni 2010; Paleologos 2012; Wiesner & Bandinelli 2014
Clivinini	*Aspidoglossa intermedia* (Dejean 1831)	S-Hs-G-U-H-Z	Nanni 2010; Wiesner & Bandinelli 2014; Cicchino 2010
Clivinini	*Clivina laeta* (Putzeys 1866)	Sp-H-Z	Paleologos 2012
Clivinini	*Paraclivina breviuscula* (Putzeys 1866)	Hs-Sp-M-O	Nanni 2010; Paleologos 2012; Cicchino 2003; Cicchino & Farina 2010
Clivinini	*Semiclivina platensis* (Putzeys 1866)	Sp-H-Z	Nanni 2010; Cicchino 2003; Cicchino & Farina 2005
Clivinini	*Whiteheadiana stenocephala* (Brullé 1838)	Sp-H-Z	Paleologos 2012
Galeritini	*Galerita collaris* (Dejean 1826)	S-Hs-G-U-M-Ow-Z	Nanni 2010; Cicchino *et al.* 2003; Cicchino 2003; Cicchino 2010
Galeritini	*Galerita lacordairei* (Dejean 1826)	Hs-Sp-U-H-Ow-Z	Nanni 2010; Cicchino 2003
Harpalini	*Anisostichus posticus* (Dejean 1829)	Hs-U-M-Ow-Se/O	Nanni 2010; Cicchino & Farina 2010
Harpalini	*Bradycellus* cfr. *Ruficollis* (Solier 1849)	U-H-O	Cicchino & Farina 2010
Harpalini	*Bradycellus* sp. *1*	Hs-H	Cicchino 2006; Cicchino & Farina 2005
Harpalini	*Bradycellus* sp. *2*	Sp-H	Cicchino 2003; 2006; 2007
Harpalini	*Bradycelus* sp. *5*	Sp-H-O	Cicchino 2006
Harpalini	*Gynandropus placidus* (Putzeys 1878)	Hs-U-H-Se/O	Nanni 2010; Cicchino & Farina 2010
Harpalini	*Polpochila pueli* (Négre 1963)	G-U-M-Se/O	Nanni 2010; Cicchino 2003
Harpalini	*Polpochila flavipes* (Dejean 1831)	Hs-Sp-U-M-Se/O	Nanni 2010; Cicchino 2003
Harpalini	*Polpochila nigra* (Gory 1833)	U-M-Se/O	Pp.
Harpalini	*Selenophorus* sp.*1*	Hs-G-U-M-O	Cicchino *et al.* 2003; Cicchino 2003
Harpalini	*Selenophorus alternans* (Dejean 1829)	Sp-M-Ow-Se/O	Pp.
Harpalini	*Selenophorus antarctioides* (Steinheil 1869)	Sp-U-M-Se/O	Paleologos 2012
Harpalini	*Selenophorus chalcosomus* (Reiche 1843)	M-Ow-Se/O	Cicchino & Farina 2010
Harpalini	*Selenophorus lugubris* (Putzeys 1878)	Sp-M-Ow	Paleologos 2012; Cicchino & Farina 2010
Lachnophorini	*Ega montevidensis* (Tremoleras 1917)	Sp-H	Cicchino 2003; 2007
Lebiini	*Apenes* sp.*3*	?	———
Lebiini	*Apenes seriatus* (Motschulsky 1864)	U-M-Z	Nanni 2010
Lebiini	*Carbonellia platensis* (Berg 1883)	Sp-U-X-Z	Cicchino & Farina 2005; Cicchino 2007
Loxandrini	*Loxandrus* sp.*1*	Sp-H-Z	Nanni 2010; Cicchino 2003; Cicchino 2006
Loxandrini	*Loxandrus audouini* (Waterhouse 1841)	Sp-H-Z	Nanni 2010
Loxandrini	*Loxandrus pseudomayor* (Straneo 1991)	Sp-H-Z	Nanni 2010; Paleologos 2012
Masoreini	*Aephnidius bonariensis* (Chaudoir 1876)	Sp-M-Z	Nanni 2010; Cicchino *et al.* 2013
Platynini	*Incagonum lineatopunctatum* (Dejean 1831)	S-Hs-M-Z	Nanni 2010; Cicchino 2003; 2006; 2010; Cicchino & Farina 2005
Platynini	*Incagonum discosulcatum* (Dejean 1828)	Hs-U-H-Z	Nanni, 2010; Paleologos, 2012; Cicchino & Farina, 2005

(*Continues*)

Table 3 (Continued)

Tribu	Species	Characteristics	Bibliography
Pterostichini	*Argutoridius abacetoides* (Chaudoir 1876)	Sp-M-Z	Nanni 2010
Pterostichini	*Argutoridius bonariensis* (Dejean 1828)	S-Hs-G-U-M-Z	Nanni 2010; Paleologos 2012; Castro *et al.* 2012
Pterostichini	*Argutoridius chilensis* (Dejean 1828)	S-Hs-G-U-M-Z	Nanni 2010; Paleologos 2012
Pterostichini	*Meraulax alatus* (Brullé 1838)	S-Hs-H-Z	Nanni 2010
Pterostichini	*Pachymorphus striatulus* (Fabricius 1792)	S-Hs-G-U-M-Z	Nanni 2010; Paleologos 2012; Cicchino & Farina 2010; Castro *et al.* 2012; Porrini *et al.* 2010
Scaritini	*Lophogenius ebeninus* (Arribálzaga 1878)	G-U-M-Ow-Z	Nanni 2010; Cicchino 2003
Scaritini	*Scarites anthracinus* (Dejean 1828)	S-Hs-G-U-M-Ow-Z	Nanni 2010; Paleologos 2012; Cicchino 2003; Cicchino 2010
Trechini	*Oxytrechus arechavaletai* (Putzeys 1870)	Sp-H-Z	Nanni 2010; Cicchino 2003

Assemblage species description and characterisation

In terms of habitat use, we found a dominance of specialists in the grasslands grazed by cattle, while Batáry *et al.* (2007) reported a dominance of generalists in grazed grasslands on the Great Hungarian Plain.

Originally, 80% of the surface of the islands of the Lower Delta were occupied by marshes ('pajonal') dominated by *S. giganteus* (Quintana & Bó 2011). Currently, willow and poplar plantations predominate in the region (Quintana 2011), with draining channels and dikes. These resulted in deep changes in wetland areas toward more terrestrial-like characteristics, the 'pampeanisation of the delta' (Kandus *et al.* 2006; Galafassi 2011). This can explain the appearance of more mesophilous (Nanni *et al.* 2014) and xerophilous species. This can be why, contrary to that expected for wetlands with a predominance of hydrophilous species (Paleologos 2012), we registered a similar proportion of mesophilous species. Importantly, despite the changes made in the region, the hydrophilic species still have a high overall occurrence. This highlights the importance of changes in hydrological regime on the proportion of both species groups in the different habitat types.

The occurrence of a single xerophilous species would be because of the fact that xerophily not only depends on soil moisture content but also another edaphic conditions, mainly soil sand content and vegetation cover. In the studied area, the structural features of the afforestations inside dykes (e.g. clumped vegetation, large patches of bare soil, high litter coverage and closed canopies) together with the presence of young soils or soils with high clay content during pedogenesis (Ceballos *et al.* 2012) facilitates soil moisture retention, thus hindering the establishment of xerophilous species.

The fact that a high percentage of the species surveyed in our work are distributed in both the Lower Delta and the surrounding Pampean Region is most likely because of the 'pampeanisation' process mentioned above, through which the original wetland conditions become more similar to those of the Pampa, mainly in hydrological, edaphic and floristic terms. There is increasing evidence that changes in the original habitat facilitate the introduction of ecologically and evolutionarily related species from adjacent ecosystems (Escobar *et al.* 2007; Rös *et al.* 2012).

In the studied area, the higher percentage of hemisynanthropic species is related to the presence of island dwellers and large producers. The synanthropic species, constituting a small percentage of the overall carabid assemblage, are also present in the southeastern neighbourhood of Buenos Aires (Cicchino *et al.* 2003).

With regards to the feeding habit, zoophagous species show a wide body-size range, reflecting the diversity in prey body sizes. The surveyed habitat types were structurally complex, providing a large number of microhabitats and therefore high prey availability (Lassau *et al.* 2005). Young Poplar Afforestations and Grasslands for cattle grazing may have a high seasonal availability of seeds because they harbour numerous grasses and broad leaved plants (Nanni 2010). Cicchino and Farina (2010) reported that some non-overwintering species inhabiting grasslands (e.g.

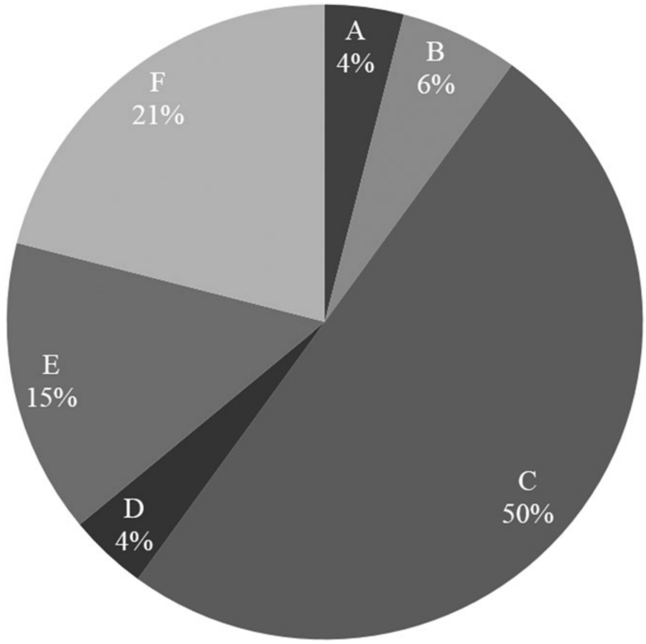

Fig. 2. Percentage of carabid species found in each distribution classes in relation to the total number of carabid species ($S_T = 48$) collected in the Lower Delta of the Paraná River, Argentina.

Table 4 Observed seasonally Carabidae richness at the Lower Delta of the Paraná River, Argentina, and total number of species expected for each season according to the Jacknife 1 and Chao 1 estimators (mean ± standard error). Inventory completeness is observed richness as a percentage of total expected richness. Singleton values are shown for each season

Season	Richness (S)	Jacknife 1	Chao 1	Singletone	Completeness (%)	
					Jack 1	Chao 1
Autumn	21	28.89 ± 0.69	25.60 ± 1.02	8	73	82
Winter	22	27.92 ± 0.54	24.50 ± 0.73	5	79	90
Spring	40	48.88 ± 0.72	45.59 ± 1.23	8	82	88
Summer	27	36.87 ± 0.75	38.17 ± 2.19	10	73	71

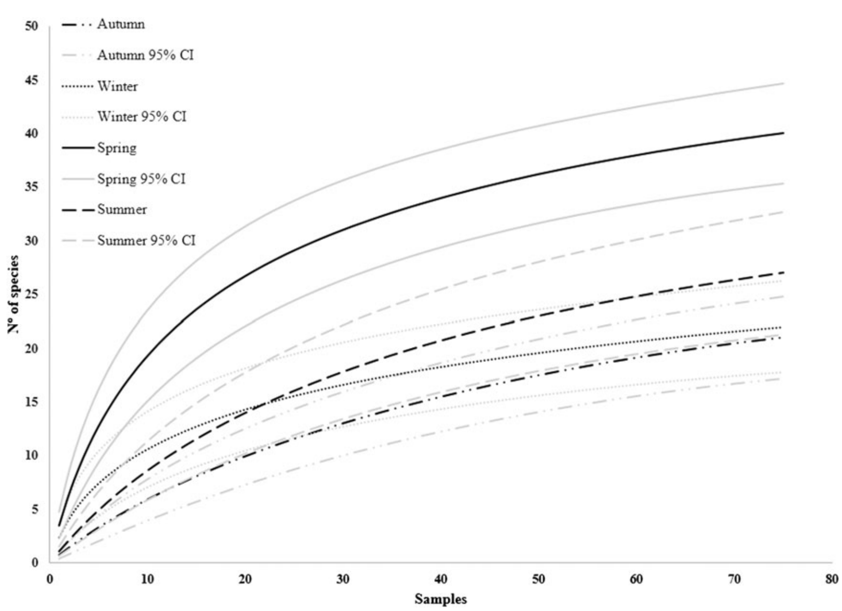

Fig. 3. Samples-based rarefaction curve for seasonally Carabidae assemblage in the Lower Delta of the Paraná River, Argentina. Black and grey lines indicate rarefaction curve and 95% bootstrap confidence intervals, respectively.

tribe Harpalini) are seed eaters during spring and summer and become omnivorous in autumn and winter.

Changes in the observed carabid seasonal richness are consistent with the result of Castro *et al.* (2012). This could be explained because most of the species has a low activity or an overwintering phase during the winter time. Anyway, there were cases in which an inverse phenological pattern was shown (e.g. *Argutoridius bonariensis*, *Argutoridius abacetoides* and *Incagonum discusulcatum*). The phenology of species would be the result of different factors such as life history and environmental variables such as temperature, humidity and diurnal period (Wolda 1988).

The greatest carabid richness and the high proportion of seed eater in spring would be related to the greatest seed production in that season. On the contrary, the lowest richness of carabid observed in autumn is coincident with the lower availability of seed. In addition, differences in species composition between autumn and winter would be because of the higher proportion of zoophagous species in the last one.

The observed singleton had a relatively high percentage (20% in spring and 38% in autumn). These rare species constituted dispersing individuals (sensu Scharff *et al.* 2003) from neighbouring habitats.

In conclusion, our study is the first report on the species of Carabidae in the Lower Delta of the Paraná River. We also provide new information on Argentinean Carabidae, including their distribution range. In addition, the current results lead us to reflect about the importance of keeping the mosaic heterogeneity as well as the hydrological regime in order to maintain the carabids' diversity in this landscape. Ongoing research will expand the knowledge of this group of beetles which are important in terms of the ecosystem services they offer as well as the possibility of detecting hotspots of biodiversity beetles in the studied region, which is considered one of the most diverse of the country.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher’s web site:

Table S1 Ecoregions wetlands, subregions and ecosystem complexes of Argentina (sensu Morello *et al.*) considered for the distribution range of the carabid species from the Lower Delta of the Paraná River.
Table S2 Acronyms for: (a) Latin-American countries and (b) Argentinean Provinces.
Table S3 Criteria used to classify the carabid species collected in the Lower Delta of the Paraná River (Argentina).