



# Effects of intensive human management on the taxonomic and functional diversity of ground beetles in a planted forest landscape

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Received: 29 March 2021 / Revised: 27 July 2021 / Accepted: 11 August 2021 /  
Published online: 21 August 2021

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## Abstract

The rapid expansion of planted forests harms native biodiversity. Few studies report the effects of replacing wetlands with planted forests on ground beetles. We analyze how the taxonomic and functional diversity of ground beetles are affected by intensive management of a planted forest landscape in the Lower Delta of the Parana River. We defined six habitat types ( $n=3$ ,  $N=18$ ): young and mature willow (YW, MW), young and mature poplar without cattle (YP, MP), young and mature silvopastoral poplar (YS, MS). Using pitfall traps ( $N=1728$ ), we recorded 35 species (1896 individuals). YW and MS reached the highest taxonomic diversity and richness. YW with more vertical heterogeneity showed higher species richness than MW. Hydrophilic species were more abundant in YW. Zoophagous species were more abundant in MS. YS, MS, and YW reached the highest functional evenness, which implies that a large part of the functional niches was used. Cattle dung and freshwater canals for livestock offer more resources for ground beetles. The planted tree species, stand age, and presence of cattle affects taxonomic and functional diversity of ground beetles. Willow and silvopastoral planted forests are the most suitable habitats for hosting wetland species. So, we recommend using willow species rather than poplar species when planted forests replace fluvial wetlands, increasing irrigation of poplar planted forests through ditches and canals, conserving or restoring different strata of understory to increase vertical heterogeneity, and maintaining the landscape heterogeneity. These management measures are essential to prevent the loss of wetland species and conserve ground beetle's diversity.

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Communicated by Andreas Schuldt.

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This article belongs to the Topical Collection: Forest and plantation biodiversity.

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**Keywords** Anthropogenic ecosystems · Carabidae · Wetland · Salicaceae · Silvopastoral

## Introduction

Rapid anthropogenic expansion through planted forest meant to intensify productivity has led to the transformation or even the disappearance of natural ecosystems (Sica et al. 2016; Evans and Turnbull 2004). The total area of forest in the world is 31 percent. The planted forest area is increasing and already represents 7 percent of the total forest area (264 million hectares) (FAO 2010). Between 2000 and 2010, the area of the planted forest increased by about 5 million hectares per year. Given the current trend, an additional increase in the planted forest area to 300 million hectares can be anticipated by 2020 (MacGregor 2002). Argentinian plantation area reached 1.2 million ha in 2015 (SENASA 2015).

It is well known that the replacement of natural ecosystems by anthropogenic ecosystems harms native biodiversity (Sica et al. 2018; Suárez et al. 2021). Anthropogenic ecosystems are relatively homogeneous and composed of one or few tree species with individuals of the same size and age. Planted forests generally support a low species diversity because of the limited number of available habitats (Stephens and Wagner 2007; Bremer and Farley 2010). However, the species diversity can be favored, with a dominance of generalist species, when the vertical heterogeneity of the planted forest understory is high (Magnano et al. 2019). The diversity of organisms is highly dependent on the heterogeneity of the landscape and the complexity of the stand (Dias et al. 2013). In this context, one of the most affected groups of animals is usually soil arthropods (Paillet et al. 2010).

Beetles of the family Carabidae (Coleoptera) have been used as indicators of natural and anthropogenic disturbances and management practices (Lövei and Sunderland 1996) because they are taxonomically well known, common in most terrestrial habitats, and can easily be collected using standard methods (Magura 2017). Also, this family provides important ecosystem services (Cicchino 2006; Paleologos et al. 2007; Kwiatkowski 2011). Studies addressing the influence of planted forests and their management on ground beetle have been reported positive (Niemela et al. 2007), negative (Magura et al. 2003) or with no effect (Magura et al. 2000) on richness and diversity in the boreal region and the Hungarian Mountain Range. However, few studies report the effects of replacing wetlands with planted forests on ground beetles. For other taxa, such as mammals and birds, ecologically sustainable planted forest management could contribute to their conservation in wetlands of the Lower Delta of the Paraná River (Fracassi et al. 2017; Magnano et al. 2019; Krug et al. 2019). Establishing how management practices affect ground beetle communities is essential for their conservation and for carrying out appropriate practices for the development of each assembly.

Species abundance, richness and diversity of ground beetles communities in planted forests are influenced by biotic factors (tree species composition, understory, canopy cover) (Chungu 2014; Kaizuka and Iwasa 2015), abiotic factors (light availability, structural and chemical characteristics of leaf litter, soil characteristics) (Magura et al. 2003; Chungu 2014) and management characteristics (type of implemented management, presence of cattle, location of the plantation within the landscape, edge effect, size and age of the stands, vicinity to other habitat types and habitat type that was replaced) (Gormally and Fahy 1998; Koivula 2001; Magura 2002; Niemelä et al. 2007; Binkley and Fisher 2012; Magura et al. 2017; Nanni et al. 2019). Seasonality could also be a determinant factor in structuring ground beetle communities (Saska et al. 2013). Furthermore, these factors modify the

diversity and abundance of functional groups of ground beetles (e.g., Allegro and Sciaky 2003; Paleologos et al. 2007; Liu et al. 2015; Magura 2017). Functional group diversity may affect the dynamics of the available resources (e.g., food and shelter), as well as the stability of the entire ecosystem in terms of resilience and resistance (Díaz and Cabido 2001). Changes in the stability of the ecosystem are of vital importance, especially when planted forests replace highly dynamic wetland environments, as in the present study. In this context, we aim to analyze how taxonomic and functional diversity of ground beetles are differentially affected by intensive management of a planted forest landscape in the Lower Delta of the Parana River, Argentina. For this, we compared ground beetles communities among land uses with different intensive management and across seasons. We hypothesize that abundance, richness, and diversity of the ground beetles change due to factors such as planted tree species with their associated environmental conditions, type of implemented management, stand age, presence of cattle, and season (hypothesis 1). We predict that abundance, richness, and diversity of ground beetles to be greatest in the habitat types with the most vertical heterogeneity. Also, we hypothesize that each planted forest has a specific set of environmental conditions (environmental filters e.g., understory, soil characteristics) that select species with specific traits associated with these (hypothesis 2). We predict more typical wetland species within the lowland planted forests than in the highland planted forests because the first preserves soil conditions similar to wetland environments.

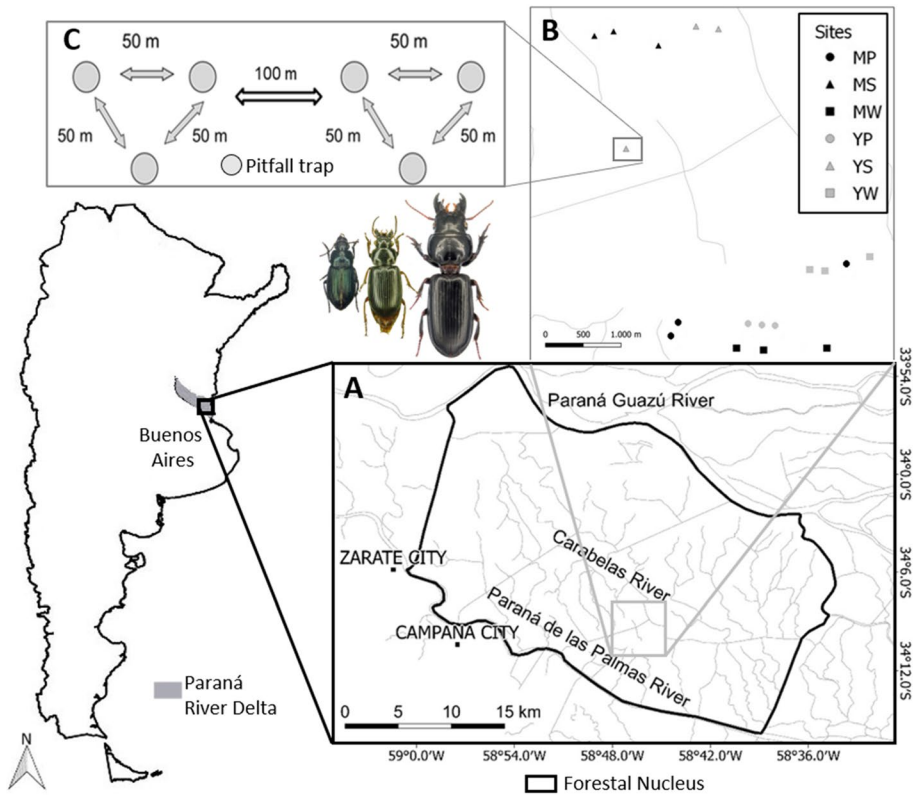
## Materials and methods

### Study area

The Parana River Delta is a wetland macrosystem located along the final 320 km of the Parana Basin (Fig. 1). Its southernmost area, the Lower Delta (33° 45'S; 58° 51'W), encompasses approximately 4500 km<sup>2</sup> of the mainland (southern Entre Rios province) and 3000 km<sup>2</sup> of islands (northern Buenos Aires province, Sica et al. 2016). The hydrological regime is dominated by floods from the Parana River, combined with floods from Gualeguay and Uruguay rivers, tidal and storm surges from the De la Plata River estuary and local rainfall events. All these events produce a distinctive hydrological signature across the area (Baigún et al. 2008).

The Lower Delta has a temperate-humid climate. The coldest month of the year corresponds to July, with an average temperature of 10.5 °C, while the warmest corresponds to January, with an average temperature of 24.4 °C. The average annual rainfall is 1066.1 mm, ranging from 230 in February to 31 mm in June (Malvárez 1999).

We focused on the insular area of the Lower Delta that has undergone a substantial transformation over more than 100 years, mainly due to hydrological changes caused by the construction of a dense network of dikes and canals for the establishment of planted forests with Salicaceae and, more recently, of silvopastoral systems (Quintana et al. 2014). As a result of these anthropogenic changes, the natural land cover composed of riparian forests and freshwater marshes had been degraded or destroyed (Quintana and Kalesnik 2008). This area represents the largest cover (c. 80,000 ha) of planted forests with Salicaceae in Argentina (Petray 2000), including willow (*Salix babylonica*, *Salix nigra* and hybrids), covering 75%, and poplar stands (*Populus nigra*, *Populus deltoides* and hybrids), covering 25% of the area (Borodowski 2006). Planted forests are not homogeneously distributed



**Fig. 1** Map of the study area: **A** Forestal Nucleus in the Lower Delta of the Paraná River, **B** habitat types, **C** diagram of the arrangement of pitfall traps within each habitat type. *MP* Mature Poplar without cattle, *YP* Young Poplar without cattle, *MW* Mature Willow, *YW* Young Willow, *MS* Mature Silvopastoral poplar, *YS* Young Silvopastoral poplar. Pictures by Cicchino: *Scarithes anthracinus* (average length 3 cm), *Polpochila flavipes* (average length 1.5 cm), *Selenophorus anceps* (average length 1 cm)

in the Lower Delta, but are concentrated in the so-called “Forest Nucleus” (Fig. 1), a 935 km<sup>2</sup>-area mainly occupied by tree-only systems, silvopastoral systems and ranches (Fracassi 2012; Quintana et al. 2014).

### Planted forest management

Planted forests of willow and poplar are different systems. Willow trees are spaced at 3 × 2 m or 3 × 3 m and are primarily used for pulp production, while poplar trees, preferred for plywood and sawn timber, are spaced at 6 × 2 m, 6 × 4 m or 6 × 6 m. In general, planted forests of willow are not managed and are planted in lowlands that can retain waterlogging, unlike planted forests of poplar that are planted in highlands with landfill. Willow stand understory is dominated by *Carex riparia* subsp. *chilensis* and *Rubus divaricatus*. Young willow stands have a greater structural heterogeneity than mature willow stands, due to complementing species such as *Eleocharis bonariensis* and *Hydrocotyle bonariensis* (Bergonzi 2019). Management of young poplar plantations includes pruning to shape and land clearing using plows and rollers (Fracassi 2012). Pruning to shape consists of cutting

the lower branches to favor the development of the tree trunk. The use of plows makes furrows in the soil to reduce compaction and eliminates the understory. The use of rollers crushes the herbaceous vegetation which reduces the competition with the young forest species. Management also involves the use of agrochemicals, which is recognized as a serious threat to biodiversity (Evans and Turnbull 2004). Mature poplar stands are not managed inside because they have a canopy closure that avoids the development of an abundant understory. Their understory is dominated by leaf litter and *Carex bonariensis*. Although young poplar stands are managed, they have abundant understory with the dominance of *Lolium multiflorum* and *Eryngium pandanifolium* (Krug 2018). The forest rotation of poplar planted forests shifts in the Lower Delta have an average of 17 years (Cobas et al. 2013). It is possible to obtain understory up to the 7th year of the rotation. From the eighth year, understory growth decreases due to the limited light penetrating the canopy (Cobas et al. 2013). Mátyás and Peszlen (1997) showed that the site conditions influence the maturation age of *Populus deltoides* implanted. In the region, juvenile to mature wood transition occurs between 7 and 9 years due to the rapid growth of Salicaceae (Borodowski 2006).

Silvopastoral systems integrate cattle husbandry with forest management (e.g., use of plows and rollers) in planted forests of poplar given their wider tree spacing. Both mature and young silvopastoral systems have canals or ditches as internal drinking fountains, unlike poplar planted forests without cattle where there is no such management. Cattle feed mainly on plants in the understory. The predominating grazing systems are continuous or involve rotations among stands. The annual average stocking rate varies between 0.3–0.5 and 0.7–1 LU/ha (LU: livestock unit) (Quintana et al. 2014). In the silvopastoral systems, the use of plows predominates over rollers. Young silvopastoral systems have a more diverse understory than mature ones, with species such as *Eryngium pandanifolium*, *Carex* spp., *Carduus* spp. and *Solanum bonariense*. The understory of mature silvopastoral systems is dominated by leaf litter. Species such as *Muhlenbergia schreberi*, *Trifolium repens* and *Hydrocotyle bonariensis* are less abundant (Krug 2018).

## Sampling design

We characterized each habitat type in terms of three variables: tree species (willow and poplar), land-use (tree-only and silvopastoral system) and stand age (young: 5–6 years; mature: 11–14 years). We defined six habitat types: Young Willow (YW; ages=5, 5, 5), Mature Willow (MW; ages=14, 14, 14), Young Poplar without cattle (YP; ages=5, 5, 5), Young Silvopastoral poplar (YS; ages=6, 5, 5), Mature Poplar without cattle (MP; ages=11, 11, 11) and Mature Silvopastoral poplar (MS; ages=11, 11, 12) (Online Resource 1). We selected three stands for each habitat type (Fig. 1) of approximately 0.5 ha each one ( $n=3$ ,  $N=18$ ). The average distances between stands were 2.6 km (Min=0.05 km; Max=5.48 km).

## Ground beetle sampling

We collected specimens using pitfall traps (Woodcock 2005) (diameter: 9 cm; height: 14 cm; volume: 600 ml). These contained 400 ml of a mixture of 2/3 of 96% alcohol and 1/3 of glycerin. We set six pitfall traps in each stand ( $N_{\text{per visit}}=108$ ) forming two triangles equal to 1.250 m<sup>2</sup>. Triangles were separated about 100 m from each other. Pitfall traps were separated about 50 m from each other (Fig. 1) and located centrally or at least 15 m away from field edges to avoid edge effect (Molnar et al. 2001). Traps were considered as

independent observations because they were placed at a distance greater than 25 m (Woodcock 2005). We conducted this study from August 2012 to August 2014. We collected pit-fall traps every 45 days, with two capture periods in all seasons ( $N=1728$ ) during two years. In the laboratory, we only counted the captured adult ground beetles and identified them up to the species level (Reichardt 1979). A reference collection was established with specimens deposited at the “Museo Argentino de Ciencias Naturales, Bernardino Rivadavia” and at the “Instituto de Investigación e Ingeniería Ambiental, UNSAM”.

## Description of traits

Functional diversity has been proposed as an important feature of communities, enabling prediction of the rate and reliability of ecosystem processes (i.e., ecosystem function and ecosystem reliability, Mason et al. 2005). We selected the following functional traits for functional diversity analysis: dependence on soil moisture, adult feeding habits and seasonality.

Dependence on soil moisture (hydrophilic, mesophilic and xerophilic species) was selected because it has a direct association with the habitat requirements of each planted forest species and their management practices. Dependence on soil moisture (Table 1) was obtained from the bibliography (Sorensen 2006; Turienzo 2006) and field observation of the authors (Nanni et al. 2017). Adult feeding habits are highly varied (zoophagous, granivorous, and omnivorous species), with the majority of predatory species being polyphagous and consuming animal tissues, either from live prey or from carrion (Lövei and Sunderland 1996). There are also species with a partially or totally phytophagous diet as well as strict granivores in which the seeds are the main food (Kotze et al. 2011). This functional trait analysis of carabid diets can provide information about prey identity and help to determine predator–prey relationships, increasing knowledge of trophic links (Jelaska et al. 2014). Adult feeding habits (Table 1) was obtained from the bibliography (Cicchino and Farina 2005; Marasas et al. 2010; Nanni et al. 2017) and the direct observation of the mandibular structure from collected adults.

Finally, knowledge of seasonal fluctuations (Table 1) in ground beetle species abundance is important for adequate agroecosystem management, because it determines the reproductive period and consequently the survival of their populations (Castro et al. 2017). Surveying carabids and other invertebrates within a range of habitats over a vast region would not only help to understand the taxonomy, natural history, and biogeography of the species present, but would also help to develop guidelines for their conservation (Cividanes 2021).

## Data analysis

We registered seasonal species richness (number of species), and we estimated seasonal species evenness and diversity. For the estimations, we used the Pielou and the Shannon–Wiener index, respectively (Pielou 1969; Shannon and Weaver 1949). We compared values of evenness and diversity with a generalized linear model (GLM) based on a Gaussian distribution with an identity link function and using a first-order autoregressive correlation matrix per replicate. We use these approaches because they are better fits than include replicate as a random factor. We considered season and habitat type as fixed factors (treatment). We modelled the variance with the varIdent function per habitat type. We analyzed the species richness with a generalized linear mixed model (GLMM) based on Poisson

**Table 1** Ground beetle species registered in a planted forest landscape in the Lower Delta of the Parana River

Tribe	Species	Traits			Hábitat type
		DSM	AFH	S	
Masoreini	<i>Aephniidius bonariensis</i>	M	Z	W	MS
Harpalini	<i>Anisostichus posticus</i>	M	Gr	Sp-W	MW-YW-MP-YS
Pterostichini	<i>Argutoridius abacetoidea</i>	M	Z	An	MW-YW-MP- MS-YS
Pterostichini	<i>Argutoridius bonariensis</i>	M	Z	An	MW-YW-MP-YP-MS-YS
Pterostichini	<i>Argutoridius</i> sp. 3	–	Z	A	MS
Pterostichini	<i>Argutoridius chilensis</i>	M	Z	W	MW-YS
Clivinini	<i>Aspidoglossa intermedia</i>	H	Z	An	MW-YW-MP-YP-MS-YS
Bembidiini	<i>Bembidion uruguayense</i>	H	Z	Sp-W-A	MW-YS
Brachinini	<i>Brachinus olidus</i>	H	Z	S	MS
Harpalini	<i>Bradycellus</i> sp. 2	H	Gr	Sp	YW-MS-YS
Lachnophorini	<i>Ega montevidensis</i>	H	Z	W	YS
Galeritini	<i>Galerita collaris</i>	M	Z	Sp-A	MS-YS
Galeritini	<i>Galerita lacordairei</i>	H	Z	Sp-S	MW-YW-MP
Platynini	<i>Incagonun discosulcatum</i>	H	Z	Sp-W-A	MW-YW-MP
Scaritini	<i>Lophogenius ebeninus</i>	M	Z	Sp-S	MW-YW-MS-YS
Loxandrini	<i>Loxandrus audouini</i>	H	Z	An	MW-YW-MP-YP-MS-YS
Loxandrini	<i>Loxandrus planicollis</i>	H	Z	W-A	MS
Loxandrini	<i>Loxandrus simplex</i>	M	Z	S	YW
Pterostichini	<i>Meraulax alatus</i>	H	Z	Sp-W-A	YW-MP
Pterostichini	<i>Metius circumfusus</i>	H	O	Sp-W	YW-MS-YS
Cicindelini	<i>Oxycheila femoralis</i>	H	Z	S	MW-YW-MS
Pterostichini	<i>Pachymorphus chalceus</i>	M	Z	W-A	MW-YP
Pterostichini	<i>Pachymorphus</i> sp. 2	–	Z	A	MP
Pterostichini	<i>Pachymorphus striatulus</i>	M	Z	An	MW-MP-YP-MS-YS
Clivinini	<i>Paraclivina breviscula</i>	M	O	Sp-W-A	MW-YW-MS-YS
Pterostichini	<i>Paranortes cordicollis</i>	M	Z	An	MW-YW-MP-YP-MS-YS
Harpalini	<i>Pelmatellus egenus</i>	M	O	W-A-S	MP
Harpalini	<i>Polpochila flavipes</i>	M	Gr	S	MS
Harpalini	<i>Polpochila nigra</i>	M	Gr	Sp-S	MS- YS
Zuehiini	<i>Pseudaptinus mimicus</i>	–	Z	Sp	YP
Scaritini	<i>Scarites anthracinus</i>	M	Z	An	MW-YW-MP-YP-MS-YS
Scaritini	<i>Scarites melanarius</i>	M	Z	An	MW-YW-MP-YP-MS-YS
Harpalini	<i>Selenophorus</i> sp. 1	M	O	W	YP
Harpalini	<i>Selenophorus anceps</i>	X	O	Sp-S	YS
Clivinini	<i>Semiclivina platensis</i>	H	Z	Sp-W	YW-MP

MP Mature Poplar without cattle, YP Young Poplar without cattle, MW Mature Willow, YW Young Willow, MS Mature Silvopastoral poplar, YS Young Silvopastoral poplar

The functional traits used for the analysis of Functional Diversity were: dependence on soil moisture (DSM), adult feeding habits (AFH) and species seasonality (S). M mesophilic, H hydrophilic, X xerophilic, Z zoophagous, Gr granivorous, O omnivorous, Sp spring, W winter, A autumn, S summer, An Annual

distribution with a log link function. We used this approach because species richness is a discrete variable. We considered season and habitat type as fixed factors (treatment) and the replicates as random factors. Including replicate as a random factor allows us to model the temporal dependence of the traps. Akaike's information and parsimony criteria were used to select the final models (Crawley 2009).

To characterize each habitat type according to the composition of beetle communities, we computed a Principal Component Analysis (PCA) with a Hellinger pre-transformation (Borcard et al. 2011). We removed all rare species, i.e., those species that were recorded only once in a single sample during the study. Rare species do not characterize the species assemblage and its contribution to the principal components analysis is insignificant because it only contains one piece of data. Later, we evaluated species contribution to each component through Pearson's correlation coefficients. To simplify the interpretation of the results, we plotted the centroids of the six habitat types for each season and the species with a significant correlation.

To evaluate and compare the different components of functional diversity in each habitat type, we assigned each species to a functional group using clusters with Gower function and Average linkage. We calculated the functional diversity indexes: functional richness (FRic), functional evenness (FEve), functional divergence (FDiv) and functional dispersion (FDis) (Mason et al. 2005). We compared them using GLMM based on a Gaussian distribution with an identity link function (Casanoves et al. 2010). We considered habitat type as a fixed factor and replicate as a random factor. We modelled the variance with the varIdent function per habitat type. Akaike's information and parsimony criteria were used to select the final models (Crawley 2009). We did all analyses with the vegan package (Oksanen et al. 2019) of the R 3.6.0 (R Core Team 2019) and the Infostat (Di Rienzo 2011).

## Results

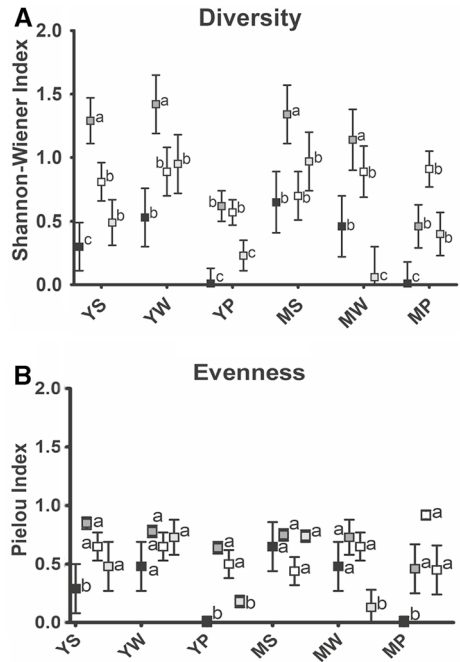
We recorded 35 ground beetle species, distributed in 24 genera, and captured a total of 1896 individuals. Table 1 shows the species list collected during the study and their functional traits. Ground beetle species abundance per habitat type were given in Online Resource 2. Mature silvopastoral poplar, young poplar without cattle and young willow were the most abundant habitat types (Online Resource 2).

The general linear model of diversity showed a significant interaction among habitat types and seasons ( $F_{15,138} = 2.15$ ;  $p = 0.0107$ ). Young and mature willow and young and mature silvopastoral poplar reached the highest diversity in spring. The lowest diversity was found in young and mature poplar without cattle during summer and in mature willow during autumn (Fig. 2). The remaining combinations of habitat types and seasons yielded intermediate values.

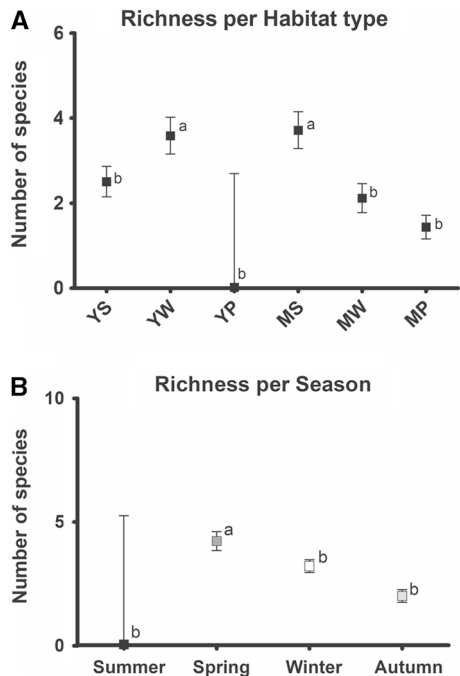
On the other hand, there were significant differences in the generalized linear model of species richness among habitat types ( $F_{51,38} = 5.09$ ;  $p = 0.0003$ ) and seasons ( $F_{3,138} = 8.00$ ;  $p < 0.0001$ ), but not significant interaction ( $F_{15,138} = 1.38$ ;  $p = 0.1637$ ). Although no significant differences were found between mature silvopastoral poplar and young willow, the former showed higher species richness (Fig. 3). Young silvopastoral poplar, mature willow and young and mature poplars without cattle did not differ significantly in species richness. Young and mature poplars without cattle exhibited the lowest species richness. When comparing among seasons, species richness was significantly higher in spring than in other seasons (Fig. 3).



**Fig. 2** Ground beetle diversity and evenness in a planted forest landscape in the Lower Delta of the Parana River (mean  $\pm$  standard error). **A** Diversity (Shannon–Wiener index), **B** Evenness (Pielou index). *MP* Mature Poplar without cattle, *YP* Young Poplar without cattle, *MW* Mature Willow, *YW* Young Willow, *MS* Mature Silvopastoral poplar, *YS* Young Silvopastoral poplar. Winter (white), Autumn (light grey), Spring (grey) and Summer (black). Different letters indicate significant differences ( $p < 0.05$ )



**Fig. 3** Ground beetle richness in a planted forest landscape in the Lower Delta of the Parana River (mean  $\pm$  standard error). **A** Richness by habitat type, **B** Richness by season. *MP* Mature Poplar without cattle, *YP* Young Poplar without cattle, *MW* Mature Willow, *YW* Young Willow, *MS* Mature Silvopastoral poplar, *YS* Young Silvopastoral poplar. Different letters indicate significant differences ( $p < 0.05$ )



There was a significant interaction between habitat type and season for the general linear model of evenness ( $F_{15,138} = 5.27$ ;  $p < 0.0001$ ). The lowest evenness was recorded for mature and young poplar and young silvopastoral poplar in summer and young poplar and mature willow in autumn. The remaining combinations of habitat types and seasons yielded the highest evenness values (Fig. 2).

The first two PCA components (PC1 and PC2) accounted for 40.92% of the total variance (24.06% and 16.86% for PC1 and PC2, respectively). *Paranortes cordicollis* was significantly correlated with the PC1, while *Scarites anthracinus* and *Argutoridius bonariensis* were significantly correlated with the PC2. *Loxandrus audouini* was significantly correlated with both components (Table 2).

Regardless of the season, ground beetle communities in willow stands are located toward the positive end of PC1 and the positive end of PC2, differing from the rest of the habitat types. PC2 ordered the ground beetle communities according to the season, with spring and summer located toward the negative end of PC2 and autumn and winter toward its positive end (Fig. 4).

Table 3 shows the abundance of individuals registered during our study by dependence on soil moisture and adult feeding habits. We observed that the abundance of zoophagous individuals was higher in the mature silvopastoral poplar. Mesophilic individuals were more abundant than hydrophilic and xerophilic individuals. Willow stand had more abundant hydrophilic individuals while poplar stand had more abundance of mesophilic individuals (Table 3).

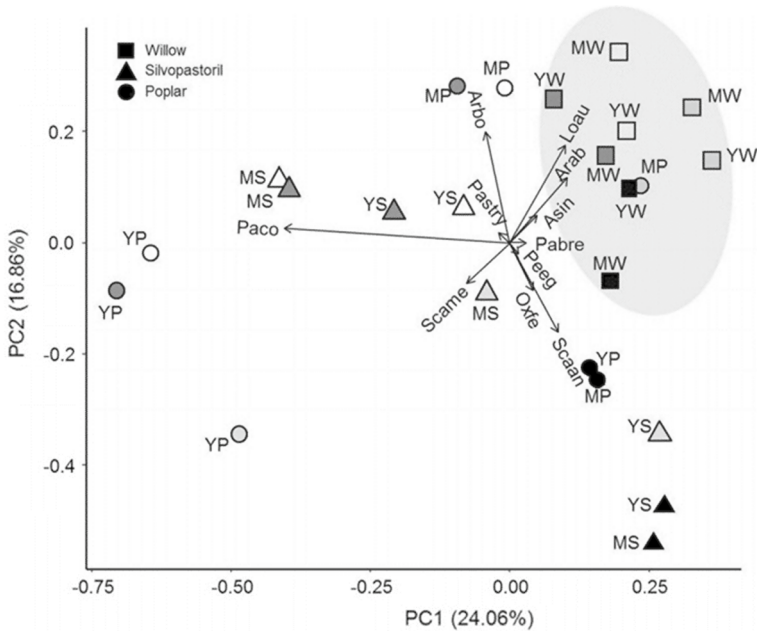
Cluster analysis revealed eight functional groups during the study period (Table 4). Group 3 was characterized by zoophagous, mesophilic with annual activity species while group 4 was characterized by zoophagous, hydrophilic with annual activity species. Although functional groups 3 and 4 were the most abundant in all habitat types, group 3 was more abundant in poplar stands and group 4 in willow stands. Group 5 was characterized by zoophagous, hydrophilic summer activity species. Group 5 was mainly related to mature stands (independently of type) and young willow. Group 7 was exclusive to silvopastoral stands and group 8 was exclusive to young silvopastoral poplar. Group 6 was all land use. Groups 1 and 2 were the less abundant and showed no particular pattern (Table 4).

The general linear model showed significant differences for the indexes of functional divergence (FDiv) and functional evenness (FEve) (FDiv:  $F_{512} = 3.86$ ,  $p = 0.0256$ ; FEve:  $F_{512} = 3.27$ ,  $p = 0.0430$ ). Young and mature silvopastoral poplar and young willow reached the highest functional evenness (Table 5). Mature poplar was the only habitat type to differentiate in terms of functional divergence, presenting the lowest values (Table 5). We did not find significant differences in functional richness (FRic) and functional dispersion (FDis).

**Table 2** Pearson correlation coefficients between ground beetle species that contributed most to the ordering and the first two principal components (PC1 and PC2) obtained by the PCA

Species	CP1	CP2
<i>Paranortes cordicollis</i>	0.76**	–
<i>Scarites anthracinus</i>	–	– 0.50***
<i>Argutoridius bonariensis</i>	–	0.44***
<i>Loxandrus audouini</i>	– 0.25***	0.41***

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



**Fig. 4** Principal component analysis (PC1 and PC2) of ground beetle species composition among habitat types in a planted forest landscape in the Lower Delta of the Parana River over the seasons. White—winter, light gray—spring, dark gray—autumn and black—summer. Gray ellipse shows willow planting sites. *MP* Mature Poplar without cattle, *YP* Young Poplar without cattle, *MW* Mature Willow, *YW* Young Willow, *MS* Mature Silvopastoral poplar, *YS* Young Silvopastoral poplar. We plotted only the species that presented a significant correlation. *Paco* *Paranortes cordicollis*, *Arbo* *Argutoridius bonariensis*, *Loau* *Loxandrus audouini*, *Scaan* *Scarites anthracinus*, *Scame* *Scarites melanarius*, *Pastry* *Pachymorphus striatulus*, *Arab* *Argutoridius abacetoides*, *Asin* *Aspidoglossa intermedia*, *Oxfe* *Oxycheila femoralis*, *Pabre* *Paraclivina breviscula* and *Peeg* *Pelmatellus egenus*

**Table 3** Abundance of ground beetle individuals registered by dependence on soil moisture and adult feeding habits per hábitat types in a planted forest landscape in the Lower Delta of the Parana River

Trait	MP	YP	MW	YW	MS	YS
Zoophagous	97	385	194	303	604	240
Granivorous	4	0	2	2	4	3
Omnivorous	2	1	3	15	8	29
Mesophilous	73	366	116	125	522	183
Hidrophilous	29	19	83	195	93	70
Xerophilous	0	0	0	0	0	19

*MP* Mature Poplar without cattle, *YP* Young Poplar without cattle, *MW* Mature Willow, *YW* Young Willow, *MS* Mature Silvopastoral poplar, *YS* Young Silvopastoral poplar

### Discussion

In general, planted forests that replace natural ecosystems harm native biodiversity (Evans and Turnbull 2004). These changes in biodiversity depend on several factors, highlighting the type of habitat replaced (Corbelli et al. 2015). In particular, when the replaced

**Table 4** Ground beetle functional groups registered in a planted forest landscape in the Lower Delta of the Parana River

Functional Group	Characteristic	Ground beetle species
G1	Granivorous, mesophilic	<i>Anisostichus posticus</i> , <i>Bradycellus</i> sp. 2
G2	Zoophagous, mesophilic, with winter activity	<i>Aepheidius bonariensis</i> , <i>Argutoridius chilensis</i> , <i>Pachymorphus chalcus</i>
G3	Zoophagous, mesophilic, with annual activity	<i>Argutoridius abacetoides</i> , <i>Argutoridius bonariensis</i> , <i>Galerita collaris</i> , <i>Pachymorphus striatulus</i> , <i>Paranortes cordicollis</i> , <i>Scarites anthracinus</i> , <i>Scarites melanarius</i> , <i>Lophogenius ebeninus</i>
G4	Zoophagous, hydrophilic, with annual activity	<i>Aspidoglossa intermedia</i> , <i>Bembidion uruguayense</i> , <i>Ega montevidensis</i> , <i>Loxandrus audouini</i> , <i>Incagoun discosulcatum</i> , <i>Loxandrus planicollis</i> , <i>Meraulax alatus</i> , <i>Semiclivina platensis</i>
G5	Zoophagous, hydrophilic, with activity in summer	<i>Galerita lacordairei</i> , <i>Oxycheila femoralis</i>
G6	Omnivorous, mesophilic, with winter and autumn activity	<i>Metius circumfusius</i> , <i>Paraclivina breviscula</i> , <i>Pelmatellus egenus</i> , <i>Selenophorus</i> sp1
G7	Granivorous, mesophilic, with activity in summer	<i>Polpochila nigra</i>
G8	Omnivorous, xerophilic, with activity in spring and summer	<i>Selenophorus anceps</i>

**Table 5** Ground beetle functional diversity (*FDisp* Functional Dispersion index, *FRic* Functional Richness Index, *FDiv* Functional Divergence index, *FEve* functional Evenness index) for each habitat type classified in a planted forest landscape in the Lower Delta of the Parana River (Mean  $\pm$  SE)

Habitat type	FDiv	FEve	FDisp	FRic
MS	0.52 $\pm$ 0.08 <sup>a</sup>	0.29 $\pm$ 0.05 <sup>a</sup>	0.1 $\pm$ 0.01 <sup>a</sup>	0.05 $\pm$ 0.01 <sup>a</sup>
YS	0.49 $\pm$ 0.08 <sup>a</sup>	0.36 $\pm$ 0.07 <sup>a</sup>	0.09 $\pm$ 0.01 <sup>a</sup>	0.04 $\pm$ 0.01 <sup>a</sup>
YW	0.44 $\pm$ 0.07 <sup>a</sup>	0.27 $\pm$ 0.06 <sup>a</sup>	0.08 $\pm$ 0.01 <sup>a</sup>	0.04 $\pm$ 0.01 <sup>a</sup>
MW	0.32 $\pm$ 0.08 <sup>a</sup>	0.18 $\pm$ 0.05 <sup>b</sup>	0.07 $\pm$ 0.01 <sup>a</sup>	0.02 $\pm$ 0.01 <sup>a</sup>
YP	0.30 $\pm$ 0.08 <sup>a</sup>	0.14 $\pm$ 0.05 <sup>b</sup>	0.07 $\pm$ 0.01 <sup>a</sup>	0.01 $\pm$ 0.01 <sup>a</sup>
MP	0.10 $\pm$ 0.08 <sup>b</sup>	0.08 $\pm$ 0.05 <sup>b</sup>	0.05 $\pm$ 0.01 <sup>a</sup>	0.01 $\pm$ 0.01 <sup>a</sup>

*MP* Mature Poplar without cattle, *YP* Young Poplar without cattle, *MW* Mature Willow, *YW* Young Willow, *MS* Mature Silvopastoral poplar, *YS* Young Silvopastoral poplar

Different letters indicate significant differences ( $p < 0.05$ )

ecosystem is a wetland, a drastic change in vegetation cover occurs and the natural hydrological regime is altered, losing the flood pulses. These changes limit the number of habitats available for wetland species (Magnano et al. 2019; Krug 2018; Nanni et al. 2019). In the Lower Delta of Parana River, there are few isolated remnants of natural grasslands and the original riparian forests have practically disappeared. The secondary forests are environments that most resemble the original riparian forests (Kalesnik and Sirolli 2011). These are abandoned planted forests of Salicaceae that were re-colonized by herbaceous, shrub, and arboreal native species and support a great number of wetland species (Magnano et al. 2019; Nanni et al. 2019). Our results indicate that planted tree species (willow or poplar) with their associated environmental conditions (light availability, soil conditions, waterlogging, understory vegetation) and the type of implemented management, contributed to the differences in ground beetles' taxonomic diversity and richness. Particular associations between planted tree species and ground beetle communities have been observed before (Day et al. 1993; Chungu 2014; Kaizuka and Iwasa 2015). However, Stastna (2012) reported no difference in ground beetle communities between willow and poplar stands, probably, since these planted forests replaced grasslands, and they were set in areas with no difference in waterlogging. In our study, planted forests replaced wetlands. So, the differences in the ground beetle communities would be because the planted forest of willow are located in lowland areas within the dams and subject to temporary floods by rains that increase the richness of hydrophilic species, typical of wetland environments such as *Loxandrus audouini* and *Aspidoglossa intermedia*. Although planted forest of willow and poplar conserve many of the ground beetle species observed in other works for secondary forests in this region (Nanni et al. 2019), there is a loss of wetland species such as *Apenes seriatus* and *Carbonellia platensis*.

Cattle inside the planted forests of poplar were another factor that influenced ground beetles' richness. On one hand, cattle dung in silvopastoral systems offers new niches for soil arthropods. In particular, it is a suitable habitat for detritivorous species with different phenology (Cabrero-Sañudo and Lobo 2003), a fact reflected in the higher abundance of prey for zoophagous ground beetle species. We found that the abundance of zoophagous ground beetle species was much higher in silvopastoral systems than in the other habitat types. On the other hand, some management activities performed in silvopastoral systems such as shape pruning and/or weed clearing using rollers are known to affect soil

microenvironmental conditions by increasing solar radiation and temperature, but also to favor the establishment of terrestrial open-habitat species (Kwiatkowski 2011; Batáry et al. 2007). Moreover, hydrophilic species found in these habitat types are likely favored by canals and ditches that act as a sink for freshwater for cattle. Alternatively, the adjacent patches of each stand could also affect the diversity due to the species flow, as seen in Magura and Lövei (2019). In future studies, adjacent patches could be incorporated at the landscape level to understand these potential interactions.

Also, ground beetles' richness was modified by the stand age. Young willow showed higher species richness compared to mature willow in agreement with Rubio (2004) for the same region. Young willow stands have more vertical heterogeneity than mature stands due to an abundant understory dominated by shrubs (Casaubón et al. 2001). Ground beetles are typical soil beetles, usually found on caves, under rocks and litter, but some groups eventually inhabit trees and shrubs (Moraes et al. 2013). So, this vertical heterogeneity would support high species diversity because of an increased number of habitats available (Hardersen et al. 2020).

Seasonality is another modelling factor of the ground beetles' richness and diversity. The spring was the most diverse and rich season for different habitat types. Although seasonality is species-specific, we detected patterns of richness for spring coinciding with active time reported for other ground beetle species in other parts of the world (Cartellieri and Lövei 2003). The environmental temperature during spring favors the activity of many ground beetles (Saska et al. 2013).

The habitat type mature poplar without cattle showed a low species diversity and richness, but the highest evenness. This suggests a stable climax community (Magurran 2005) resulting from the lack of forestry management practices. In addition, generalist species are most likely favored in highlands-where poplar stands are planted- and by the absence of cattle, because in the other habitat types they may compete with flood-tolerant, specialist species. Such predominance of generalist species has been previously reported for other planted forests of poplar with similar management practices (Ulrich et al. 2004; Stasna 2012). The low evenness of the community in young poplar (with a single dominating species, *Paranortes cordicollis*) is in line with that reported by Allegro and Sciaky (2003) for this habitat type. This result would be due to the presence of a dense cover of herbaceous vegetation that dominates the understory and affects the locomotion of medium- to large-sized species (Allegro and Sciaky 2003).

Thereby, the richness and diversity of the ground beetles change due to factors such as planted tree species with their associated environmental conditions, type of implemented management, stand age, presence of cattle, and season, as suggested in our hypothesis 1.

Functional evenness may be seen as the degree to which the biomass of a community is distributed in niche space to allow effective utilization of the entire range of resources available to it (Mason et al. 2005). The high functional evenness observed in young willow, and young and mature silvopastoral poplar implies that a large part of the functional niches was used. This situation would indicate an uniform exploitation of the niche space occupied by the different functional groups in these habitat types (Mason et al. 2005). The lowest functional divergence of mature poplar was likely because it is a stable climax community with a few dominant species, as mentioned above. Besides, the planted tree species determine the functional groups of the ground beetle. The planted tree species are an environmental filter, due to differences in water-logging. These differences are reflected in the dependence on soil moisture of groups 3 (mesophilic species) and 4 (hydrophilic species). Also, both groups include annual zoophagous species. The high abundance of top predators suggests that the study habitat

types harbor a large number of prey species and are environmentally complex (Liu et al. 2015). The xerophilic species *Selenophorus anceps*, the only member of the functional group 8, is unexpected in a wetland ecosystem. The finding of a terrestrial species in young silvopastoral poplar reflects the deep changes in the environmental conditions caused by the ongoing anthropogenic activities (Porrini et al. 2014) contributes to wetland desiccation. Alternatively, the appearance of this species could be due to the dispersal from other neighboring environments (Scharff et al. 2003), or the dispersal, mediated by anthropic actions such as the movement of machinery from the mainland to the islands. It is worthy of noting that the ground beetle functional groups represented in each habitat type are conditioned by environmental filters (Keddy 1992) associated with the management practices used according to the tree species (e.g., construction of dams and other hydraulic structures, use of plows and rollers to reduce the understory), as we hypothesized.

In conclusion, the planted tree species with their associated environmental conditions, stand age, and presence of cattle inside the plantations have relevant implications for planted forest management and taxonomic and functional diversity of ground beetles in the Lower Delta of the Parana River. Based on our results, planted forests of willow (set in lowland areas) host a greater number of hydrophilic species (typical of wetland) than planted forests of poplar. So, we recommend using willow species rather than poplar species when planted forests replace fluvial wetlands. Planted forests of willow are flood-resistant, thus if planted in lowlands can retain waterlogging. In fluvial wetlands, planted forests of willow are not managed, favoring occurrence of hydrophilic ground beetles. Silvopastoral planted forests were also habitat types suitable for the development of some hydrophilic species, probably due to freshwater sources for cattle. For this reason, increasing irrigation of poplar planted forests without cattle through the addition of ditches and canals would increase soil moisture, thus favoring hydrophilic species. Several of these ground beetles are potential predators of forest pests (Nanni et al. 2015). Therefore, if their populations are abundant, they could become natural enemies of pest species that are detrimental to production (Nanni et al. 2021). Also, other works showed that adding canals and ditches within poplar planted forests has a positive effect on the diversity of other taxa (e.g., mammals and birds) (Fracassi et al. 2017; Krug et al. 2019). Conserving or restoring different strata of understory to increase vertical heterogeneity would increase the number of habitats available for ground beetles, for example, reducing weed cleaning (e.g., use of plow and roller). Finally, the maintenance of heterogeneous landscape mosaic with different species trees, stand age, and silvopastoral systems could host almost the entire community of ground beetles found in secondary forests (Nanni et al. 2019). We recommend carrying out these management measures throughout planted forests that replace fluvial wetlands in areas with similar climate and conditions. These management measures favor ground beetle diversity, particularly hydrophilic species whose niche is limited by being in a planted forest landscape under intensive management. We believe in the need to implement management practices that are ecosystem friendly and that guarantee the conservation of biodiversity and the sustainable use of these modified fluvial wetlands.

**Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1007/s10531-021-02273-w>.

**Acknowledgements** We thank the Instituto de Investigación e Ingeniería Ambiental (IIIA), CONICET-UNSAM. We are grateful to the Las Carabelas staff of Papel Prensa S.A. and to the Gómez family for allowing access during this field study.

**Author contributions** AN, AC, RQ: Conceptualization, Methodology: AN; Formal analysis and investigation: AN, PK; Writing—original draft preparation: AN, PK; Writing—review and editing: AN, PK, AC, RQ; Funding acquisition: RQ; Resources: RQ, AC; Supervision: RQ. All authors read and approved the final manuscript.

**Funding** This work was supported by the projects PICT Bicentenario 2227 and PICT 2982 of the National Agency for Science and Technology Promotion, Argentina, and PIP 0092 of the National Council for Scientific and Technological Research (CONICET).

**Data availability** The generated and analysed datasets during the current study are available from the corresponding author on reasonable request.

## Declarations

**Conflict of interest** The authors declare that they have no competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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