

# Seed bank composition in a secondary forest in the Lower Delta of the Paraná River (Argentina)

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## ABSTRACT

The native forests once occupying the coastal levees of the Lower Delta islands of the Paraná River (in Argentina) have been replaced by commercial forests. Many of those forests have been abandoned, resulting in secondary forest formation that is subject to numerous invasive exotic species. *A priori* observations suggest that successional trends do not lead to recovery of the original forest. The aim of the present study was to analyze the role of invasive exotic species in these environments and the likelihood of recovery of the original forest cover. Therefore, we examined the composition of the seed bank and of the standing vegetation, as well as the population structure of tree species. Secondary forests are described as being in an intermediate successional stage, with few exotic species (mainly trees) but with a high abundance of standing vegetation and seed banks. These exotic species will likely continue to successfully predominate in different forest strata over the next stages. Because of the low density of native tree species, it is difficult to predict their future persistence. In conclusion, ecological restoration strategies will be needed in order to increase native tree species richness and biodiversity of the forests in the Lower Delta of the Paraná River.

**Key words:** Chinese privet (*Ligustrum sinense*), invasive species, post-abandonment regeneration, riparian forest, seedling emergence

## Introduction

Seed banks contain viable propagules stored above or below the soil (Thompson & Grime, 1979). Several studies have analyzed the importance of different environmental factors, as well as the size and composition of soil seed banks, in various ecosystems (Bakker 1989; Bertiller 1992; Albrecht & Pilgram 1997; Jalili *et al.* 2003). The role that seed banks play in secondary successions has been studied since the mid-20th century, and it is considered a key factor to ensure the regeneration of plant cover following disturbances (Baker 1989; Chapman & Chapman 1999; Luzuriaga *et al.* 2005). In the last few decades, there has been growing interest in soil seed bank composition in forest ecosystems (Milber 1995; Holmes & Cowling 1997; Vallés *et al.* 2005), because of the potential of seed banks to restore original forests (Onaindia & Amezaga 2000; Urretavizcaya & Defosé 2004), as well as their strong influence on the composition and diversity of ecosystems after the commercial harvesting of timber (Roberts 1981; Kalesnik 2001; Decocq *et al.* 2004).

The degree of association between the composition of seed banks and that of the standing vegetation can be used

to predict the recovery trends of plant communities (Holmes & Cowling 1997; Albrecht & Pilgram 1997; Decocq *et al.* 2004). In mature forests, the composition of the seed bank usually differs from that of the canopy vegetation (Arévalo & Fernández-Palacios 2000), the seed banks exhibiting a higher proportion of early successional or pioneer species (Hanlon *et al.* 1998; Arévalo & Fernández-Palacios 2000) than of mature forest species (Fenner 1985), because most shade-tolerant species do not develop persistent seed banks (Onaindia & Amezaga 2000).

Ecosystem restoration potential has also been studied solely by analyzing seed bank composition (Middleton 2003; Decocq *et al.* 2004). Seed banks in areas subjected to anthropic modifications can be composed almost entirely of invasive exotic species, decreasing the chance that native species will recover. For instance, the seed banks of mature deciduous forests subjected to management are composed mainly of exotic species, which constitute over 80% of the total seed density (Leck 1989).

In the study area of this work (island levees of the Lower Delta of the Paraná River), the original forest vegetation

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had been almost entirely replaced by commercial forests of willow and poplar (Burkart 1957; Kalesnik 2001; Vallés *et al.* 2005). In the last few decades, many of those forests were abandoned because of socioeconomic difficulties affecting the region (Kalesnik & Malvárez 2003; Vallés *et al.* 2005). Despite the fact that certain areas have long been abandoned (for over 30 years), the original forest has not been able to recover. Instead, a mixed secondary forest dominated by invasive exotic species has spontaneously developed. Many of these species have been introduced for ornamental purposes, such as the Asian species Japanese honeysuckle (*Lonicera japonica*), glossy privet (*Ligustrum lucidum*) and Chinese privet (*Ligustrum sinense*), as well as the European elm-leaf blackberry (*Rubus ulmifolius*). These species often coexist with low densities of native tree species seedlings and saplings, such as laurel (*Nectandra falcifolia*; Kalesnik 2001), “canelón” (*Rapanea lorentziana*; Kalesnik & Malvárez 2003) and Mexican olive (*Blepharocalyx tweediei*; Kalesnik *et al.* 2009). This secondary forest can be considered a “neo-ecosystem”, a term coined by Morello *et al.* (2000) to characterize semi-natural open or wooded areas where dominant invasive exotic species are accompanied by native species.

The main goal of the present study was to analyze the role of invasive exotic species in levee forests of the Lower Delta and the likelihood of recovery of the original forest, locally referred to as the Monte Blanco forest. The seed bank composition was estimated by differentiating between invasive exotic species and native species. Regeneration trajectories for the recovery of communities were defined by analyzing the similarities between the seed bank and the standing vegetation species.

Our main hypothesis was that the invasive process, occurring in the Lower Delta of the Paraná River at a regional level, is evidenced by the seed bank composition of secondary forests. As a consequence, the dominance of invasive exotic species would continue and the probability of recovery of the original Monte Blanco native species would be low.

## Materials and methods

### Study area: the Buenos Aires Province Lower Delta

The Lower Delta islands are located along the final stretch of the Paraná River Delta, at the point where the Paraná River divides into two main distributaries, Paraná Guazú and Paraná de las Palmas (Figure 1). The area extends from the city of Ibicuy (59°20'W; 33°42'S) to the mouths of the Paraná Guazú (58°24'W; 34°S) and Luján Rivers (58°32'W; 34°26'S) at the Río de la Plata. The islands form a growing delta over the Río de la Plata estuary (Iriondo & Scotta 1979; Parker & Marcolini 1992) covering a total area of 2,071.06 km<sup>2</sup> (Latinoconsult 1972).

The temperate climate is characterized by rainfall throughout the year and an average temperature above 22°C during the warmest month. The average annual temperature is approximately 17°C, ranging from 6°C to 30°C (Servicio Meteorológico Nacional 1980). The hydrological regime of the area is influenced by the Paraná and Uruguay Rivers and the Río de la Plata estuary (Latinoconsult 1972; Mujica 1979). However, the Paraná River regime is determined mainly by tropical and subtropical rainfall in its upper basin, exhibiting seasonal variations in water levels, which begin rising in September and reach peak levels in March (DNCP 1983).

The main hydromorphic soil types in the levees are humic and subhumic gley soils, as well as new alluvial soils (Bonfils 1962). According to the United States Department of Agriculture soil taxonomy, these soil types correspond to poorly developed mollisols under an aquic regime.

Sampling was performed in a secondary forest located on the banks of the Carabelas River (Figure 1). The site is an open Salicaceae forest that has not been logged for 20 years and in which the original vegetation has been replaced by exotic tree species and, to a lesser extent, by native species. Although our data were obtained during 2001, it should be noted that subsequent studies have not shown any variation from these data (Kalesnik *et al.* 2009).

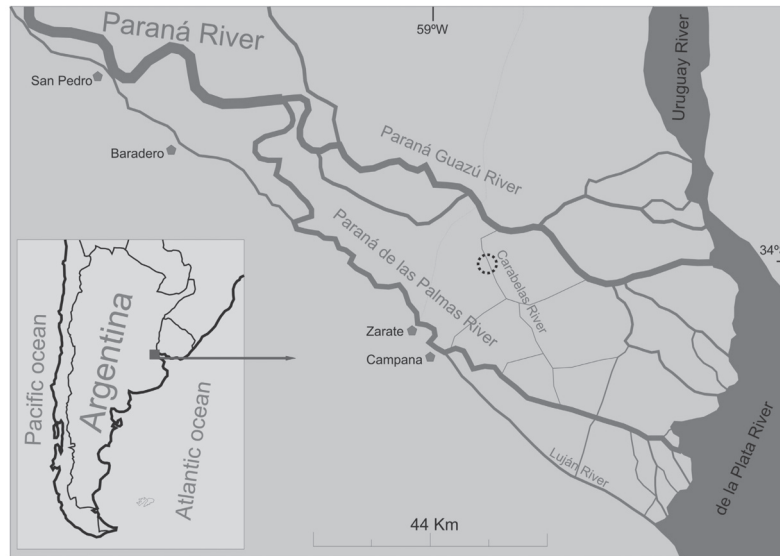
### Sampling design and data collection

#### Seed bank

Four 10 × 10 m plots were randomly set at the site in February of 1999. Forty circular soil core samples (10 cm in diameter and 5 cm in depth) were collected from the topsoil layer, ten samples from each plot (two from each corner and two from the center of the plot). The soil core samples were collected by inserting a PVC tube into the ground. The samples were immediately stored into plastic bags and labeled. Seedling emergence and direct seed counts were both used to determine seed bank structure and composition. For each plot, one corner sample and one center sample were used for each method, yielding a total sampled surface area of 1570 cm<sup>2</sup>.

#### Seedling emergence

Twenty soil samples were cold stratified by storing them at 5°C for two weeks, in order to break the typical dormancy of many temperate climate seeds (Schneider & Sharitz 1986; Houle & Phillips 1988). In March, the samples were allowed to germinate in plastic trays inside a greenhouse. The trays contained inert sand (2.0 cm under the samples and 0.5 cm over) to maintain humidity conditions. Soil samples were spread over the trays to maximize the likelihood of seedling emergence. We also assembled four control trays containing only inert sand. The trays were rotated twice a



**Figure 1.** Study area: Lower Delta of the Paraná River (Argentina). Sampling site is indicated by a dotted circle.

week, by row and by column, in order to homogenize the environmental variables in the greenhouse. For each tray, the emerging seedlings were counted and then transferred to plastic pots outdoors for identification.

#### *Direct seed count*

The remaining 20 samples were sifted twice, after which the seeds were counted. Large plant fragments were discarded during the first sifting. Seeds were then separated by species using a 1-mm mesh sieve. This technique was performed mainly to identify *L. sinense* seeds, the principal invasive species in the area (Kalesnik *et al.* 2009), which do not germinate using the previous method (Vallés *et al.* 2005) and whose quantification was assumed to be of importance for this study.

#### *Standing vegetation*

Species cover was estimated for each 10 × 10 m plot using a modified Braun Blanquet scale (Mueller-Dombois & Ellenberg 1974). Species identification and origin were established according to the nomenclature devised by Cabrera (1963-1968), Burkart (1957, 1979, 1987) and Cabrera & Dawson (1944). The life-form types used were based on Barkman (1988).

The numbers of individuals of each tree species for each pre-determined age class were counted. Age class distribution considered three groups: adults (diameter at breast height > 5 cm), saplings (diameter at breast height < 5 cm, height > 1.30 m) and seedlings (height < 1.30 m). Saplings and seedlings were sampled in a smaller 2 × 2 m plot at the center of the larger (10 × 10 m) plot.

Patterns in the population structure and spatial distribution of the tree species—frequent reproducers; recent

incorporation or recent invaders; and nomadic or relictual individuals—were identified on the basis of previous data (Knight 1975; Saxena & Singh 1984). The future composition of the secondary forest was predicted based on the relative density of seedlings, saplings and adult trees found in the standing vegetation. Relative tree species density in the seed bank was also taken into account for the predictive analysis.

#### *Data analysis*

##### *Seed bank*

Seed bank species richness was calculated as the sum of species identified on the basis of the seedling emergence and direct seed count techniques. Similarly, in our comparative analysis of seed density in the bank and seed bank species richness for each life-form type and origin, we used both methods.

*Standing vegetation* - Total species richness, as well as species richness discriminated by life form and origin, was estimated as the sum of the species identified during sampling. Average species cover was estimated by determining the arithmetic mean for all plots. For comparative analysis, the cover for each life form and origin was calculated as the sum of all species belonging to the respective group and normalized to 100%.

##### *Seed bank and standing vegetation comparison*

Similarity between seed bank and standing vegetation composition in the secondary forest was estimated by the qualitative Sørensen similarity index (Magurran 1988). Similarity was also analyzed for each life-form type using

the same index, although we considered species only according to their life form. For both analyses, calculation of the similarity index took into account the total number of species identified in all four plots.

### Tree species density

Relative densities of tree species identified in the seed bank and in the secondary forest structure were analyzed in order to determine the possible future composition of the canopy. Thus, it is possible to study whether dominant species in each forest stratum are likely to sustain their dominance over time or if they will be replaced by other species. For the comparison between native and exotic species, total density was calculated as the sum of standing vegetation, seedling emergence and seed count in the seed bank.

### Statistical analysis

The data did not meet the normality assumption and therefore required square-root transformation [ $y = \sqrt{(x + 0.5)}$ ]. Because the data distribution was still non-normal after this transformation, a non-parametric Mann-Whitney test was performed for all variables to compare native and exotic origins. The XLSTAT software, version 7.5.2 (Addinsoft, Paris, France) was used for all analyses.

## Results

### Seed bank

From the 1570 cm<sup>2</sup> of secondary forest soil sampled, a total of 369 seeds were germinated, corresponding to 52 different species and equivalent to 2349 germinated seeds/m<sup>2</sup> (Table 1). Although *L. sinense* seeds did not germinate in any of the samples, high densities of that species were found in all samples by direct count, totaling 197 seeds (1254 seeds/m<sup>2</sup>). If the results of both methods are considered, the species richness in the seed bank was 53 species: five tree species (three of which were exotic); 47 herbaceous species—38 broadleaf (four exotic), seven graminoid (two exotic); and two equisetoid (both native); and one native creeper species. On average, 28.8 species germinated per plot, with an average density of 3603 seeds/m<sup>2</sup>, including *L. sinense* seeds quantified by direct count (Table 2).

As can be seen in Table 2, the number of native species was significantly higher than was that of exotic species ( $p=0.019$ ). However, seed density did not differ by species origin ( $p>0.05$ ). All types of native herbaceous species outnumbered the exotic species ( $p<0.05$ ) and their seed density was similarly higher ( $p<0.05$ ). Among these, *Solanum deltaicum* showed the highest number of germinated seeds. Tree species and broadleaf herbaceous species accounted for the majority of seeds in the bank. Although species richness did not vary by species origin ( $p>0.05$ ), the density of exotic

tree species was significantly greater than was that of native tree species ( $p=0.020$ ), particularly due to *L. sinense*. Creeper species showed the lowest richness and seed density values and did not vary by species origin ( $p>0.05$ ). No seedling emergence was observed in the four control trays.

### Comparison between standing vegetation and seed bank

The total species richness in standing vegetation was 40 species (Table 1): ten tree species (five of which were exotic); two shrub species (one exotic); 24 herbaceous species—17 broadleaf (one exotic), one native equisetoid, and six graminoid (five native); and four creepers (three native).

On average, 18.5 species were found per plot (Table 3). Although native species outnumbered exotic species ( $p=0.019$ ), the latter showed a higher mean cover value ( $p=0.021$ ). Among the broadleaf herbaceous species, number and cover were higher for native species than for exotic species ( $p=0.018$  for both). For the remaining life-form types, the number of species did not differ by origin. Nevertheless, the mean cover was higher for exotic trees (predominantly *L. sinense* and *Fraxinus* sp.) and creepers (predominantly *Lonicera japonica*) than for their native counterparts ( $p=0.021$  for both).

For all species in the seed bank and standing vegetation, the Sørensen similarity index was 38.7%. When differentiating between life forms, we found that similarity was 0% for shrubs and creepers, 29% for broadleaf species, 53.3% for trees, 66.7% for equiseta, to 76.9% for graminoid species.

Seed density was higher for exotic tree species than for native tree species ( $p=0.020$ ), mainly because 96.6% of the seeds were of *L. sinense*, compared with only 1.5% for native tree species. Among seedlings and saplings, relative density was also dominated by *L. sinense* with a significant smaller proportion of native tree species ( $p=0.046$ ). When considering adults, the density of exotic tree species was significantly higher than for native species ( $p=0.050$ ), once again because of *L. sinense* dominating the middle stratum of the forest (Table 4).

By integrating the previous results and analyzing the population structure patterns of the different tree species, *Fraxinus* sp. can be regarded as a frequent reproducer, seedlings and saplings outnumbering adults (Table 4). Seeds of *Fraxinus* sp. were also found in the seed bank, which suggests continued dominance of the canopy of the secondary forest by this species.

The remaining tree species composing the canopy, both exotic and native, showed a relictual pattern, with no seedlings or saplings found in the population structure. The only exceptions were *Morus alba* (exotic) and *Sapium haemospermum* (native), which were identified in the seed bank (Table 4).

With regards to species in the middle stratum of the secondary forest, *L. sinense* corresponded to a frequent reproducer that has a relatively higher proportion of seedlings

**Table 1.** Seed density in the seed bank and standing vegetation cover in four plots within a secondary forest of the Lower Delta of the Paraná River (Argentina).

| Species   | Germinated or counted seeds/m <sup>2</sup> |      |        |       | Standing vegetation cover, % |        |
|---|--|------|--------|-------|------------------------------|--------|
|   | (N=4)                                      |      |        |       | (N=4)                        |        |
|   | O  | LF   | Mean   | SD    | Mean                         | SD     |
| <i>Alternanthera philoxeroides</i> (Mart.) Griseb.            | N  | BL** | 12.7   | 14.7  |                              |        |
| <i>Amorpha fruticosa</i> L.                                   | E  | S    |        |       | 0.250                        | 0.500  |
| <i>Aster squamatus</i> (Spreng.) Hieron.                      | N  | BL** | 6.4    | 12.7  |                              |        |
| <i>Baccharis phyteumoides</i> (Less.) DC                      | N  | BL** |        |       | 1.503                        | 1.729  |
| <i>Blepharocalyx salicifolius</i> (Kunth) O. Berg             | N  | T    | 19.1   | 38.2  |                              |        |
| <i>Boehmeria cylindrica</i> (L.) Sw.                          | N  | BL** |        |       | 0.003                        | 0.005  |
| <i>Canna glauca</i> L.  | N  | BL** |        |       | 0.003                        | 0.005  |
| <i>Carduus acanthoides</i> L.                                 | E  | BL** |        |       | 1.875                        | 3.750  |
| <i>Carex riparia</i> Curtis                                   | N  | G**  | 19.1   | 24.4  |                              |        |
| <i>Centunculus minimus</i> L.                                 | E  | BL** |        |       | 0.750                        | 0.500  |
| <i>Cestrum parqui</i> L'Hér.                                  | N  | S    |        |       | 0.003                        | 0.005  |
| <i>Citrus aurantium</i> L.                                    | E  | T    | 6.4    | 12.7  |                              |        |
| <i>Conyza</i> sp. Less.                                       | N  | BL** | 146.4  | 84.1  | 1.500                        | 1.732  |
| <i>Cyperus</i> sp. 1  | N  | G**  | 89.1   | 67.4  | 0.250                        | 0.500  |
| <i>Cyperus</i> sp. 2  | N  | G**  | 146.4  | 96.1  | 0.250                        | 0.500  |
| <i>Cyperus</i> sp. 3  | N  | G**  | 19.1   | 12.7  |                              |        |
| <i>Diodia brasiliensis</i> Spreng.                            | N  | BL** | 6.4    | 12.7  | 4.125                        | 2.250  |
| <i>Eclipta prostrata</i> (L.) L.                              | N  | BL** | 19.1   | 24.4  |                              |        |
| <i>Eleusine indica</i> (L.) Gaertn                            | E  | G**  | 25.5   | 29.4  |                              |        |
| <i>Erechtites hieracifolia</i> (L.) Raf. ex DC.               | N  | BL** | 31.8   | 32.0  |                              |        |
| <i>Eryngium pandanifolium</i> Cham. & Schltdl.                | N  | G**  | 31.8   | 32.0  | 0.750                        | 1.500  |
| <i>Erythrina crista-galli</i> L.                              | N  | T    |        |       | 9.000                        | 9.823  |
| <i>Fragaria vesca</i> L.                                      | E  | BL** | 82.8   | 56.5  |                              |        |
| <i>Fraxinus</i> sp. L.  | E  | T    | 6.4    | 12.7  | 60.375                       | 24.008 |
| <i>Galium aparine</i> L.                                      | N  | BL** |        |       | 0.003                        | 0.005  |
| <i>Gamochaeta spicata</i> (Lam.) Cabrera                      | N  | BL** | 76.4   | 55.0  |                              |        |
| <i>Hemarthria altissima</i> (Poir.) Stapf & C.E. Hubb         | N  | G**  | 38.2   | 32.9  | 0.003                        | 0.005  |
| <i>Hydrocotyle bonariensis</i> Lam.                           | N  | BL** | 19.1   | 38.2  | 0.003                        | 0.005  |
| <i>Iris pseudacorus</i> L.                                    | E  | G**  | 31.8   | 48.2  | 1.000                        | 1.414  |
| <i>Juncus</i> spp. L.   | N  | E**  | 70.0   | 108.8 | 0.253                        | 0.498  |
| <i>Ligustrum lucidum</i> W.T. Aiton                           | E  | T    |        |       | 0.250                        | 0.500  |
| <i>Ligustrum sinense</i> Lour.*                               | E  | T    | 1254.1 | 917.5 | 87.500                       | 0      |
| <i>Lonicera japonica</i> Thunb.                               | E  | C    |        |       | 21.375                       | 16.815 |
| <i>Ludwigia peruviana</i> (L.) Hara                           | N  | BL** | 127.3  | 55.0  | 0.003                        | 0.005  |
| <i>Mikania</i> sp. Willd.                                     | N  | C    |        |       | 0.253                        | 0.498  |
| <i>Mimosa bonplandii</i> (Gillies ex Hook. & Arn.) Benth.     | N  | T    | 12.7   | 14.7  |                              |        |
| <i>Morus alba</i> L.  | E  | T    | 19.1   | 12.7  | 0.250                        | 0.500  |
| <i>Myrceugenia glaucescens</i> (Cambess.) D. Legrand & Kausel | N  | T    |        |       | 0.750                        | 1.500  |
| <i>Nicotiana longiflora</i> Cav.                              | N  | BL** | 12.7   | 25.5  |                              |        |
| <i>Orthosia virgata</i> (Poir.) E. Fourn.                     | N  | C    |        |       | 0.003                        | 0.005  |
| <i>Oxalis brasiliensis</i> Lodd.                              | N  | BL** | 12.7   | 25.5  | 0.003                        | 0.005  |
| <i>Passiflora coerulea</i> L.                                 | N  | C    | 6.4    | 12.7  |                              |        |
| <i>Phyla canescens</i> (Kunth) Greene                         | N  | BL** | 6.4    | 12.7  |                              |        |
| <i>Plantago</i> sp. L.  | N  | BL** | 171.9  | 110.8 | 1.000                        | 1.414  |
| <i>Polygonum hydropiperoides</i> Michx.                       | N  | BL** | 6.4    | 12.7  |                              |        |
| <i>Ranunculus apiifolius</i> Pers.                            | N  | BL** | 6.4    | 12.7  |                              |        |

Continue



Table 1. Continuation.

|  |   |      |               |               |        |        |
|--|---|------|---------------|---------------|--------|--------|
| <i>Ranunculus bonariensis</i> Poir.  | N | BL** | 6.4           | 12.7          |        |        |
| <i>Rapanea</i> sp.   | N | T    |               |               | 0.750  | 1.500  |
| <i>Rorippa hiliariana</i> (Walp) Cabrera   | N | BL** | 44.6          | 60.2          |        |        |
| <i>Rubus</i> spp. L.   | E | BL** | 19.1          | 24.4          |        |        |
| <i>Sapium haematospermum</i> Müll. Arg.  | N | T    | 6.4           | 12.7          | 6.250  | 8.292  |
| <i>Senecio bonariensis</i> Hook. & Arn.  | N | BL** |               |               | 0.750  | 1.500  |
| <i>Solanum deltaicum</i> Cabrera   | N | BL** | 458.4         | 108.0         | 26.005 | 31.217 |
| <i>Solanum sarrachoides</i> Sendtn.  | N | BL** | 6.4           | 12.7          |        |        |
| <i>Soliva sessilis</i> Ruiz & Pav.   | N | BL** | 31.8          | 24.4          |        |        |
| <i>Stachys gilliesii</i> Benth.  | N | BL** | 25.5          | 36.0          |        |        |
| <i>Stigmaphyllon littorale</i> A. Juss.  | N | C    |               |               | 0.253  | 0.498  |
| <i>Tradescantia fluminensis</i> Vell.  | N | BL** |               |               | 0.503  | 0.574  |
| <i>Trifolium repens</i> L.   | E | BL** | 12.7          | 14.7          |        |        |
| <i>Triglochin striata</i> Ruiz & Pav.  | N | E**  | 101.9         | 55.0          |        |        |
| <i>Verbena bonariensis</i> L.  | N | BL** | 19.1          | 24.4          | 0.253  | 0.498  |
| 9 herbaceous species in the seed bank  | X | BL** | 318.3         | 60.6          |        |        |
| 1 creeper in the seed bank   | X | C    | 12.7          | 14.7          |        |        |
| 4 herbaceous species in the standing vegetation  | X | BL** |               |               | 0.760  | 1.493  |
| <b>Total number of germinated seeds</b>  |   |      | <b>2349.1</b> | <b>1601.6</b> |        |        |
| <b>Total number of seeds by direct count (only for Chinese privet, <i>L. sinense</i>).</b> |   |      | <b>1254.1</b> | <b>917.5</b>  |        |        |

O – origin; LF – Life Form; SD – standard deviation; N – native; E – exotic; X – unidentified species; T – tree; S – shrub; BL – broadleaf; G – graminoid; E – equisetoid; C – creeper.

\*Direct count; \*\*herbaceous species.

Table 2. Mean species richness of native and exotic species density in the seed bank of a secondary forest of the Lower Delta of the Paraná River (Argentina), by life form.\*

|   | Life form    | Native                  | Exotic                  | Unidentified        | Total                  |
|---|--------------|-------------------------|-------------------------|---------------------|------------------------|
| Richness/100 m <sup>2</sup>               | Trees        | 0.8 ± 1.0 a             | 2.0 ± 0.8 a             | 0.0 ± 0.0           | 2.8 ± 1.5              |
|   | Herbaceous   |                         |                         |                     |                        |
|   | Broadleaf    | 11.8 ± 0.5 a            | 2.5 ± 1.0 b             | 4.5 ± 1.9           | 18.8 ± 2.8             |
|   | Graminoid    | 4.0 ± 0.8 a             | 57.3 ± 32.0 b           | 0.0 ± 0.0           | 5.0 ± 0.8              |
|   | Equisetoid   | 1.5 ± 0.6 a             | 0.0 ± 0.0 b             | 0.0 ± 0.0           | 1.5 ± 0.6              |
|   | Creeper      | 0.3 ± 0.5 a             | 0.0 ± 0.0 a             | 0.5 ± 0.6           | 0.8 ± 0.5              |
|   | <b>Total</b> | <b>18.3 ± 1.5 a</b>     | <b>5.5 ± 1.3 b</b>      | <b>5.0 ± 2.4</b>    | <b>28.8 ± 4.0</b>      |
| Germinated + counted seeds/m <sup>2</sup> | Trees        | 19.1 ± 24.4 a           | 1279.6 ± 827.6 b        | 0.0 ± 0.0           | 1298.7 ± 848.6         |
|   | Herbaceous   |                         |                         |                     |                        |
|   | Broadleaf    | 1279.6 ± 225.3 a        | 133.7 ± 43.5 b          | 318.3 ± 60.6        | 1731.6 ± 182.4         |
|   | Graminoid    | 324.7 ± 78.8 a          | 0.3 ± 0.5 b             | 0.0 ± 0.0           | 382.0 ± 108.0          |
|   | Equisetoid   | 171.9 ± 96.1 a          | 0.0 ± 0.0 b             | 0.0 ± 0.0           | 171.9 ± 96.1           |
|   | Creeper      | 6.4 ± 12.7 a            | 0.0 ± 0.0 a             | 12.7 ± 14.7         | 19.1 ± 12.7            |
|   | <b>Total</b> | <b>1801.6 ± 293.6 a</b> | <b>1470.6 ± 890.3 a</b> | <b>331.0 ± 46.5</b> | <b>3603.3 ± 1101.5</b> |

\*“a” differs significantly from “b” (Mann-Whitney Test, p<0.05).

**Table 3.** Mean species richness of native and exotic species density in standing vegetation of a secondary forest of the Lower Delta of the Paraná River (Argentina), by life form.\*

|                                   |            | Native        | Exotic        | Unidentified | Total       |
|-----------------------------------|------------|---------------|---------------|--------------|-------------|
| Richness/100 m <sup>2</sup>       | Trees      | 2.5 ± 0.6 a   | 2.8 ± 0.5 a   | 0.0 ± 0.0    | 5.3 ± 1.0   |
|                                   | Shrubs     | 0.8 ± 0.5 a   | 0.3 ± 0.5 b   | 0.0 ± 0.0    | 1.0 ± 0.8   |
|                                   | Herbaceous |               |               |              |             |
|                                   | Broadleaf  | 5.8 ± 3.4 a   | 0.0 ± 0.0 b   | 1.8 ± 2.1    | 7.8 ± 5.6   |
|                                   | Graminoid  | 1.3 ± 1.5 a   | 0.5 ± 0.6 b   | 0.0 ± 0.0    | 1.8 ± 2.1   |
|                                   | Equisetoid | 0.5 ± 0.6 a   | 0.0 ± 0.0 a   | 0.0 ± 0.0    | 0.5 ± 0.6   |
|                                   | Creepers   | 1.3 ± 1.3 a   | 1.0 ± 0.0 b   | 0.0 ± 0.0    | 2.3 ± 1.3   |
|                                   | Total      | 12.0 ± 6.3 a  | 4.8 ± 1.3 b   | 1.8 ± 2.1    | 18.5 ± 9.0  |
| Relative cover/100 m <sup>2</sup> | Trees      | 8.9 ± 7.7 a   | 66.1 ± 13.6 b | 0.0 ± 0.0    | 75.0 ± 20.6 |
|                                   | Shrubs     | 0.3 ± 0.2 a   | 0.1 ± 0.3 b   | 0.0 ± 0.0    | 0.5 ± 0.4   |
|                                   | Herbaceous |               |               |              |             |
|                                   | Broadleaf  | 13.6 ± 13.2 a | 0.0 ± 0.0 b   | 0.3 ± 0.6    | 13.9 ± 13.7 |
|                                   | Graminoid  | 1.2 ± 1.7 a   | 0.4 ± 0.6 a   | 0.0 ± 0.0    | 1.6 ± 2.2   |
|                                   | Equisetoid | 0.1 ± 0.2 a   | 0.0 ± 0.0 a   | 0.0 ± 0.0    | 0.1 ± 0.2   |
|                                   | Creepers   | 0.2 ± 0.3 a   | 8.6 ± 5.6 a   | 0.0 ± 0.0    | 8.8 ± 5.5   |
|                                   | Total      | 24.5 ± 8.5 a  | 75.2 ± 9.1 a  | 0.3 ± 0.6    | 100.0 ± 0.0 |

\*“a” differs significantly from “b” (Mann-Whitney Test,  $p < 0.05$ ).

**Table 4.** Population structure (seed density in the seed bank, as well as the spatial distribution of seedlings, saplings and adults) of tree species in a secondary forest of the Lower Delta of the Paraná River (Argentina).\*

| Species   | Origin | Seed bank            | Seedlings           | Saplings        | Adults        |
|---|--------|----------------------|---------------------|-----------------|---------------|
| <i>Blepharocalyx salicifolius</i> (Kunth) O. Berg             | N      |                      | 25.0 ± 25.0         |                 |               |
| <i>Erythrina crista-galli</i> L.                              | N      |                      |                     |                 | 1.0 ± 1.7     |
| <i>Fraxinus</i> sp. L.  | E      | 636.6 ± 1273.2       | 16.7 ± 28.9         | 17.3 ± 13.3     | 2.7 ± 0.6     |
| <i>Ligustrum lucidum</i> W.T. Aiton                           | E      |                      |                     |                 | 0.3 ± 0.6     |
| <i>Ligustrum sinense</i> Lour.                                | E      | 125415.0 ± 81123.8** | 54883.3 ± 56594.5   | 350.0 ± 278.4   | 33.3 ± 28.9   |
| <i>Mimosa bonplandii</i> (Gillies ex Hook. & Arn.) Benth.     | N      | 1273.2 ± 1470.2      |                     |                 |               |
| <i>Morus alba</i> L.  | E      | 1909.9 ± 1273.2      |                     |                 | 0.3 ± 0.6     |
| <i>Myrceugenia glaucescens</i> (Cambess.) D. Legrand & Kausel | N      |                      | 8.3 ± 14.4          |                 |               |
| <i>Rapanea</i> sp.  | N      |                      |                     | 0.7 ± 1.2       | 0.3 ± 0.6     |
| <i>Sapium haematospermum</i> Müll. Arg.                       | N      | 636.6 ± 1273.2       |                     |                 | 0.3 ± 0.6     |
| Overall total   |        | 129871.3 ± 84864.3   | 54933.3 ± 56637.0   | 368.0 ± 277.6   | 38.3 ± 28.9   |
| Total native species  |        | 1909.9 ± 2438.1 a    | 33.3 ± 28.9 a       | 0.7 ± 1.2 a     | 1.7 ± 2.1 a   |
| Total exotic species  |        | 127961.5 ± 82759.2 b | 54900.0 ± 56623.4 b | 367.3 ± 276.6 b | 36.7 ± 27.4 b |

\*“a” differs significantly from “b” (Mann-Whitney Test,  $p < 0.05$ ); \*\*direct count.

and saplings than of adult plants. This short tree species (3–5 m) showed a distinctive high density for all population stages considered and is therefore likely to dominate the middle stratum of the forest in the future.

## Discussion

The present work represents the first description of the type of seed banks that species of this secondary forest can develop, allowing a better understanding of the role of exotic species in such environments. Particularly, *L. sinense* can develop transient or type II seed banks during the winter months (Thompson and Grime, 1979), with germination occurring only in the spring. Our sample collection period (February 1999, which is fall in the southern hemisphere) and the fact that seeds of this species lose viability relatively quickly is in agreement with the aforementioned assumption.

Contrarily, *Fraxinus* sp. forms seed banks classified as type III (*sensu* Thompson & Grime 1979), also known as type B (*sensu* Nakagoshi 1985), in which seeds germinate immediately after being released during the fall. A small fraction of seeds permanently incorporate into the seed bank, which would account for the results of our seed emergence analysis. *Fraxinus* sp. also show traits of the *Fagus* type, as defined by Nakagoshi (1985), which is a shade-tolerant, deciduous tree species with large seeds and type A or B seed banks (types II or III according to Thompson & Grime 1979).

The occurrence of *R. ulmifolius* in the seed bank was noteworthy, despite being absent from the standing vegetation. This case is compatible with persistent seed bank types (type IV according to Thompson & Grime 1979), in which a low proportion of seeds germinate upon being dispersed and the remaining vast majority are incorporated into the seed bank. This strategy is typical of dominant species in disturbed environments (Thompson 1998). In analyzing successional trends, Nakagoshi (1985) described the *Rubus* type as a functional group composed of shade-intolerant shrubs with a short life-span and seed dispersal by birds. In the event of disturbances (e.g., weeding), *R. ulmifolius* can germinate and invade forests.

In the forest studied, the species similarity of the seed bank and standing vegetation (38.7%) was similar to that reported by Hopfensperger (2007) for temperate and tropical forests (31% on average for both). This degree of similarity represents an intermediate successional state, because mature forests usually consist of small seed banks composed of species absent from the standing vegetation (Nakagoshi 1985; Thompson 1998).

The exotic tree species, acting as invasive species in the secondary forest, showed a population structure that is compatible with a frequent reproducer pattern and a prominent presence in the seed bank. The results of our seed bank analysis underscore the notion that exotic species will

continue to dominate all strata of the secondary forest in future generations. The colonization success of *Ligustrum* species is most likely attributable to seed dispersal by birds, as reported by Montaldo (1993) for similar regions.

When we compared our results with those obtained by other authors (Gunther *et al.* 1984; Schneider & Sharitz 1986; McGraw 1987; Titus 1988; Goodson *et al.* 2002; Nicol *et al.* 2003; Leck & Schütz 2005; Richter & Stromberg 2005), we found that the species richness of the seed bank in the secondary forest we studied here was high (53 species), particularly in broadleaf herbaceous life forms. Our seed bank also showed a high estimated seed density (3603 seeds/m<sup>2</sup>), not only due to the herbaceous species but also due to trees. Although tree species richness in the seed bank was low, we observed considerable tree seed density (1299 seeds/m<sup>2</sup>), mainly due to three exotic tree species.

The invasive nature of exotic species was not reflected in the total seed bank richness, because native species outnumbered exotic species, mainly because of a high proportion of native herbaceous species. This notwithstanding, the high abundance of exotic tree seeds compensated for the total seed densities when we discriminated between species by their origin.

In summary, the secondary forests in the study area showed a low number of exotic species, mainly trees, but there was high species abundance, in standing vegetation as well as in soil seed banks. One explanation for this scenario is the ubiquity of *L. sinense*. This species can be responsible for severely reducing species richness and tree regeneration (Merriam & Feil 2002), because of shading and allelopathic effects, a high degree of phenotypic plasticity and its strong tendency toward asexual reproduction (Grove & Clarkson 2005; Pokwinski 2008). The significantly low density of tree species native to the original forests, both in standing vegetation and seed banks, will likely lead to their disappearance from those forests. Even the few native species composing the canopy exhibited a relictual pattern and are therefore not expected to be components of the canopy in the future.

The secondary succession observed in these abandoned commercial forests can be considered a natural and spontaneous passive restoration process (Rey Benayas & Camacho Cruz 2004) that will not result in the regeneration of the original Monte Blanco forest. Therefore, strategies focused on active forest restoration measures (Maestre *et al.* 2001; Rey Benayas 2005) are needed in order to increase biological diversity and native tree species richness in the secondary forests of the Lower Delta.

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