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5 Impact of *Ligustrum lucidum* on the soil seed bank in invaded subtropical seasonally
6 dry woodlands (Córdoba, Argentina).

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26 **Abstract**

27

28 The impact of invasive species on below ground flora may differ from that on the above
29 ground vegetation. Recent reviews of invaded and native communities emphasize the
30 need for more comprehensive information on the impacts of plant invasion on soil seed
31 banks. *Ligustrum lucidum* is one of the most important invasive woody species in several
32 ecosystems of Argentina; however, its impact on soil seed bank communities has not
33 been studied. Here we analyzed differences in species richness, total seed density and
34 species composition (total, native and exotic species) in the soil seed bank of native and
35 invaded woodlands, in two different seasons. We also analyzed differences in similarity
36 between standing vegetation and soil seed banks of both woodland types. The study was
37 carried out in the Chaco Serrano woodlands of Córdoba, central Argentina. Our main
38 results indicate differences in *L. lucidum* woodland composition and a reduction in both
39 richness and total density of species in the soil seed bank compared to the native
40 woodlands, independently of the sampling season. Moreover, a higher abundance of
41 certain exotic species in the soil seed bank was observed in *L. lucidum* woodlands,
42 particularly in spring. Finally, low similarity between soil seed bank and the established
43 vegetation was observed in both woodland types. From a management perspective, it
44 seems that passive restoration from soil seed banks of *L. lucidum* might be coupled with
45 active addition of some native woody species and control of other exotic species.

46

47 **Keywords:** alien species - exotic species – invaded soil seed banks –soil seed bank-
48 vegetation relationship- species composition- woody invasion

49

50 **Introduction**

51 The impact of invasive species on below ground flora –e.g., seeds and fungi–
52 may differ from that on the above ground vegetation, due to different interactions
53 between biotic and abiotic factors (Gioria et al. 2014). The soil seed bank, a key strategy
54 for ecosystem resilience, plays a central role in the persistence of plant populations in
55 highly variable and disturbed environments (Frieswyk and Zedler 2006; Scott et al. 2010;
56 Gioria et al. 2012 and references there in). The soil seed banks of invaded communities
57 are strongly indicative of the long-term implications of plant invasions (e.g., persistence
58 of the invader within the community through its own soil seed bank, facilitation of the
59 presence of other exotic species) and the capacity of the resident community to buffer
60 against the full or partial displacement of resident species (biotic resistance) (Gioria et al.
61 2014). In addition, having information about the soil seed bank thus lead toward different
62 management strategies (Dremann and Shaw 2002; D' Antonio and Meyerson 2002;

63 Skowronek et al. 2014); for example different approaches must be applied if the soil seed
64 bank of an invaded community is mostly composed by exotic species or if it is composed
65 mainly by natives.

66 Exotic species can modify soil seed bank composition directly, through their own
67 seeds contribution, and indirectly, either by creating different microhabitats under their
68 canopy (e.g., modifying seed viability through changes in light and nutrient levels;
69 Giantomasi et al. 2008; Gioria and Osborne 2009a; González-Muñoz et al. 2012), or by
70 altering the communities of dispersers, predators or decomposers (Ayup et al. 2014;
71 Furey et al. 2014). Recent reviews concerning the role of soil seed banks in invaded and
72 native communities emphasize the need for more comprehensive information about the
73 impacts of plant invasion on soil seed banks in order to understand long-term implications
74 of plant invasions (Gioria et al. 2012, 2014). So far, studies on soil seed bank have shown
75 that invasion by exotic species with structural dominance, such as trees and shrubs, result
76 in lower species richness and density, and differences in species composition (Holmes
77 and Cowling 1997; Holmes 2002; Mason et al. 2007; Marchante et al. 2011; Gioria et al.
78 2014). Moreover, the changes induced by exotic species in the community could facilitate
79 the arrival of new exotic species to the invaded community (Giantomasi et al. 2008;
80 González-Muñoz et al. 2012), an effect currently named ‘invasional meltdown’ (*sensu*
81 Simberloff and Von Holle 1999; Simberloff 2006). Accordingly, invaded communities
82 have been found to have a higher richness and/or abundance of seeds of exotic species
83 (Gioria et al. 2012; González-Muñoz et al. 2012).

84 Soil seed bank characteristics in native and invaded communities are generally
85 recorded at a single time of the year (Holmes and Cowling 1997; Mason et al. 2007;
86 Giantomasi et al. 2008; Marchante et al. 2011; Gonzalez-Muñoz et al. 2012; Skowronek
87 et al. 2014; Kundel et al. 2014; Tererai et al. 2014; but see Gioria and Osborne 2009a,
88 2010). However, composition, richness or density of species in the soil seed bank could
89 vary at different times of the year (Gioria and Osborne 2010), particularly in areas with
90 seasonal climates, where native species dispersal peak generally occurs at the end of the
91 rainy season (Fenner 1998; Li et al. 2012) and many exotic species show phenological
92 segregation from natives (Godoy et al. 2009; Wolkovich and Cleland 2010). Finally, most
93 studies describe an overall low similarity between the aboveground vegetation and the
94 soil seed banks both in native and invaded communities (Holmes and Cowling 1997;
95 Mason et al. 2007; Giantomasi et al. 2008; Gioria and Osborne 2009a; Skowronek et al.
96 2014; but see González-Muñoz et al. 2012). Such low similarity might be given by the
97 predominance of annuals in soil seed banks, whereas perennial species dominate the
98 aboveground vegetation (Meers et al. 2012 and references therein). Indeed, the fact that
99 contrasting growth forms characterize the above and belowground vegetation has been

100 described both in native and invaded communities (Vilá and Gimeno 2007; Vosse et al.
101 2008). Therefore, studies on soil seed banks in invaded ecosystems and the relationship
102 between soil seed banks and the established vegetation, considering two different seasons
103 and accounting for plant growth forms, may improve our understanding of the effect of
104 invasive species on seed banks.

105 Previous studies on soil seed bank that compare sites invaded by woody species
106 with areas dominated by natives have been performed mostly in fynbos or riparian areas
107 of South Africa (Holmes and Cowling 1997; Holmes 2002; Gaertner et al. 2011; Tererai
108 et al. 2014) and in European dunes and woodlands (Marchante et al. 2011; González-
109 Muñoz et al. 2012; Skowronek et al. 2014). This information, however, is very scarce for
110 subtropical woodlands, particularly in South America (but see Giantomasi et al. 2008). In
111 the mountain Chaco Serrano Woodlands of Córdoba (central Argentina) the Asiatic tree
112 *Ligustrum lucidum* W. T. Aiton is widely spread, forming extensive mono-specific
113 woodlands (i.e., with more than 80% of the vegetation cover), where it grows together
114 with several exotic species (Hoyos et al. 2010; Giorgis et al. 2011; Gavier-Pizarro et al.
115 2012). The dispersal peak of *L. lucidum* in this system occurs during the dry winters,
116 unlike most native species, which disperse in the warm and rainy season (Gurvich et al.
117 2005; Ferreras et al. 2008; Tecco et al. 2013). Several studies have assessed the
118 ecological strategies underlying the success of this invader, both in Argentina and other
119 parts of the world (Lichstein et al. 2004; Tecco et al. 2006, 2007; Ferreras et al. 2008;
120 Long et al. 2009; Aslan et al. 2012; Aguirre-Acosta et al. 2014; Aragón et al. 2014; Ayup
121 et al. 2014). However, to our knowledge there is no information on the impact of this
122 invader on the soil seed bank of invaded communities. Here, we aim to answer the
123 following questions: (1) Are *L. lucidum* woodlands modifying soil seed bank composition
124 and reducing seed richness and total density as compared to the native woodlands? Could
125 the same pattern be observed if samples are taken in autumn or spring? (2) Is there a trend
126 towards higher exotic seed richness, total density or differences in exotic species
127 composition in the soil seed banks of *L. lucidum* woodland than in native woodlands? (3)
128 Does the similarity between the soil seed bank and the established vegetation differ
129 between native and *L. lucidum* woodlands?

130 We hypothesize that in a subtropical ecosystem with dry winters the structural
131 dominance of the invasive tree *L. lucidum* is associated to differential soil seed bank
132 characteristics compared to the native soil seed banks. In particular, we expect differences
133 in species composition, lower seed density and richness in soil seed banks of *L. lucidum*
134 woodlands. Moreover, as many exotic species can show phenological segregation from
135 natives in this and other seasonal regions (e.g. Tecco et al 2013, Godoy et al. 2009;
136 Wolkovich and Cleland 2010) those seed banks differences might vary with seasons. In

137 addition, and given previous evidence on facilitation among exotic species in invaded
138 woodlands (Simberloff and Von Holle 1999; Simberloff 2006) we predict higher richness
139 and abundance of exotic species in soil seed banks of *L. lucidum* than in those of native
140 woodlands. Finally, as in most woody systems, we expect to find an overall low
141 similarity between soil seed banks and standing vegetation in both woodlands.

142

143 **Methods**

144

145 ***Study area and nature of L. lucidum invasion in the region***

146 The study was conducted in the Chaco Serrano woodlands, near the cities of Río
147 Ceballos and Salsipuedes, Córdoba, central Argentina. Mean annual precipitation in the
148 area is 885 mm (ranging from 635 to 1129 mm) with most rainfall concentrated in the
149 warmest months, from October to April (Casco and Lado unpublished data). Mean
150 temperature is 22° C in summer and 9° C in winter (De Fina 1992). Potential natural
151 vegetation in the area is a low xerophytic woodland (Luti et al. 1979), but the original
152 cover has been converted into a mosaic of open woodlands, shrublands and grasslands due
153 to the expansion of human settlement, agriculture, logging, and burning (Gavier and
154 Bucher 2004). In addition to the changes in vegetation, more than 16% of tree and shrub
155 species of the Chaco Serrano Woodland of Córdoba (28 of 171) are exotics, with the most
156 common being (in order of decreasing frequency): *Gleditsia triacanthos*, *Ligustrum*
157 *lucidum*, *Morus alba*, *Pyracantha angustifolia*, *Pinus elliotii*, *Melia azedarach*, *Ulmus*
158 *pumila* and *Cotoneaster franchetii* (Giorgis et al. 2011).

159 *Ligustrum lucidum*, Oleaceae ("glossy privet"), is an ornamental evergreen and
160 shade-tolerant Chinese tree, with bird-dispersed fleshy-fruits, that invades woodlands and
161 grasslands in southern South America (Montaldo 1993; Mazia et al. 2001; Lichstein et al.
162 2004; Hoyos et al 2010; Gavier-Pizarro et al 2012) and other regions of the world
163 (Richardson and Rejmánek 2011). In the Chaco Serrano Woodland of Córdoba, *L. lucidum*
164 was introduced at the beginning of the 20th century as an ornamental tree (Hoyos et al.
165 2010; Giorgis et al. 2011) and has spread exponentially since then, occupying 12% of the
166 forested area in 2001 and 20% in 2006 (Hoyos et al. 2010; Gavier-Pizarro et al. 2012). The
167 dispersal period of *L. lucidum* in low mountain Chaco woodlands range from May to the
168 end of September (Ferrerías et al. 2008), unlike most native species, which disperse in the
169 warm and rainy season, mostly from November to April (Gurvich et al. 2005; Tecco et al.
170 2013). *L. lucidum* displays a profuse fruit production (Ferrerías et al. 2008) that may
171 constitute a highly important mechanism for the species expansion and persistence. In
172 addition, it also has sprouting capacity (Lichstein et al. 2004) which may difficult the
173 management of this species.

174

175 ***Experimental design***

176 In 2012, 12 sites were selected within the study area, half of them corresponding to
177 native woodlands (located in areas defined by the following coordinates 31°7'9.4'' to
178 31°10'37.2'' S and 64°17'8.8'' to 64°20'29.1'' W). The other six sites were woodlands
179 dominated by *L. lucidum* (hereafter exotic woodlands), with more than 80% cover of *L.*
180 *lucidum* (Supplementary material Table 1) (the exotic woodlands were distributed in an
181 area compromised by the coordinates 31°7'10.4'' to 31°10'38.3'' S and 64°17'19.1'' to
182 64°20'18.4'' W). The native and *L. lucidum* woodlands were within the same altitudinal
183 strip (730 to 930 m a.s.l). The soils are all entisols (Cioccale 1999) and the soil depth was
184 in a range of 5 to 20 cm. In addition, the sites of both woodlands types have a gentle slope
185 (from 2 to 20 %) and low livestock density. At each site, a 20 x 20 m sample plot was
186 established, where soil seed bank samples were extracted and established vegetation was
187 characterized in terms of floristic composition.

188

189 ***Soil seed bank sampling and greenhouse experiment***

190 Characterization of the soil seed bank involved two sampling dates at different points in
191 time. The first sampling was conducted in autumn (May 2012), which is the end of the
192 dispersal period of most native species and coincides with the end of the rainy season. The
193 second sampling was performed in spring (November 2012), which is nearly 45 days after
194 the end of the dispersal period of *L. lucidum*. This second sampling date ensured that most
195 *L. lucidum* seeds were in the soil and coincided with the beginning of the rainy season.

196 Six soil seed bank samples were taken from each 20 x 20 m plot (totaling 72 samples
197 for each sampling date) on each sampling date. Each sample was taken with a soil core of
198 10 cm in diameter and comprised the first 5 cm of the soil, including the litter layer. The
199 upper 5-cm soil depth is where most of the viable seeds accumulate (Giantomasi et al. 2008
200 and references therein; Buonopane et al. 2013).

201 Once collected, soil samples were sieved through a mesh (0.5 x 0.5 cm) to remove plant
202 fragments and stones. The samples were stored in a cold room at 5°C during a month
203 because species in this area may need cold stratification for breaking seed dormancy
204 (Baskin and Baskin 1998; Giantomasi et al. 2008). Soil samples were then spread over 2
205 cm of sterilized sand in plastic trays (20 x 25 cm) (Funes et al. 2001) and placed randomly
206 in a greenhouse at an average temperature of 25 °C. Trays were kept moist using an
207 irrigator system and randomized every 15 days. In addition, trays were stirred several times
208 during the experiment to promote seed germination. Six trays containing only sterilized
209 sand were also included to evaluate possible seed contamination within the greenhouse
210 (Giantomasi et al. 2008; Marchante et al. 2011). For samples collected on both sampling

211 dates, seedling emergence was recorded weekly for one year, identifying and counting the
212 number of emerged seedlings. If necessary, seedlings were transplanted for correct
213 identification.

214

215 *Vegetation survey*

216 Vegetation surveys to evaluate composition, species richness and abundance were
217 conducted in each plot within each woodland type in February 2013. Percentage cover of
218 all vascular species was recorded using a scale starting from 0.05 (less than 1%), 1, 2, 3, 5,
219 8, and 10 and, from there, incrementing every 5 % up to 100 %. This survey could not be
220 performed in 2 of 12 sites: one of the native sites was logged and vegetation in one of the
221 exotic sites was damaged due to a hail storm. The soil seed bank and the established
222 vegetation were compared considering species abundance, richness, and abundance of
223 species within each growth form (i.e., tree, shrub, climber, forb and grass).

224 Nomenclature of plant species follows the «Catálogo de las Plantas Vasculares del
225 Cono Sur» (Zuloaga et al. 2008) and their update «on line» (www.darwin.edu.ar). Species
226 were classified as native or exotic as well as by the different growth forms based on
227 Zuloaga et al. (2008) and Giorgis et al. (2011).

228

229 *Data analysis*

230 We used a combination of statistical procedures that have been found to be most
231 appropriate in recent assessments of patterns in soil seed bank data (Gioria and Osborne
232 2009ab, 2010; Skowronek et al. 2014; Tererai et al. 2014). Richness and density of species
233 in the soil seed bank (total, native and exotic) in both sampling seasons were compared
234 using generalized linear models in Infostat (Di Rienzo et al. 2013) and its interface to R (R
235 2.15.0, R development core team 2012). Seedling density was analyzed as a function of
236 “Woodland type” (exotic/native woodlands). A Poisson error structure was used with a log
237 link function for total, native and exotic richness in autumn. For the rest of the response
238 variables a quasi-Poisson error structure was used due to over-dispersion.

239 A Permutational Multivariate Analysis of Variance (PERMANOVA, Anderson 2001)
240 was used to quantify the differences in species composition between the soil seed banks of
241 both types of woodlands in each sampling season, both for the whole pool of species, and
242 for natives, exotics and woody exotics separately. The advantages of this method over
243 traditional parametric methods of multivariate data analysis is that it provides a direct
244 additive partitioning of variation as in traditional linear models, while maintaining the
245 flexibility and lack of formal assumptions of non-parametric methods (Gioria and Osborne
246 2010). The test was performed using 9999 permutations and Bray-Curtis was used as
247 distance measures. Similarity Percentage Analysis (SIMPER, Clarke 1993) based on Bray-

248 Curtis similarity (Clarke 1993) was used to identify the species that most contributed to the
249 average dissimilarity between exotic and native woodlands. This procedure computes the
250 average contribution of each species to the overall dissimilarity between two groups
251 (Gioria and Osborne 2010; Skowronek et al. 2014). Non-metrical Multidimensional
252 Scaling (NMDS) was used as an ordination method to visualize multivariate pattern in the
253 data of soil seed bank and the established vegetation (Gioria and Osborne 2009a). NMDS
254 was performed based on Bray Curtis similarity measure. For PERMANOVA, SIMPER and
255 NMDS the density of seeds was square-root transformed in order to reduce the contribution
256 of the most abundant species to differences between groups. These analyses were
257 performed using PAST 2.1 (Hammer et al. 2001).

258 Sørensen coefficient index was used for comparing the species in the soil seed bank and
259 the established vegetation within each study site (Skowronek et al. 2014). The indices were
260 statically compared through a Mann Whitney analysis performed in Infostat (Di Rienzo et
261 al. 2013). In addition, we performed Spearman correlations to detect the similarities
262 between soil seed banks and the established vegetation of each study site, but considering
263 the abundance or cover of species, (i.e., seedling density in the soil seed bank vs. cover of
264 established vegetation). The correlations were performed in PAST 2.1 (Hammer et al.
265 2001). Finally, differences among growth forms in soil seed banks of both woodland types
266 in each study season were analyzed with generalized lineal models. The density of
267 seedlings was analyzed as a function of “Growth forms”. A Poisson error structure was
268 used with a log link function, but a quasi-Poisson error structure was used due to over-
269 dispersion in the response variables. Percentage of vegetation cover was analyzed with a
270 general linear model; however, as the data showed heterocedasticity of variance, it was
271 modeled by applying the variance function of identity (VarIdent in Infostat; Reyna and
272 Wall 2014). Fisher least significant difference (LSD) was used as a posteriori test. The
273 GLMs were performed in Infostat (Di Rienzo et al. 2013) and its interface to R (R 2.15.0,
274 R development core team 2012). In all the analyses, differences were considered significant
275 at $p < 0.05$.

276

277 **Results:**

278

279 ***Soil seed banks***

280 A total of 159 species (29 exotic and 130 native species) were found in the soil seed
281 banks of both woodland types. Among them, 107 and 110 species were found in the soil
282 seed banks of the native woodlands and 68 and 77 species were found in the soil seed
283 banks of the exotic woodlands in autumn and spring, respectively. Soil seed banks of both
284 woodland types shared 53 species in autumn and 58 in spring. There was a high proportion

285 of exotic species among the 10 most abundant species in the exotic woodland soil seed
286 banks (Table 1). This was particularly evident in the sampling performed in spring, in
287 which seven of the 10 most abundant species were exotic (Table 1; see the complete list of
288 species and their abundances in Supplementary material Table 1).

289

290 *Soil seed bank richness and abundances*

291 Soil seed banks of native woodlands showed significantly higher total richness and
292 seed density than exotic woodlands, both in autumn and spring (Fig. 1). The same pattern
293 was observed in the analysis including only native species (Fig. 1). The analysis that
294 included only exotic species showed non-significant differences in seedling density and
295 richness in the soil seed bank between woodlands types (Fig. 1).

296

297 *Species composition in the soil seed bank*

298 Species composition and relative abundance of the soil seed banks of the exotic
299 woodlands differed from that of the native woodlands (Fig. 2), mostly in autumn. In
300 addition, higher dispersion among soil seed banks of native woodlands –i.e., higher
301 dispersion on coordinate 1- in relation to *L. lucidum* woodlands was observed in both
302 seasons, although more pronounced in autumn. PERMANOVA showed that species
303 composition and relative abundance differed significantly both in autumn ($F=2.27$, $p=0.01$)
304 and in spring ($F=2.02$, $p=0.02$). Accordingly, SIMPER analysis showed a high average
305 dissimilarity between exotic and native woodland soil seed banks both in autumn and
306 spring (70.3 % in both seasons; Table 2). In autumn, coinciding with the end of the
307 dispersal period of most native species, mainly native species (with the exception of
308 *Duchesnea indica*) made the greatest contribution to the differentiation between soil seed
309 banks of both woodland types. In spring, and in coincidence with the end of the dispersion
310 of most exotic species, more than half of the species that showed the higher contribution to
311 dissimilarities between soil seed banks types were exotic (Table 2).

312 PERMANOVA showed a similar result between both types of soil seed banks when
313 the analysis included only native species, indicating that native and exotic woodlands
314 differed in the composition of native species within their soil seed banks. This pattern was
315 statistically significant in autumn ($F=2.47$, $p=0.004$) and marginally significant in spring
316 ($F=1.64$, $p=0.07$).

317 The comparison of the composition of exotic species in the soil seed banks between
318 types of woodland (i.e., PERMANOVA analysis performed only with exotic species)
319 showed non-significant differences in autumn ($F=1.41$, $p=0.13$) but it did show significant
320 results in spring ($F=1.99$, $p=0.01$). Differences in soil seed bank composition of exotic
321 species between woodland types was significant in both seasons, when only woody species

322 were considered (PERMANOVA, $F=4.47$; $p=0.009$; $F=2.07$; $p=0.01$ for autumn and
323 spring, respectively).

324

325 ***Relationships between soil seed bank and established vegetation***

326 A clear differentiation in composition and relative abundance of species in the
327 established vegetation of both woodland types was observed (NMDS; Supplementary
328 material Fig 1). The Sørensen coefficients of similarity between the soil seed banks and the
329 established vegetation were low in both woodland types, regardless of the sampling season
330 (Table 3). However, there was a marginally significant tendency of higher similarity in the
331 native woodlands in relation to the exotic ones in the autumn sampling. Correlations
332 between seedling density in the soil seed banks and the established vegetation cover
333 showed low r values in all sites of each woodland type, although most of them were
334 significant (Supplementary material Table 2).

335 The established vegetation of the native woodlands was mainly composed of trees,
336 shrubs and graminoids, whereas that of the exotic woodlands was dominated by trees (Fig.
337 3a). The relative importance (mean density) of growth forms within the soil seed bank was
338 similar in both seasons in the native woodland. The native soil seed bank showed a similar
339 pattern to that of the established vegetation (except for trees), with a dominance of
340 graminoids followed by forbs and to a lesser degree by shrubs (Fig. 3b, c). In the exotic
341 woodland, the dominance of growth forms in the soil seed banks differed between
342 sampling seasons (Fig 2b, c). Density of forbs and grasses was similarly important in both
343 seasons but dominance of trees was higher in spring (i.e., November, end of dispersal of
344 many exotic species). The dominance of trees in the exotic soil seed bank in spring (170.71
345 ± 240.11 seeds per m^2) matched the overall dominance of trees in the established
346 vegetation of the exotic woodlands (Figure 2a).

347

348 **Discussion**

349 Soil seed bank is strongly related to the long-term implications of plant invasions
350 and the biotic resistance of native communities (Gioria et al. 2014). *Ligustrum lucidum* is
351 recorded as woody invader in several regions of the world (Richardson and Rejmánek
352 2011). In this study we focused on the impact of this species in the soil seed banks when
353 invading subtropical woodlands with dry winters. In accordance with our hypothesis, we
354 found that woodlands dominated by *L. lucidum* show differences in floristic composition
355 and lower richness and total density of species in the soil seed bank as compared to the
356 native woodlands, independently of the sampling season. This suggests that the overall
357 impact of the invasion in this system is similar to the patterns described for other invasive
358 species in contrasting ecosystems of the world such as Fynbos, riparian or coastal

359 ecosystem (Holmes and Cowling 1997; Vosse et al. 2008; Gioria and Osborne 2009a,
360 2010; González-Muñoz et al. 2012). In this study, although exotic richness and density
361 was not higher in the invaded community as expected, certain exotic species with high
362 invasive potential did show a higher abundance within soil seed banks of *L. lucidum*
363 woodlands, particularly in spring. This finding highlights the relevance of evaluating soil
364 seed bank characteristics at least in two different seasons, an approach which is not
365 commonly found in soil seed banks studies comparing native and invaded areas (but see
366 Gioria and Osborne 2009a; 2010). Finally, as expected, low similarity between soil seed
367 bank and the established vegetation was observed in both woodland types.

368

369 ***Impoverishment of soil seed bank in exotic woodlands in two sampling seasons***

370 The soil seed banks of woodlands dominated by *L. lucidum* showed a lower total
371 seed density and richness, as well as differences in species composition compared to
372 native woodlands. Previous studies comparing native and exotic soil seed banks reported
373 similar patterns to those described here (Holmes and Cowling 1997; Vosse et al. 2008;
374 Gioria and Osborne 2009a, 2010; González-Muñoz et al. 2012; Gioria et al. 2014; but see
375 Kundel et al. 2014). Lower bird diversity in relation to native forest has been described in
376 other areas invaded by *L. lucidum* in Argentina (Ayup et al. 2014). This suggests that a
377 lower number of bird dispersers could be entering *L. lucidum* communities and, in turn,
378 could partly explain the reduction in plant species richness and density in the soil seed
379 bank observed in our study. In addition, changes in vegetation structure imposed by this
380 species, which translate in reduced light availability (Hoyos et al. 2010), and high litter
381 production (Furey et al. 2014), could be related to the pattern observed in our study.
382 Indeed, both light reduction and litter accumulation have been suggested as responsible
383 for the depletion of the soil seed banks in areas invaded by other exotic species (Gioria
384 and Osborne 2010; González-Muñoz et al. 2012).

385 The identity of the most abundant species differed between woodland types, with
386 many exotic species dominating the soil seed bank of the exotic woodland, particularly in
387 spring (Table 1). Moreover, in spring, exotic species were highly important for
388 distinguishing both types of communities (Table 2). In addition, three of the most
389 abundant exotic species, apart from *L. lucidum*, were present in both sampling seasons,
390 suggesting a high persistence of those exotic seeds in the soil of *L. lucidum* woodlands
391 (Thompson and Grime 1979). Even though, *L. lucidum* seeds were present in the exotic
392 seed bank in both seasons, its density was notably higher after its dispersal in spring
393 (November). This is congruent with a previous study that shows that seeds of this species
394 have a low persistence in the soil (Long et al. 2009). In future studies it would be

395 interesting to include different soil layers which could provide a clearest scenario about
396 the persistence of native and exotic seeds within those types of soil seed banks.

397 Native species seem to be driving the main differences in composition between
398 woodlands throughout the year, whereas exotic species might add further differences in
399 spring. Accordingly, when native species were considered separately in the analysis,
400 differences among woodland soil seed banks persisted in both seasons. However, in both
401 woodland types, higher seed density of native species was observed in autumn (May)
402 (Fig. 1). This trend is consistent with the dispersal timing of native species in the region.
403 Indeed, because the dispersal period of most natives ends in autumn, a lower amount of
404 native seeds is expected in the soil in spring, particularly due to a depletion of species
405 with transient seeds. In addition, the differences obtained in spring may be influenced by
406 certain exotic species, whose relative abundance in *L. lucidum* woodlands was notably
407 high in that season—e.g., *Morus alba*, *Duschesnea indica*. This is partly due to the
408 coincidence of *L. lucidum* dispersal with the dispersal of other woody exotic species in
409 the area (Tecco et al. 2013), and probably other non-woody exotic species whose
410 phenology in the area has still not been thoroughly studied.

411

412 ***Exotics in L. lucidum soil seed bank: invasional meltdown or invasional***
413 ***interference?***

414 There is growing evidence suggesting that some established invaders enhance the
415 arrival of other exotic species into the invaded community (Simberloff and Von Holle
416 1999; Richardson et al. 2000; Simberloff 2006). Some studies have suggested this
417 facilitation in soil seed banks of invaded communities (Marchante et al. 2011; González-
418 Muñoz et al. 2012; Gioria et al. 2014). In our study, *L. lucidum* woodlands did not
419 differed from natives woodlands in either the total richness or the density of exotic
420 species within their soil seed bank. However, some differences were observed in the
421 composition of exotic species, particularly in spring (November) where a higher
422 abundance of certain exotic species could be observed (Table 1). Some exotic woody
423 species, which commonly act as drivers of mayor changes in the invasion process
424 (Crooks 2002; Skowronek et al. 2014), were found in high abundance in the soil seed
425 banks of the exotic woodlands in both seasons. In particular, the high abundance of the
426 invasive tree *Morus alba* warns about the potential direction of community regeneration
427 from the soil seed bank in *L. lucidum* woodlands. All in all, these results suggest that *L.*
428 *lucidum* could be exerting some kind of facilitation over certain exotic seeds, like *M. alba*
429 and *D. indica*, which is in line with the “invasional meltdown” hypothesis (Simberloff
430 and Von Holle 1999; Richardson et al. 2000; Simberloff 2006). However, the low cover
431 of those exotic species in the established vegetation of exotic woodlands suggests that

432 some factors may hinder seed germination and establishment (Supplementary material
433 Table 1). The later pattern could be interpreted as an “invasional interference”, acting at
434 the recruitment phase between those exotics seeds and *L. lucidum* (Yang et al. 2011;
435 Rauschert and Shea 2012; Kuebbing and Nuñez 2014). Specific experimental approaches
436 would be necessary to test these hypotheses and the underlying mechanisms.

437

438 ***Relationship between the soil seed banks and the established vegetation***

439 Our results are in agreement with studies reporting low similarity indices between
440 soil seed bank and established vegetation in forest areas (Hopfensperger 2007) as well as
441 with studies comparing soil seed banks in native and invaded areas (Mason et al. 2007;
442 Giantomasi et al. 2008; Gioria and Osborne 2009a; Skowronek et al. 2014). Moreover,
443 low correlation coefficients were found between seedling abundance and vegetation cover
444 of the established community. However, we found a trend towards higher similarity
445 between the soil seed bank and the established vegetation of native woodlands in autumn
446 in relation to woodlands dominated by *L. lucidum*. In our study, this might be explained
447 by the fact that autumn coincides with the end of the dispersal period of most of the
448 native species. In exotic woodlands, with the exception of *L. lucidum*, most species found
449 in the soil seed bank, even those that were abundant (many of them exotics), were rare in
450 the established vegetation (Supplementary material Table 1).

451 The species present in the soil seed banks of both woodland types had different
452 growth forms, with this difference being stressed in spring (Fig. 3 b,c). In the soil seed
453 banks of the exotic woodlands, species belonging to all growth forms were present. Trees
454 prevailed over the other forms, particularly in autumn, whereas in spring, forbs and
455 grasses were also abundant. These findings together with the great dominance of trees in
456 the standing vegetation (Fig. 3a), mainly *L. lucidum* (Supplementary material Table 1),
457 suggest that this invader is hindering germination or establishment of other growth forms.
458 On the other hand, a lower representation of dominant woody species was observed in the
459 soil seed bank of native woodlands in relation to the established vegetation, in both
460 seasons (e.g., *Acacia caven*, *Celtis ehrenbergiana*, *Condalia buxifolia*, *Xanthophillum*
461 *coco*, *Lithraea molleoides*), which is in line with previous findings in the study area
462 (Giantomasi et al. 2008). These results warn that if a disturbance occurred, those native
463 woody species might have low possibilities of regeneration from the soil seed bank. A
464 reduced canopy cover could thus be expected, which probably facilitates future invasion
465 events (Mason et al. 2007). However, we cannot discard the possibility that germination
466 requirements for some species may not have been met in the greenhouse, which may
467 explain the absence of seedlings from those species (Marchante et al. 2011) or that the

468 number of samples per replicate was scarce to detect woody species in the native
469 woodland (Sheng et al. 2014).

470

471 ***Final remarks and management implications***

472 In invaded woodlands, resilient ecosystems are feasible to be restored passively if
473 their soil seed banks resemble their native vegetation and have a high richness and
474 density of seeds (Frieswyk and Zedler 2006). In our study, soil seed banks of *L. lucidum*
475 woodlands presented a lower abundance of native species and a higher abundance of
476 certain exotic species than the soil seed banks of native woodlands. Then, if a
477 management strategy is to be performed (e.g., removing adults) careful monitoring of
478 new exotic recruitment has to be considered because those managed exotic communities
479 could easily change into a new invaded area (Mason et al. 2007). Despite the lower
480 richness and abundance in *L. lucidum* soil seed bank, several native species were found at
481 both sampling times, suggesting that soil-stored seed banks still offer a potential for
482 driving regeneration of part of the native plant community (Tererai et al. 2014).
483 Nevertheless, some key native woody species need to be actively added to the system,
484 which is a common practice in many other ecosystems in which restoration from the soil
485 seed bank is considered (Mason et al. 2007; González-Muñoz et al. 2012).

486 On the other hand, we found some exotic species in the soil seed bank of the
487 native woodlands. Those seeds may exist as soil seed bank “sleeper cells”, waiting for
488 proper conditions to begin an invasion process (Fisher et al. 2009). So, while native cover
489 remains intact, introduced species could have difficulties in germinating and/or
490 establishment, but the occurrence of disturbances might facilitate the expression of their
491 invasive capacity (Fisher et al. 2009). In this respect, it is important to consider that *L.*
492 *lucidum* forms important seedling banks and its adults have resprouting capacity, both of
493 which could further aid the species’ regeneration and recovery in this invaded woodland
494 after a disturbance event (Lichstein et al. 2004).

495 The end of the native dispersal period, in autumn, seems to be a suitable time to
496 perform a management strategy in the exotic woodlands due to a lower abundance of
497 exotic species in their soil seed banks. However, a thorough study of seed dispersal is
498 necessary in order to have a clearer scenario of what seeds arrive to the exotic
499 communities in each month. In addition, as previous studies suggested that ecosystem
500 functions (e.g., soil nutrient cycling, water flow) may be modified with invasion
501 (Gaertner et al. 2011; González-Muñoz et al. 2012; Aragón et al. 2014; Furey et al. 2014),
502 it is necessary to perform ecosystem studies in order to determine the feasibility of
503 restoration and the strategies that may be needed.

504

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510

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700

701 **Figures Captions**

702 **Fig. 1** Species richness and density (seedling per m²) within the seed banks of the exotic *L. lucidum*
703 woodlands and the native Chaco Serrano woodlands of Córdoba, Argentina. Means (\pm standard
704 deviations) of richness and seed density for the two sampling periods of autumn (May) and spring
705 (November) are provided for all species recorded in the community (a and d) as well as for native (b
706 and e) and exotic species (c and f). p values are provided when significant differences between native
707 (n=6) and exotic *L. lucidum* woodlands (n=6) were found. Black bars: *L. lucidum* woodlands and white
708 bars: native woodlands.

709

710 **Fig. 2** Non-metrical Multidimensional Scaling (NMDS) on species composition and relative
711 abundances within the seed bank of exotic (*L. lucidum*) woodlands and native woodlands of the Chaco
712 Serrano of Córdoba, Argentina. NMDS were performed for the seed bank communities sampled in (a)
713 autumn (stress value = 0.19) and (b) spring (stress value = 0.15). Black symbols= exotic woodlands;
714 White symbols= native woodlands.

715

716 **Fig. 3** Representation of the different growth forms in the established vegetation (a), in the seed banks
717 sampled in autumn (b) and in spring (c) in native and exotic woodlands. Black bars: *L. lucidum*
718 woodlands and white bars: native woodlands. Different letters indicate significant differences among
719 growth forms within each woodland type (Fisher least significant difference (LSD)); capital letters
720 indicate differences among growth forms within *L. lucidum* woodlands, lowercase letter indicate
721 differences among growth forms within native woodlands.

722

Table 1 Most abundant species in the soil seed banks of the exotic *L. lucidum* woodlands and the native Chaco Serrano woodlands of Córdoba, Argentina. Species density per m² is provided for the sampling in autumn (May) and spring (November). Species are ordered by their abundances and exotic species are highlighted in bold. Species growth form is indicated as T (trees), S (shrub), AG (annual grasses), PG (perennial grasses), AF (annual forb), PF (perennial forb). Species that are shared by both seed bank types are indicated with an *.

Exotic woodlands	Growth form	Density per m2	Native woodlands	Growth form	Density per m2
Autumn					
<i>Oxalis conorrhiza</i> *	PF	671.43	<i>Cyperus incomtus</i> *	PG	2350
<i>Cyperus incomtus</i> *	PG	646.43	<i>Gamochaeta calviceps</i> *	AF/PF	1532.14
<i>Gamochaeta calviceps</i> *	PF/AF	357.14	<i>Baccharis glutinosa</i>	AF	1196.43
<i>Duschesnea indica</i>	PF	346.43	<i>Digitaria ciliaris</i>	AG	717.86
<i>Eustachys retusa</i>	PG	253.57	<i>Exhalimolobos weddellii</i>	PF	632.14
<i>Oplismenus hirtellus</i>	PG	185.71	<i>Oxalis conorrhiza</i> *	PF	607.14
<i>Leonurus japonicus</i>	AF	128.57	<i>Cyperus aggregatus</i>	PG	596.43
<i>Ligustrum lucidum</i>	T	92.86	<i>Eragrostis mexicana</i>	AG	425
<i>Triodanis perfoliata</i>	AF	85.71	<i>Lepidium bonaerensis</i>	AF	371.43
<i>Morus alba</i>	T	78.57	<i>Chromolaena hookeriana</i>	S	332.14
Spring					
<i>Cyperus incomtus</i> *	PG	889.29	<i>Cyperus incomtus</i> *	PG	3989.29
<i>Duschesnea indica</i>	PF	675	<i>Gamochaeta calviceps</i> *	AF/PF	1467.86
<i>Morus alba</i>	T	625	<i>Fleischmannia prasiifoli</i>	PF	603.57
<i>Gamochaeta calviceps</i> *	AF/PF	250	<i>Baccharis glutinosa</i>	PF	417.86
<i>Talinum paniculatum</i>	PF	228.57	<i>Lepidium bonaerensis</i>	AF	360.71
<i>Ligustrum lucidum</i>	T	207.14	<i>Exhalimolobos weddellii</i>	PF	317.86
<i>Chenopodium album</i>	AF	103.57	<i>Iresine diffusa</i>	PF	235.71
<i>Sonchus asper</i>	AF	92.86	<i>Oxalis conorrhiza</i>	PF	225
<i>Leonurus japonicus</i>	AF	67.86	<i>Cantinoa mutabilis</i>	PF	207.14
<i>Conyza bonariensis</i>	PF	64.29	<i>Eragrostis mexicana</i>	AG	178.57

Table 2 Species that showed the highest contribution to dissimilarities between native and *L. lucidum* soil seed bank in autumn (May) and spring (November) (SIMPER results; 25 % of cumulative contribution is shown). Species are ordered by their contribution within each sampling season. Mean density of *L. lucidum* and native woodlands is provided. Exotic species are highlighted in bold.

Sampling season	Species	Contribution	Cumulative Contribution	Mean density of seeds in <i>L. lucidum</i> soil seed bank*	Mean density of seeds in native soil seed bank*
Autumn	<i>Cyperus incommutus</i>	3.53	5.02	646.43	2350
	<i>Gamochaeta calviceps</i>	2.40	8.43	357.14	1532.14
	<i>Chromolaena hookeriana</i>	1.92	11.16	7.14	332.14
	<i>Duchesnea indica</i>	1.9	13.86	346.43	92.86
	<i>Lorentzianthus viscidus</i>	1.84	16.48	7.14	278.57
	<i>Exhalimolobos weddellii</i>	1.79	19.03	0	632.14
	<i>Digitaria ciliaris</i>	1.79	21.56	17.86	717.86
	<i>Baccharis glutinosa</i>	1.66	23.92	3.57	1196.43
Spring	<i>Cyperus incommutus</i>	4.28	6.09	889.29	3989.29
	<i>Duchesnea indica</i>	2.78	10.04	675	78.57
	<i>Fleischmannia prasiifoli</i>	2.23	13.21	7.14	603.57
	<i>Gamochaeta calviceps</i>	2.15	16.27	250	1467.86
	<i>Ligustrum lucidum</i>	2.07	19.21	207.14	3.57
	<i>Morus alba</i>	1.94	21.96	625	0
	<i>Talinum paniculatum</i>	1.71	24.4	228.57	171.43

*The square root of these values was used for the analysis

Table 3 Sørensen coefficients of similarity between soil seed banks and established vegetation in native and exotic woodlands of the Chaco Serrano woodland of Córdoba. Mean coefficients of similarities and standard deviations are provided for both sampling seasons in autumn (May) and spring (November).

Sorensen coefficients of similarity				
Sample season	Exotic woodlands	Native woodlands	W	<i>p</i>
Autumn	0.18 ± 0.14	0.36 ± 0.05	18	0.06
Spring	0.25 ± 0.11	0.32 ± 0.08	24	0.55





