The role of bioclimatic features, landscape configuration and historical land use in the invasion of an Asian tree in subtropical Argentina

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Abstract

Context: Knowing which factors determine the spread of plant invaders is a relevant issue in global ecology. Cultural landscapes both influence and are affected by exotic species. Although bioclimatic boundaries, seed sources and landscape configuration all control the invasion process, they have been mostly studied separately and independently from their distant drivers.

Objectives: We followed a multiscale approach to describe the invasion dynamics of the Asian tree (*Ligustrum lucidum*) in subtropical NW Argentina cultural landscapes by: (1) identifying the potential bioclimatic area of invasion, (2) mapping the currently invaded area in peri-urban focal sectors, and (3) quantitatively describing the landscape-scale patterns of invasion in relation to environmental and cultural variables.

Method: Niche models were used to map potential invasion area, remote sensing, GIS and field surveys to map patterns of invasion and their association to landscape and environmental variables.

Results: Climate suitability to *L. lucidum* extends over important ranges of the studied area, but currently invaded areas are mostly restricted to clusters around the main cities. The historical and demographic features of cities (e.g., date foundation, population) are important in predicting invaded forest location and spread. At local scale, invasion is associated to abandoned fields nearby urban centers, roads and rivers.

Conclusions: The invasion patterns of *L. lucidum* reflect the combined effect of historical socioeconomic connections between Asia and America, as well as the local cultural landscape history and configuration. Teleconnected cultural landscapes need to be explored as a theoretical framework for the study of biological invasions in the Anthropocene.

Keywords: Invasive species; *Ligustrum lucidum*; Species distribution; Telecoupled cultural landscapes.

Introduction

Species invasions can become a distinctive feature of newly created cultural landscapes, as they change from a mostly wild to mostly anthropogenic one (Sadori et al. 2010). Most of the arrivals of exotic species into their new ranges appear to result from intentional or accidental exchanges between distant regions via different pathways, depending on sociocultural factors (Hulme et al. 2008; Hulme 2009). Once introduced, their establishment and spread result from the complex interaction between new habitat and species characteristics. Successful invasions that spread into natural systems are the result of the cultural landscape construction that includes the biocultural dimension: a physically, culturally, and historically determined environment. Humans have been transporting plants species among regions for millennia. These interchanges were extremely important among Asia, Europe and Africa along the silk route, as well as between Europe and America after Columbus, and they have had unprecedented magnitude and complexity across the globe in recent decades (Hulme 2009). Purpose driven exchanges include, for example, species with agricultural, medicinal or ornamental value. However, some of these species are able to spread into natural and seminatural ecosystems affecting ecological functions and biodiversity (Vitousek et al. 1996; Bellard et al. 2013) as an unplanned, and frequently undesirable, side effect of the cultural landscape construction.

Cities are a particularly important feature of the cultural landscapes, regulating the multiple connections and flows between people and ecosystems that strongly affect species invasion. Cities act as attraction centers for the introduction of desirable and undesirable species and then as sources of propagules for the peri-urban environment (Altson and Richardson 2006; Botham et al. 2009; Wang et al. 2011). For example, gardening, urban forestry or horticulture regulate the location of seed sources, increase the propagule pressure and reduce the probability of invasion failure by temporally protecting potential invaders from unsuitable environmental conditions until they adapt to local conditions (Mack 2000; Pyšek

53 and Richardson 2010; Hulme 2011; Pergl et al. 2016). Recent studies found that human

54 population and wealth (Pyšek et al. 2010, Decker et al. 2012), as well as the historical legacy

55 (Essl et al. 2011) are strong predictors of a wide range of invasive species distribution.

56 Therefore, it is expected that cities and anthropogenic peri-urban landscapes play a key role in

57 the introduction and spread of invasive species.

58   The capacity of a particular species to colonize areas depends on the interaction among

59 propagule availability, dispersal capacity, population growth potential, and landscape

60 heterogeneity (Vilá et al. 2008; O´Reilly-Nugent et al. 2016). In this sense, biological (e.g.

61 intrinsic species attributes, life history traits) (Grotkopp and Rejmánek 2007; Leishman et al.

62 2007; Peñuelas et al. 2010) and environmental factors (climate, topography, hydrology) are

63 important drivers that interact with human activities and determine the geographical extent of

64 plant invaders in their novel distribution range (Rejmánek and Richardson 1996; Thuiller et al.

65 2006). For example, human disturbances can regulate resource availability (e.g. light, soil

66 nutrients), affecting ecosystem invasibility and often enhancing the competitive availability of

67 invasive species (Karalius and Alpert 2010; Standish et al. 2008). Furthermore, changes in

68 landscape configuration (e.g. replacing forests by grasslands, increased of roads, etc) can affect

69 dispersal barriers and corridors and thus, the spread pattern (Miller et al. 2015). This results in

70 higher invasion rates in fragmented landscapes than in continuous and unconnected areas (Vilá

71 and Ibañez 2011). When the cultural landscape construction results in strongly modified

72 environmental conditions, they can overwhelm the influence of climate and natural physical

73 environment (e.g. soils, hydrology or topography) (Chiron et al. 2009; Sharma et al. 2010;

74 Fuentes et al. 2015). Cities and peri-urban areas are characterized by distinctively intensive

75 features of the cultural landscape. In addition to present-day landscape configuration, invasions

76 are often associated with the historical changes in land-use (Mosher et al. 2009; Vilá and

77 Ibañez 2011). Although biophysical factors and their interaction with city dynamic can be very

78   relevant to understand biological invasion processes as side effects of cultural landscape

79   development, they have been largely explored separately.

80   The cultural landscape construction in the subtropical humid forest of northwest

81   Argentina, Yungas ecoregion, experienced a major change with the Spanish arrival in the

82   region in the 16th century. As a result of the territory reconfiguration implemented during

83   colonial times, the main productive activities and population shifted from the highlands in the

84   Pre-Hispanic and early Hispanic period, to the forested humid flatlands of the foothills. Much

85   of the lowland and lower montane forests with flat topography were deforested for agriculture

86   and grazing, and the main urban centers were located nearby. These areas include the three

87   province capital cities of the region: San Miguel de Tucumán, Salta, and San Salvador de Jujuy,

88   with approximately 900,000, 600,000 and 300,000 inhabitants, respectively (INDEC 2010).

89   During the past decades, several montane areas near these urban centers experienced

90   abandonment or disintensification of agriculture and livestock grazing, which resulted in the

91   expansion of secondary forests (Grau et al. 2008; Gutiérrez-Angonese and Grau 2014). Parts of

92   these new forests are dominated by exotic tree species. A large proportion of them are

93   originally from SW Asia, including *Ligustrum lucidum* W. T. Aiton (Oleaceae), the most

94   aggressive and fast growing tree species in this area (Grau and Aragón 2000; Aragón and

95   Morales 2003; Easdale et al. 2007). *Ligustrum lucidum* was possibly introduced primarily for

96   urban shade, gardening, living fences and windbreaks. One of the first records in Argentina

97   dates to c.1900 (Montti et al. 2016). The extent of *L. lucidum* forests and the drivers of the

98   invasion are still not well documented. Here, we follow a multiscale approach to explore the

99   dynamics of this invasion into cultural landscapes in NW Argentina, with particular emphasis

100   on the role of cities and distant connections between native and novel ranges of distribution of

101   this species. Specifically in this study, we pursued the following objectives: 1) to identify the

102   potential area of invasion by *L. Lucidum* in the Yungas ecoregion of Argentina using ecological

103   niche distribution models; 2) to map, quantify and describe current invaded area in this

104 ecoregion by using satellite images in three peri-urban focal zones; and 3) to quantitatively

105 describe the spatial and temporal patterns of *L. lucidum* forest invasion at local scale, linking

106 environmental and cultural landscape features in the largest peri-urban sector of the region: San

107 Miguel de Tucumán and Sierra de San Javier.

108

109 **2. Methodology**

110 *2.1. Studied species*

111   *Ligustrum lucidum* or Chinese glossy privet is an evergreen tree native of the south of

112 the Yangtze River in China, where it grows in different climates and soil types between 0 to

113 2900 m.a.s.l, in full sunlight, as well as in shaded understory (Chang et al. 1996). *L. lucidum*

114 has been extensively cultivated for different purposes (e.g., traditional medicine, culturing

115 wax-insects to obtain white wax, furniture) for a long time in China. Because of its particular

116 functional traits (eg. fast growth rate, tolerance to air pollution), it is regarded as a great

117 landscaping plant and it is used extensively as an ornamental in streets and gardens around the

118 world (Guilhermetti et al. 2013). But it is also considered a successful global invader outside

119 its native range (Panetta 2000; Aslan et al. 2012; Montti et al. 2016).

120 *2.2. Study area*

121   Our study focuses on Yungas ecoregion, the humid native forests of northwestern

122 Argentina (-22.25ºS to -27.95ºS, -64.22º to -65.65ºW) (Fig.1a). The climate is subtropical with

123 a monsoon regime of precipitation (dry winters, rainy summers) (Brown et al. 2001).

124 Temperature and precipitation are controlled by topography; the average annual temperature is

125 high in the eastern piedmont (20ºC) and decreases with elevation. Precipitation exceeds 1100

126 mm per year (Bianchi 1981), 78% concentrated in the months of November to March.

127 Additional supply of water, particularly during the dry season, comes from fog or horizontal

128 rain (Hunzinger 1997). The native humid forest that *L. lucidum* replaces has a high proportion

129   of evergreen and semi-deciduous tree species, with *Ocotea porphyria*, *Blepharocalyx*

130   *salicifolius*, *Pisonia ambigua* and *Cedrela lilloi,* as dominant tree species (Grau et al. 2010;

131   Brown et al. 2001; Blundo et al. 2012). For the purpose of this study, three spatial scales of

132   analysis were considered: I) Regional: including all Yungas distribution in Argentina, c. 5.2

133   million ha; II) Sub-regional: three pre-selected focal zones or sectors where invasion was

134   notorious covering 408,500 ha aprox. and III) Local: that include the most affected sector by

135   the invasion, near to 120,000 ha, the peri-urban region of San Miguel de Tucumán (Fig. 1a).

136   *2.3. Potential distribution of Ligustrum lucidum at regional scale*

137   We generated a potential distribution map at regional scale based on recently observed

138   presence records, climatic variables and maximum entropy algorithm implemented in Maxent

139   3.3.1 (Phillips et al. 2006). This map represents the distribution of suitable climatic conditions

140   for *L. lucidum* in our study area. Maxent has proven to produce more reliable results than other

141   comparable methods such as Bioclim, Domain or Garp (Wisz et al. 2008). This reliability has

142   been confirmed by its high capacity to predict novel presence for not so well-known species

143   (Pearson et al. 2007) and to predict the outcome of introductions of invasive species outside the

144   native range (Ficetola et al. 2007; Rödder et al. 2008; Rödder and Lötters 2009). We initially

145   considered 127 presence records of *L. lucidum* collected from fieldwork (50%), national

146   herbarium specimen data examined by the authors (35%) and well as other records reported in

147   the literature throughout the study area (15%). Obviously erroneous occurrence points (e.g.

148   coordinates outside the studied area under which they had been listed) and duplications

149   resulting from the merger of records from the different sources were removed. In the case of

150   invasive species, most records tend to be collected where high densities of people and

151   researchers occurs. This sampling bias may influence the prediction of the model. Therefore,

152   we removed randomly presence records that were geographically close together trying not to

153   leave records in adjacent cells. As a result, not all presence records collected were used in

154   model calibration (60 presences records).

155   First, we obtained an initial set of 10 models setting Maxent with hinge and quadratic

156   features and cross-validation, using 90% of presence data to fit the model and the remaining

157   10% for model validation given the small number of presence points. In addition, we

158   disaggregated potentially clustered/repeated presence records by randomly selecting one per

159   grid cell. In order to characterize the "background" of environment available to the species, we

160   restricted the area only to the study region (Merow et al. 2013). This initial set was used to

161   identify variables with minimal or no contribution to overall model taking into account the

162   predictive efficacy using the jackknife test of variable importance, variable response curves

163   and percent contribution of each variable in the model. Only environmental variables with

164   relatively low collinearity (i.e., Pearson correlation values lower than 0.7 considering only the

165   cells with presence data) and greater biological significance were selected. The average

166   training gain values of selected variables were examined once again and the variables showing

167   the lowest decrease in gain values when omitted from the full model were removed. These

168   variables correspond to a subset of 19 climatic variables from the WorldClim database

169   (http://www.worldclim.org/; Hijmans et al., 2005), that were projected at a 30 arc second

170   (approximately 1 km^2) spatial resolution.

171   The model´s performance was evaluated using the area under the receiver operating

172   characteristic curve (AUC). An AUC value of 0.5 indicates that the performance of the model

173   is no better than random, while values closer to 1.0 indicate better model performance (Phillips

174   et al. 2006). To obtain a model we ran Maxent with 100 replicate using the reduced set of

175   variables and the same setting. Then the 10 models with greatest AUC values were selected and

176   averaged to obtain the final model. Finally, to generate a binary prediction of occurrence it was

177   necessary to choose a threshold. Because no single procedure is recommended to select

178   thresholds, we used a *maximum training sensitivity plus logistic threshold* to cut-off. This

179   criterion has been described as the most objective to identify optimal habitats when only

180   presence data are available (Liu C et al. 2013). Pixels with a value higher than the selected

181   threshold were considered presence data, meaning that they harbored the appropriate climate

182   conditions for the species. We used ArcGis 10.1 and Spatial Analysis tool to construct the final

183   model.

184   *2.4. Current distribution of Ligustrum lucidum* forest at sub-regional scale

185   To evaluate and quantify the current distribution of *L. lucidum* forests we surveyed the

186   whole Yungas ecoregion in Argentina and identified three focal zones where invasion was

187   notorious (i.e. where several hectares of monodominant forest are present). These sectors

188   included the peri-urban landscapes around the most important cities, centered in the localities

189   of Yala (Jujuy province), San Lorenzo (Salta province) and Sierra de San Javier (Tucumán

190   province). These study sectors were included in two subsets of Landsat TM images: scene path

191   231/row 77 for Yala and San Lorenzo and scenes path 231/row 78 and 79 (mosaic) for Sierra

192   de San Javier. Four images were selected for each sector corresponding to January, July,

193   August and December 2010 to maximize potential differences in phenology between native

194   and exotic forest. Images were almost cloudless; the remaining few clouds (less than 10% in

195   two images in one date) were masked. Landsat image proved an excellent alternative at low

196   cost to mapping spread of *L. lucidum* forests and was previously used by Hoyos et al. (2010)

197   and Gavier-Pizarro et al. (2012) in more seasonal forests of Argentina at higher latitude. The

198   images have 30 x 30 m spatial resolution and were orthorectified and georeferenced using GPS

199   points obtained in the field (geopositional error <10 m) and converted to the official coordinate

200   system of Argentina (Gauss-Krügger POSGAR94 System, zone 3). The six multispectral bands

201   of the Landsat images were combined into a single multi-temporal stack with resulting 24

202   bands for each study area. The stack of bands also included the NDVI (Normalized Difference

203   Vegetation Index) and the hill shade image, obtained from the DEM (digital elevation model)

204   resampled to match the spatial resolution to a 30 x 30 m pixel, which allows modelling the

205   shadows caused by the topography. As a result, final staked images included 26 layers of

206   information: 24 multispectral bands+ NDVI+hill shade. Images were obtained from the

207   *Instituto Nacional de Pesquisas Espaciais* (INPE, http://www.dgi.inpe.br/CDSR/). Lastly,

208   multi-temporal images for the three sites were clipped to cover the interest sectors leaving a

209   surface of 106,183 ha for Yala and San Lorenzo sector, and 248,305 ha for Sierra de San Javier.

210   Land cover maps were derived using the non-parametric classifier Support Vector

211   Machine (SVM) (Hsu et al. 2007). SVM defines a hyperplane that separates points

212   corresponding to two different classes in a multidimensional space (Foody and Mathur 2004;

213   Huang et al. 2002). In our case, land cover was classified into five classes: 1-Forest (including

214   Yungas and dry forest, but also a small proportion of tree plantations), 2-*L. lucidum* forest, 3-

215   Urban, 4-Water, and 5-Others (agriculture, grassland, mix agriculture, citrus and perennials

216   plantation, cleared, roads and bare soil). *L. lucidum* forests differ substantially in structural and

217   physical characteristics from native forest (Grau et al. 2010). *L. lucidum* canopies are evergreen

218   and closed, resulting in higher absorption in the visible domain and higher reflection in the

219   near-infrared domain and thus present high NDVI (Zamora Nazca et al. 2014). During

220   fieldwork in 2010, we identified training areas used to parameterize a SVM classifier. This

221   methodological approach was previously used to classify our study species in other region of

222   Argentina by Gavier-Pizarro et al. (2012).

223   2.5. *Ligustrum lucidum relationship invasion with environment and land-cover changes at sub-*

224   *regional and local scale*

225   Based on the current distribution map of the *L. lucidum* forests in the three focal sectors

226   (section 2.4) the landscape structure of these invaded stands was analyzed using the

227   FRAGSTATS software (McGarigal and Marks 1995) at sub-regional scale. The selection of

228   metrics was based on their ability to characterize various aspects of fragmentation such as:

229   class area (sum the area of all fragments per class), mean patch size (an index of

230   fragmentation), number of patches (an indicator of several ecological processes and landscape

231   heterogeneity), total edge length (indicator of patch complexity), average nearest-neighbor

232   distance and mean proximity index. Additional information on these metrics and detailed

233   mathematical description can be found in McGarigal and Cushman (2002). In addition, we

234   used ArcGis 10.1 and Spatial Analysis tool to compute descriptive statistics and explore the

235   relationship between geographic distribution of *L. lucidum* forest patches and variables such as

236   slope, elevation, temperature, precipitation and distance to roads, rivers and urban areas. We

237   also explored the relationship between *L. lucidum* forests per sector (SSJ, SJ and Y), population

238   and cities´ features as time of foundation and size by fitting linear regression. Population data

239   was extracted from official data of Censo Nacional de Población, Hogares y Viviendas 2010.

240   INDEC-Instituto Geográfico Nacional (IGN, http://www.sig.indec.gov.ar/censo2010/).

241   Additionally, to enrich the discussion we combined *Ligustrum* sub-regional map and urban data

242   with the data from Córdoba city extracted from Gavier-Pizarro et al. (2012) where *L. lucidum*

243   invasion has been reported.

244   To analyze the influence of past land-uses on forest invasion and to assess the invasion

245   rate we worked at local scale in Sierra de San Javier (SSJ) and San Miguel de Tucumán city,

246   the most affected sector by the invasion. San Miguel de Tucumán is the largest political,

247   economic and cultural urban center in NW Argentina. For this analysis, we used an additional

248   set of land cover history data that we combined with our *L. lucidum* forests areas for 2010. The

249   series of land cover maps previously made for SSJ by Gutiérrez-Angonese and Grau (2014)

250   and Gutiérrez-Angonese (2015) were derived from Landsat MSS and TM images (30 x 30 m of

251   spatial resolution) from 1972 to 2010, selecting early-spring cloud-free images with a temporal

252   frequency of four to five years (1972, 1977, 1981, 1986, 1992, 1996, 2001, 2006 and 2010).

253   All Landsat images were image-to-image spatially co-registered and atmospherically corrected

254 using DOS method (Song et al 2001). Images were classified by applying the machine learning

255 algorithm Random Forest (Breiman 2001), using the Random Forest Package (Liaw and

256 Wiener 2002) in the R statistical Software (R Development Core Team, 2014). For this map

257 land cover was classified into seven categories 1-Montane forest (SMF) that we called here

258 Yungas forest, 2-Dry forest or "Chaco" (DF), 3-Montane grassland (MG), 4-Anthropogenic

259 grassland and shrubland (AG), 5-Sugar cane (SC), 6-Citrus plantations (CP) and 7-High-to-

260 medium density urban areas (UR). Final accuracy estimation OOB (out of bag) ranges from

261 8.8-12.6% of error in TM scenes and 12.9-18.8% in MSS scenes (Gutiérrez-Angonese and

262 Grau 2014). To combine our data with the land cover history, we used our map of invaded

263 areas by *L. lucidum* in 2010 as a reference. The set of data from Gutiérrez-Angonese and Grau

264 (2014) and Gutiérrez-Angonese (2015) was used to estimate the temporal trajectory of the

265 invasion and the previous land cover for the areas that end being *L. lucidum* forests in 2010. In

266 the Gutiérrez-Angonese and Grau (2014) and Gutiérrez-Angonese (2015) data, different land

267 covers were discriminated (see above), but *L. lucidum* forests were not discriminated from

268 native forest (Yungas). Therefore, the map of *L. lucidum* forests in 2010 was used as a mask to

269 extract the information from the history land cover maps and the invasion rate was estimated

270 assuming that the class "SMF" in the Gutiérrez-Angonese and Grau data corresponds to *L.*

271 *lucidum* forests.

272   Additionally, to investigate the factors that were associated with past invasion patterns

273 of *L. lucidum*, we performed a multiple logistic regression using the presence of *L. lucidum*

274 forests in 2010 as a binary dependent variable, and two sets of independent environmental and

275 land use variables derived from the map of 1972 (Eastman, 2016) (Table 2). A stratified sample

276 (selecting 10% of the pixels) was applied to reduce the inherent spatial autocorrelation of

277 spatial data (i.e. locations close to each other exhibit more similar values than those further

278 apart). Model fit was evaluated through the pseudo-R^2 coefficient, ranging from 0 to 1 (values

279 greater than 0.2 means a good fit, Eastman 2016), representing the percentage of variance

280   explained in non-linear functions. Additionally, the contribution of each independent variable

281   to explain the probability of occurrence of *L. lucidum* forests in 2010 was assessed by

282   obtaining the standardized coefficients (b') of each variable, which allows comparing variables

283   with one another, regardless of the unit of measurement for each variable. Standard coefficients

284   were quantified using the formula proposed by Lesschen et al. (2005). The higher the 'b' value

285   the more the corresponding variable contributes to explain the presence of *Ligustrum* forests in

286   its current location.

287

288   **3. Results**

289   The model of potential *L. lucidum* distribution at regional scale (Fig. 1b) had a good

290   overall accuracy with an AUC of 0.82 for independent data. Four variables were used in the

291   setting of final model of the predictive map with different relative contribution: Bio 14:

292   Precipitation of the driest month (56%), Bio 1: Annual mean temperature (25%), Bio12:

293   Annual precipitation (12%) and Bio 6: Minimum temperature of the coldest month (7 %). The

294   spatial model generated only by these environmental variables suggests that the study area

295   presents a high climatic suitability, almost overlapping in some part with the distribution of

296   Yungas ecoregion in Argentina (Fig. 1b). This is not surprising, given that *L. lucidum* tolerate a

297   wide range of environmental conditions (Chang et al. 1996).

298   Despite its wide potential distribution range, *L. lucidum* forest patches were limited in

299   2010 to three "hotspots" of invasion in the peri-urban areas of the largest cities (Fig. 2). The *L.*

300   *lucidum* forests covered approximately 700 ha in 2010, that represents 0.22% of the total forest

301   area (324,000 ha) in these three sectors and was distributed in several patches (relatively

302   discrete forest areas) with mean patch size of < 0.6 ha (Table 1). Although the mean patch size

303   was small, a high proportion of the invaded forests were distributed in large patches (between 2

304   to 38 ha, that represent more than 50% of the total invaded area). Sierra de San Javier in

305   Tucumán has the largest area of *L. lucidum* forests, and Yala the smallest one. The spatial and

306 spectral resolution of the Landsat TM images (30 m) did not allow us to detect young or mixed

307 forest of *L. lucidum*, and only monodominant-invaded forest was detected, mapped and

308 analyzed. Landscape indices appear related to the size of the total invaded area per sector. We

309 observed an increase in mean patch size and a decrease in distance to nearest-neighbor from Y

310 to SSJ (less to more invaded areas; Table 1); indicating a process of forest patch coalescence

311 (inverse of fragmentation) as the area of *L. lucidum* forests increases.

312   At sub-regional scale, the current *L. lucidum* forests were located between 15-19 °C

313 mean annual temperature and 600-900 annual precipitation and in areas with gentle slopes (Fig

314 3a, b, c). However, a particular distribution pattern was observed when considering elevation:

315 *L. lucidum* forests were concentrated in two distinct altitudinal ranges: low elevation foothills

316 (around 500 m.a.s.l) and mountain ridges and slopes (between 1000 and 1500 m.a.s.l) (Fig. 3

317 d). Additionally, *L. lucidum* forest patches were less common as distance to roads and rivers

318 increase (Fig. 3 e, f). Along the three sectors, a sturdy relationship with variables associated to

319 cities was observed: *L. lucidum* forests extent appeared to be influenced by different urban

320 features such as age of city foundation, size, urban population and population density of the

321 three more important cities located in the Yungas. This relationship holds when the data for the

322 city of Córdoba is included (Fig. 4).

323   At local scale, patches of *L. lucidum* forest were distributed in seven clusters around

324 San Miguel de Tucumán city and Sierra de San Javier, mostly located at the top and bottom of

325 the mountain range (Fig. 3d and Fig. 5). The distribution of *L. lucidum* forests cover in 2010

326 and the land-cover changes observed since 1972, indicate that the species doubled its area

327 during this period from 306 to 620 ha. The invasion process apparently varied in intensity

328 through time, with two main expansion pulses, during 1986-1992 and after 2001 (Fig. 6 a). The

329 expansion occurred mainly over citrus plantation (CP, 43%, Fig 6 b) located at the foothills.

330 Other anthropic uses such as agricultural grasslands (AG) or sugar cane (SC) were

331 comparatively less invaded by *L. lucidum* forests, representing 8 and 11 % of net changes

332   respectively. Among natural ecosystems *L. lucidum* expansion occurred mainly over montane

333   grassland (MG, approximately 34%) distributed at the top of SSJ.

334   At local scale, precipitation and elevation were the best environmental predictors to

335   explain the presence of *L. lucidum* forests. In addition, at this spatial scale there was also a

336   negative relationship between new *L. lucidum* forests and slope (Pseudo-R^2=0.66, Table 2).

337   However, according to the logistic regression analysis, land cover variables were better

338   predictors than environmental factors to explain the presence of *L. lucidum* forests in Sierra de

339   San Javier, (Table 2, b' coefficient). Among these variables, distance to *L. lucidum* forests in

340   1972 was the variable that better explained the probability of occurrence of *Ligustrum* forests

341   in 2010. Many patches were close to the initial foci of invasion, irrespectively of whether these

342   patches were previously occupied by other uses, showing that this species´ spread involves a

343   spatial "contagious" pattern. In addition, the invasion was enhanced in areas near to roads, CP,

344   DF, SC and UR, land covers mainly distributed in the piedmont of SSJ, and away from MG or

345   AG (located at the top of SSJ) during the 1970s (Table 2).

346

347   **Discussion**

348   At the classical ecological or landscape scales, controls of plant succession can be

349   categorized in three main groups of factors: i) site availability, ii) differential species

350   performance and iii) species availability (Pickett et al. 1987). Exotic plant invasions can be

351   considered a particular component of plant succession, in which species availability plays a key

352   role, and in turn, is regulated by mechanisms that operate at global scale and are dependent on

353   socio-political variables in addition to biophysical ones. Thus, understanding plant invasion

354   and its effects in framing emerging cultural landscapes, depends on the co-occurrence of

355   factors that operate a different spatial scales, from global to local and that includes: i) suitable

356   environmental and climatic conditions, ii) human induced conditions/cultural landscape, and

357   iii) human propagule introduction, "pressure"; and a posteriori landscape scale dispersal. In this

358   study, we explored these different components as controls of the invasion of the Asian tree *L.*

359   *Lucidum* in the Argentinian Yungas ecoregion. Cities are a prominent and increasingly

360   important cultural feature of landscapes and regions, since they regulate economic and political

361   activities and concentrate human population that in turn has influential decisions over

362   ecosystems. Our study point out the potential role of cities as key controls of the interaction

363   between invasive species availability (largely anthropogenic) and landscape characteristics that

364   control colonization and dispersal.

365   *Suitable environmental and climatic conditions*

366   The influence of environmental variables in invasive species distribution is well known

367   (e.g. Gormley et al. 2011; Xu 2015). The results of our niche modelling (Fig. 1b) suggested

368   that Yungas ecoregion in NW Argentina (mainly in Tucumán province) has suitable climatic

369   conditions for the expansion of this species. *Ligustrum lucidum* forests current distribution,

370   however, only occupies a minor and aggregated portion of this potential range, despite the

371   species has been present in the region for more than a century. This could reflect the "lag

372   phase" in biological invasions (Aikio et al. 2010). Although our understanding of causality is

373   still limited, dispersal barriers coupled with the original location of seed sources rather than

374   climatic conditions appear to be the main restriction to a widespread distribution. In its native

375   range, *L. lucidum* experiences more extreme climatic conditions than in subtropical Argentina

376   (from wet-warm to temperate) and grows up to 2500 m.a.s.l (Chang et al.1996). As a result,

377   and according with niche conservationism (Peterson 2003; Thuiller et al. 2005), it is possible

378   that this species presents advantageous adaptations to diverse environmental conditions.

379   Furthermore, it has been documented that exotic species can broaden their native-range

380   ecological niche during the process of invasion (e.g. Broennimann et al. 2007; Fitzpatrick et al.

381   2012; Essl et al. 2009). If this is the case of *L. lucidum*, we could expect major expansions of

382   the current distribution area into the Argentinian Yungas, but also in other ecosystems such as

383   dry forest or natural grasslands. The potential capacity of *L. lucidum* to invade places under

384   different and contrasting environmental and vegetation conditions is supported by examples of

385   invasions in other places of Argentina including sectors of dry forest in Córdoba (Gavier-

386   Pizarro et al. 2012), grasslands in Buenos Aires (Ghersa et al. 2002) and riparian forest in Entre

387   Rios (Torresin et al. 2013). In this work, we only sampled a subset of *L. lucidum*´s large

388   geographic range. Thus, other environmental and climatic predictors may be important to

389   explain the distribution at bigger scale studies (i.e. country, continental or global).

390   *Human induced conditions/cultural landscape*

391   We identified three hotspots of invasion in the Argentinian Yungas, with Sierra de San

392   Javier as the one experiencing the most advanced invasion (with more than 600 ha of

393   homogeneous monodominant *L. lucidum* forest) and Yala the least. Although this represents

394   only 0.22% of the studied Yungas forest cover, there are many potential sources of invasion

395   along this ecoregion. Landsat images provided an excellent data source to map *L. lucidum*

396   invasion in dry seasonal forests (Hoyos et al. 2010; Gavier- Pizarro et al. 2012), but in partially

397   evergreen mountain ecosystems, it showed limitations for mapping young or mixed stands,

398   which could not be reliably discriminated from native forests. Previous works using remote

399   sensing in Sierra de San Javier showed the same limitation (Grau et al. 2008). In addition,

400   small patches (<0.5 ha), even those highly dominated by *L. lucidum* were not detected due to

401   the medium-spatial resolution of Landsat images. However, based on our extensive field

402   knowledge, we are confident that our map captures the main patterns of *L. lucidum* invasion,

403   showing the largest invaded forest patches.

404   In Sierra de San Javier particularly, citrus plantations (in the foothills) and grasslands

405   (mainly distributed close to the mountain top) were the land cover types over which *Ligustrum*

406   forests expanded more aggressively. Expansion occurred at a higher rate between 1986 and

407   1992 and after 2001 (Fig. 6). During the 1940s, a small touristic village was developed in

408   Sierra de San Javier, and in 1948 the National Government, legally expropriated nearly 10,000

409   hectares to create a university project and a Natural Reserve. As a consequence, 36 private

410   owners abandoned their agricultural land. However, the development failed to materialize; this

411   history of land use may have produced the initial introduction of seed sources and availability

412   of potentially colonized fields. Then, during 1973 through a Resolution of the National

413   University of Tucumán, the Biological Park Sierra de San Javier, a protected area that belonged

414   to the University was created, and many areas were abandoned (Gutiérrez-Angonese and Grau

415   2014), creating opportunities for the second pulse of invasion. Although we do not have strong

416   evidence to link directly the first and second pulses of invasion, our interpretation of the

417   observed pattern is that political conservation decisions taken several years before invasion

418   pulse could have unintentionally promoted the spread of *L. lucidum* by creating adequate local

419   environmental conditions and encouraging the abandonment of agriculture and grazing fields.

420   A similar pattern was found in another area by Gavier-Pizarro et al. (2012). In addition to

421   formal conservation practices, the combination of abandonment of marginal agriculture and the

422   expansion of sub-urban residential areas after the rapid economic growth during the beginning

423   of the 21st century may have favored the second expansion pulse.

424   *Ligustrum lucidum* monodominant forests close to peri-urban areas of large urban

425   centers, present a strong spatial association with roads and rivers and with urban areas of larger

426   size and higher population density (Fig. 3 and 4, Table 1). Roads and rivers often act as

427   corridors along which invasive species can spread (Wang R et al. 2011) and cities as reservoir

428   of seed sources. Large urban areas of the Yungas ecoregion, appeared to have favored *L.*

429   *lucidum* invasion likely by hosting large seed sources since the species is intensively used for

430   urban forestry and vegetated fences near recently disturbed areas (e.g. in association to urban

431   development), or recently abandoned agriculture lands (as agriculture becomes non-

432   competitive in comparison to urban land uses) (Davis et al. 2000; Theoharides and Dukes

433   2007; Hufbauer et al. 2012). Importantly, the relationship between *L. lucidum* invaded area and

434   cities size is consistent with the scaling attribute of cities (Bettencourt 2013), that explains

435   several properties of urban systems considering variables such as green areas, transport

436   infrastructure, human interaction, among others. This pattern is more evident if we combine

437   our data with the *L. lucidum* cover around Córdoba city described by Gavier-Pizarro et al.,

438   (2012) (see Fig. 4). This relationship confirms that *L. lucidum* responds to the scaling rule

439   proposed for city systems and could be considered as a side effect linked with the urban centers

440   dynamics and functioning. It is also worth noting that even though *L. lucidum* showed strong

441   association with peri-urban forest transition and land abandonment, and that the urban areas

442   grew during the last decades, the expansion of new forest has slowed down in recent times

443   (Gutiérrez-Angonese 2015); probably because newly abandoned agriculture areas are

444   becoming scarce. However, our results should be considered a conservative estimate of the

445   present invaded forests. Recent field data shows that *L. lucidum* is expanding into mature

446   native forest (Malizia et al. in press), revealing that invasion could occur by other ways unable

447   to be detected by standard remote sensing methods.

448   *Propagule pressure and dispersal*

449   Our results suggest that humans and their activities are the main control of landscape

450   features influencing *L. lucidum* distribution pattern. Urban areas play an important role as *L.*

451   *lucidum* propagule sources, and roads and rivers enhance dispersion and increase propagule

452   pressure into sites suitable for invasion, such as abandoned fields. The invasion across the

453   cultural landscape followed a contagious pattern, with a strong decrease of invasion probability

454   with distance from pre-existing *Ligustrum* stands. Consistently, previous studies suggested this

455   pattern also could be consequence of propagule pressure conditions and seed dispersal

456   mechanism at a micro local scale (Aragón and Morales 2003; Powell et al. unpublished work).

457   In others words, urban and peri-urban areas present a relatively high abundance of *L. lucidum*

458   as a result of widespread cultivation by humans in gardens and streets, and the availability of

459 invasion prone sites. *L. lucidum* invasion into areas nearby seed sources, can later achieve

460 persistence by two mechanisms. First, this species has a high growth rate and effective

461 vegetative reproduction (Grau and Aragón 2000; Aragón and Groom 2003), which helps

462 competitively displacing native species (Malizia et al. in press). Second, *L. lucidum* produces

463 massive fruit crops that fall and germinate underneath the parental tree (Aragón and Groom

464 2003). In addition, *L. lucidum* produces fruits during the winter (when native fruit offer is

465 scarce) and its seeds are frequently eaten and dispersed by birds (Aragón and Groom 2003).

466 *Turdus rufiventris* a medium-sized passerine, which is the most abundant fruit-eating bird

467 species in the southern Argentinian Yungas, disperses seeds beyond canopy proximity, using

468 native trees or abandoned citrus plantations as perches (Blendinger et al 2012; Ayup et al.

469 2014). Also as Powell et al. (unpublished work) confirmed recently, seeds dispersed by birds

470 presented different spatial patterns depending on their handling technique and the tree density

471 influenced the number of seeds and their dispersal distance. The combination and relative

472 contribution of these factors to control invasion spread needs to be better understood in order to

473 refine models of invasion and develop future scenarios.

474 *Telecoupled cultural landscapes as a modifier of site and species availability to explain the L.*

475 *lucidum invasion*

476   Several studies described the biological traits that confer advantages to *L. lucidum* over

477 the native species (Aragón and Groom 2003; Aragón and Morales 2003; Tecco et al. 2006;

478 Easdale et al. 2007; Ferreras et al. 2008). Here, we showed that, human activities are also key

479 factors controlling its expansion in Argentinian Yungas. As different studies revealed, human-

480 assisted propagule movements and disturbances related to the development of cultural

481 landscapes could be more important in shaping the invasion process than the invasive species'

482 traits themselves (Chytrý et al. 2008a, b). This suggests that tree invasion should be tackled

483 from a multidisciplinary focus that includes the human dimension view and the dynamic

484   processes associated with it (i.e., social, economic, geographic, historic and landscape

485   ecology), in order to develop a comprehensive theoretical framework on how these factors

486   operate during the invasion process at different stages and spatio-temporal scales.

487   Based in our multiscale analysis we argue that invasions have a strong interaction with

488   "telecoupled cultural landscapes". The concept of "telecouplings" has been recently developed

489   to study the links between distant socio-environmental systems and the environmental

490   modifications related with distant drivers (Liu J et al. 2013). The concept is used to study land

491   use change processes (e.g., Gasparri and le Polain 2014) and urban-rural interactions (Deines et

492   al. 2016); it was proposed as potentially important to explain species invasions (Liu J et al.

493   2013). In the telecoupling frame, cities are crucial elements to articulate the interaction

494   between the telecoupled systems (Seto et al. 2012). Cities concentrate the main fluxes of

495   information, energy and materials, as well as the most powerful decisions. Therefore cities and

496   peri-urban zones are particularly prone to result into "telecoupled cultural landscapes'' where

497   invasive plants such as *L. lucidum* could play the role of incorporating biological features from

498   distant locations and creating novel ecosystems. In this scenario, peri-urban areas are expected

499   to be the first ones affected.

500   Under this framework, to better understand why *L. lucidum* became a successful

501   invasive species in Argentina it is advisable to consider the long and intermittent telecouplings

502   operating between China and Americas, and particularly Argentina. Since the 1600´s,

503   sociocultural and economic telecoupling between Asia and the Americas has been intensive,

504   especially related with the interchange of natural resources. For example, American silver

505   enhanced Chinese economy particularly on final of Ming and beginning of Qing Dynasties

506   (Flynn and Giráldez 2002; Flynn et al. 2003); and American crops species (maize, potato,

507   sweet potato) helped mitigating human famine and changed human population dynamic

508   (mainly in eighteenth century). In addition, sugar cane from SE Asia influenced socioeconomic

509   organization and food habits in America (Mann 2006). Nowadays, both areas continue with

510   some relationships that not only favor international trade of material resources (i.e. China is the

511   main soybean importer from Argentina), but also important flows of people, information and

512   cultural aspects (as garden diversity composition, type of food, natural medicine, etc). Three of

513   the cities described here, in which the surrounds are being invaded by *L. lucidum* forests (Salta,

514   San Miguel de Tucumán and Córdoba), have more than 1% of their population composed by

515   Asian people (INDEC 2010). Also, these cities and San Salvador de Jujuy, were important

516   nodes of the trade route known as the ''Hispanic American china silk route'' used to commerce

517   different goods from Asia during the colonial times (Bonialian 2014). Essl et al. (2011)

518   emphasizes that the impact of human activities and socio economy legacy on species invasion

519   can often exhibit a considerable time lag. For these reasons, we argue that historical flows and

520   connections between native (China) and novel ranges (Argentina) need to be studied as

521   relevant drivers of cultural landscape change and *L. lucidum* invasion.

522

523   **Conclusions**

524   Two main conclusions emerge from this study: First, a multiscale approach is necessary

525   to explain invasive species distributions. Second, the interaction at multiple-scale between

526   biophysical variables and factors involved in the development of cultural landscapes is crucial

527   to explain invasive species success. As a corollary, we suggest that a better developed inclusion

528   of cultural aspects into the theory of invasion is a priority.

529   Our results suggest that at regional scale, Yungas ecoregion of NW Argentina presents

530   climatic conditions adequate for *L. lucidum* expansion. However, for the invasion to develop it

531   is necessary the co-occurrence of other factors. In the studied area invaded ranges are clustered

532   around the regional major cities and according to scale rules (i.e., the bigger the city, the larger

533   the invaded area), thus suggesting that major urban centers in the Yungas ecoregion could

534   create particular conditions in their surrounding areas that increase invasibility. The

535   mechanisms that explain the relationship between cities size and *L. lucidum* invaded area are

still unclear and need more research; but the contagious pattern of invasion suggests that propagule pressure and biological mechanisms (as seed dispersion and vegetative reproduction) can play a key role. Although we only evaluated recent historical factors of land use change in relation to trees invasion, we suggest that understanding the longer-term historical legacy of socioeconomic teleconnections between Asia and the Americas may provide useful insights for the development of a framework of teleconnected cultural landscapes, a potentially important concept for the geographical socioecology of the Antropocene.

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801

802   **Tables**

803   **Table 1.** Spatial patterns of *L. lucidum* forests (LF) and other land-cover classes around three

804   study areas in NW Argentina at sub-regional scale (**Y**: Yala; **SL**: San Lorenzo and **SSJ:** Sierra

805   de San Javier).

Variables	Y	SL	SSJ
Land-cover class (ha)			
Total study area	104,801	103,591	246,732
Urban	4,796	5,260	8,333
Forest (F)	85,301	75,842	162,901
L. lucidum forest (LF)	11	36	667
Other	14,693	25,134	76,130
Spatial analysis of L. lucidum forests			
Rate of LF/F (%)	0.01	0.03	0.3
Number of LF patches	82	238	1053
Mean patch size (ha)	0.13	0.15	0.63
Total border/total area (m)	0.11	0.10	0.05
Average nearest-neighbor distance (m)	1099	462	231
Mean proximity index	0.34	0.82	11.4

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809   **Table 2.** Results of multiple logistic regression at local scale

810   (Dependent variable= Presence of *L. lucidum* forests in 2010; Independent variables=

811   environmental condition and distance to different land cover in 1972)

Variables	b'	mean	sd
Intercept	-3.97		
Environmental Variables			
Elevation (m.a.s.l.)	5.99	781.2	383.20
Mean annual precipitation (mm from *WorldClim*)	2.00	923.0	94.25
Slope (%; 100% = 45°)	-1.88	17.5	23.18
Aspect (°)	0.13	121.9	100.09
Land use/cover Variables			
Distance to rivers (m)	-0.77	1198	1054.71
Distance to roads (m)	-6.21	1247	1277.46
Distance to areas with *L. lucidum* in 1972 (m)	-182	3218	2619.89
Distance to Montane grassland (m)	7.67	4299	5204.82
Distance to urban areas in 1972 (m)	-2.21	6895	5950.52
Distance to Sugar cane (m)	-2.38	861	1252.18
Distance to Citrus plantations (m)	-5.06	639	1062.34
Distance to Dry forest (m)	-3.36	1831	2350.33
Distance to Anthropogenic grassland (m)	2.31	2835	3849.53

Pseudo-R^2	0.66

812   b' (Standard coefficient) represent the contribution of each independent variable to explain the

813   probability of occurrence of the dependent variable and was calculated according to Lesschen

814   et al. (2005). Pseudo-R^2 = 1 indicates a perfect fit. Pseudo-R^2 greater than 0.2 is considered a

815   relatively good fit.

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Figure Captions

Figure 1: a) Location of the study area in Argentina at three different scales: (I) regional, (II)

sub-regional and (III) local, b) Original Yungas ecorregion (native forest) and map of potential

L. lucidum distribution in NW Argentina.

Figure 2. *Ligustrum lucidum* forests current distribution and different land covers at sub-

regional scale. ■ Water† (lakes, lagoons, dams and rivers), ■ Urban (cities, roads and others

built-up areas), ■ Forest (native perennial and deciduous forests and tree plantations), ■ *L.*

lucidum forests (mono-specific and mature secondary forest). ■ Others (all other cover types

(i.e. extensive agriculture, grassland, mix agriculture, citrus and perennials plantation, sugar

cane crops, cleared, roads and bare soil). † This class was considered as "other" in most of the

analyses, figures, and tables. Black circles show areas with *L. lucidum* forests.

Figure 3. *Ligustrum lucidum* forests (ha) and environmental or distance variables in the three

peri-urban areas of NW Argentina (Y: Yala, SL: San Lorenzo, SSJ: Sierra de San Javier) at sub-

regional scale.

Figure 4. Relationship between urban features and *Ligustrum lucidum* forests by in the three

peri-urban areas of NW Argentina (Y: Yala, SL: San Lorenzo, SSJ: Sierra de San Javier) and

Córdoba city (Cba). Data presented was transformed to natural logarithm (LN) in all cases.

Data for Córdoba was obtained from Gavier-Pizarro et al 2012. Population data was extracted

from official data of INDEC. Censo Nacional de Población, Hogares y Viviendas 2010.

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856 **Figure 5**. Land cover type spatial distribution in 2010 at local scale. Black circles highlight

857 areas that present *Ligustrum lucidum* forests. The small maps in the lower left corner shows the

858 location of Tucumán province in Argentina and the location of surveyed area at local scale

859 inside the province.

860

861 **Fig. 6.** Local scale study in Sierra de San Javier (Tucumán). a) Area invaded by *Ligustrum*

862 *lucidum* in each date during the period 1972-2010. b) Area of land cover classes replaced by *L.*

863 *lucidum* forests during the period 1972-2010. The values express the relative percentage of

864 each land cover over the total invaded area during the period. MG: mountain grassland, CP:

865 citrus plantations, AG: anthropogenic grassland, DF: dry forest and SC: sugar cane
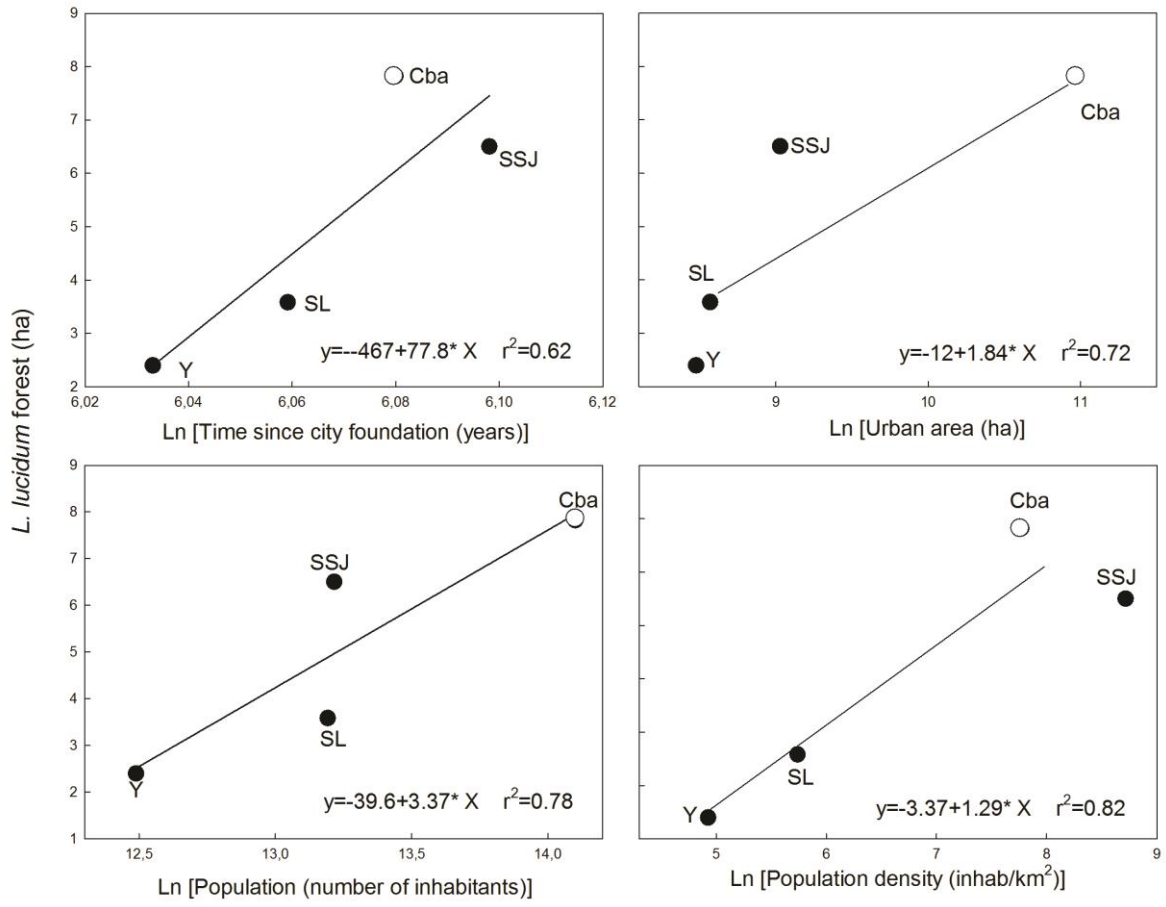
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878   **Figures**

879   Figure 1.

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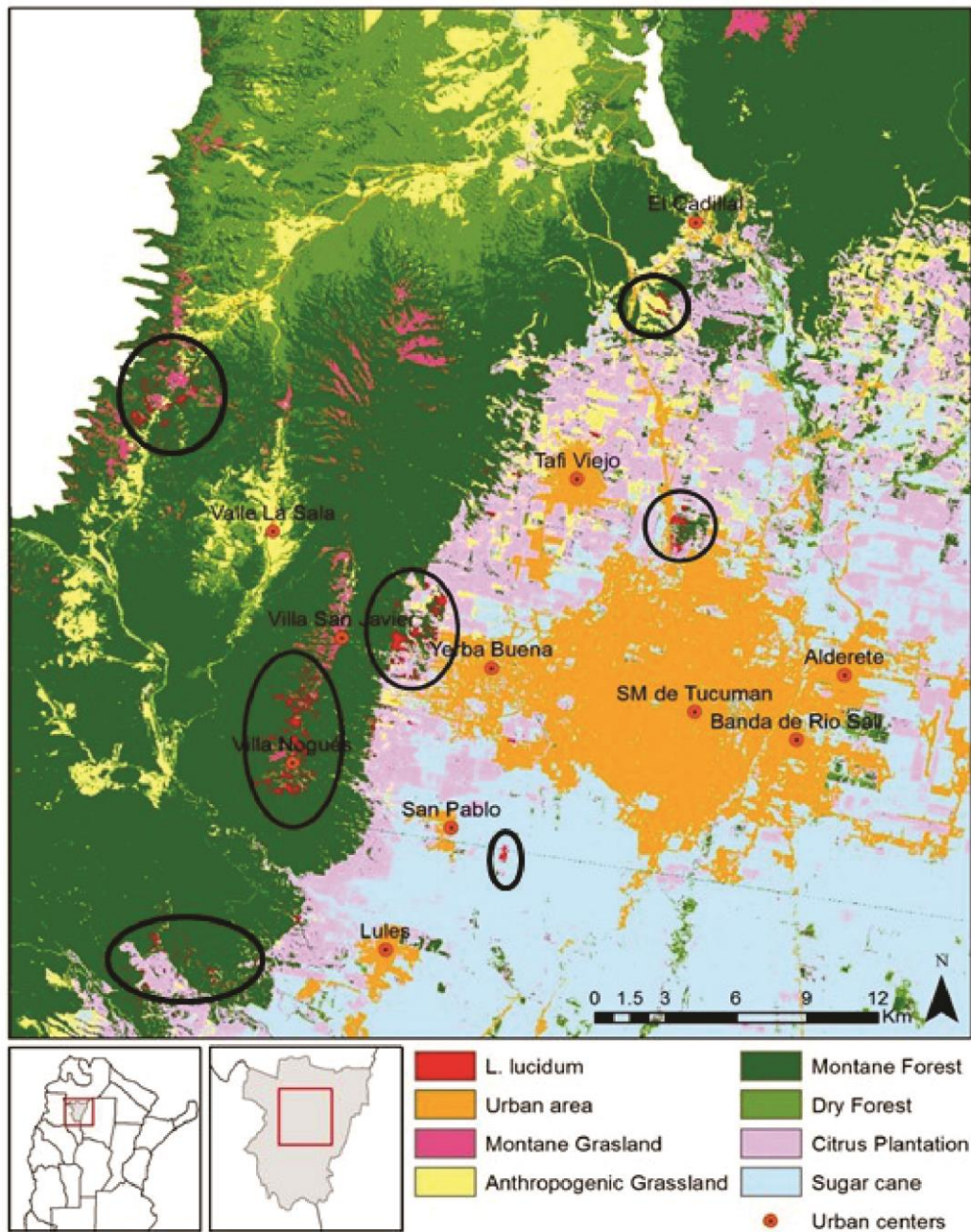886
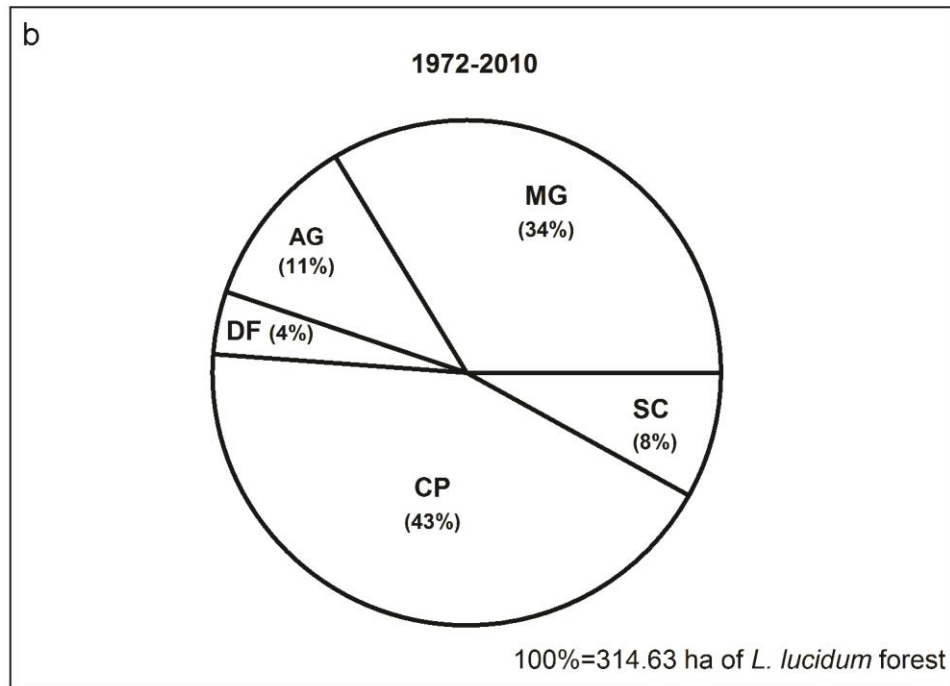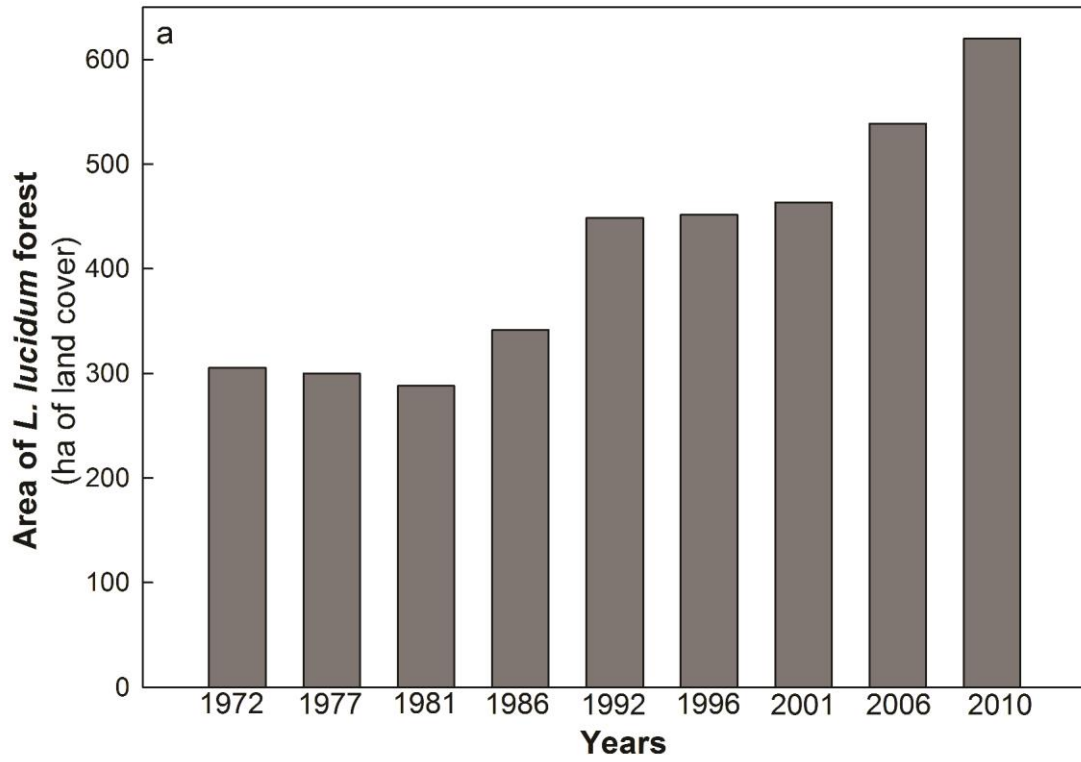
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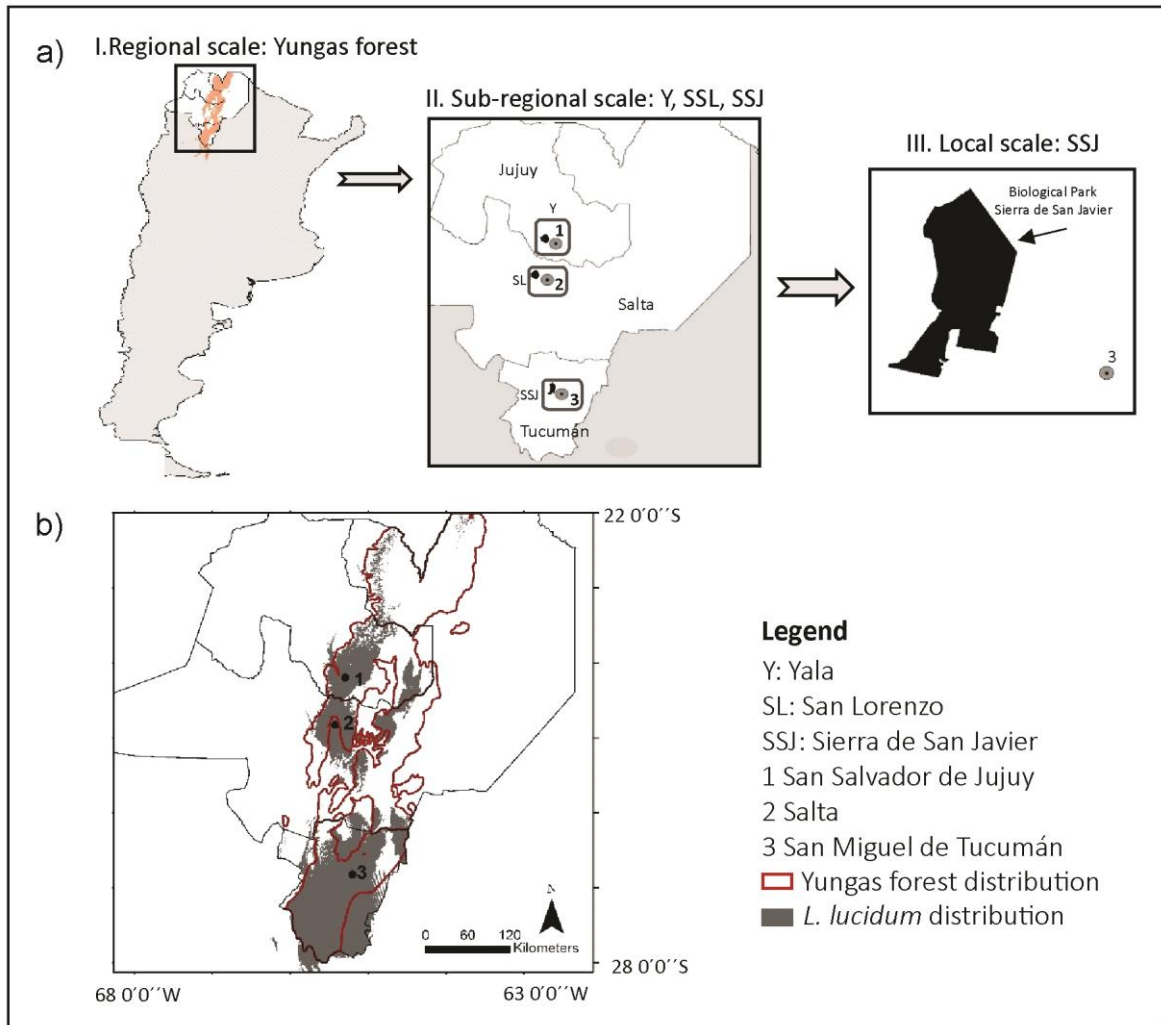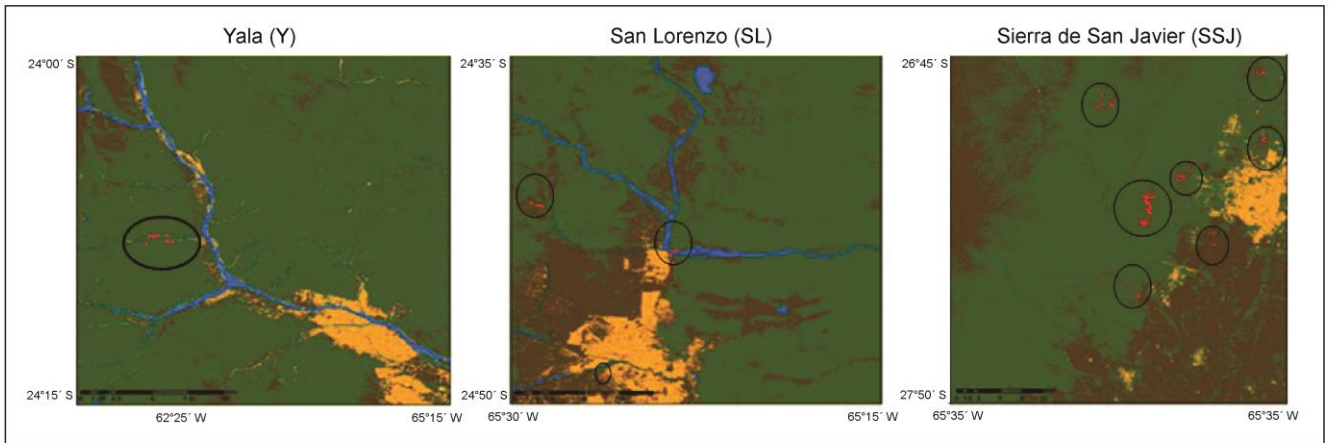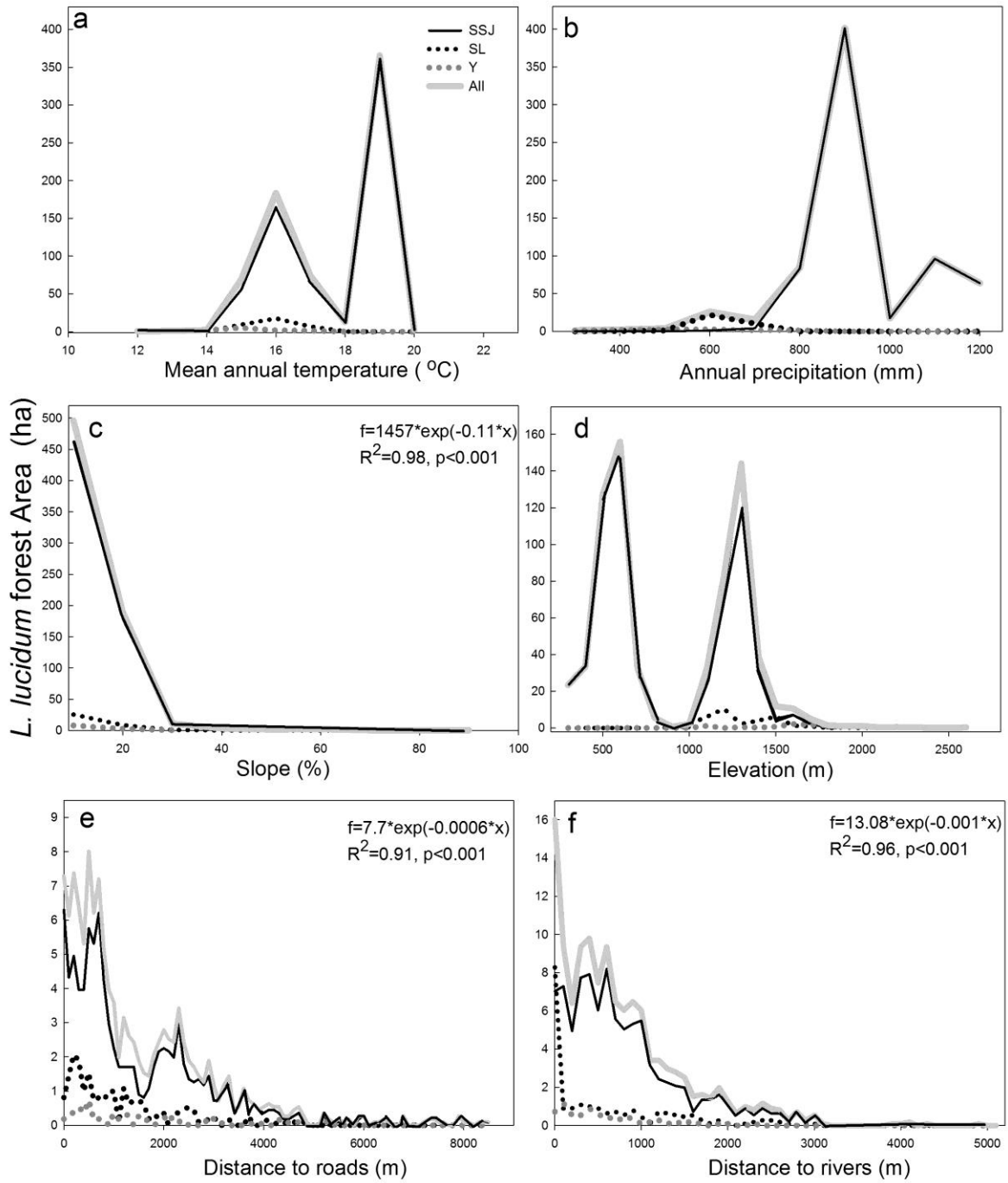
892   Appendices

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894   Appendix 1. Area (ha) of different land cover categories at different past date for total area invaded by

895   *L lucidum* (LF) at 2006. DF: Dry forest or "Chaco forest", MG: Montane grassland, AG: Anthropogenic

896   grassland and shrubland, SC: Sugar cane, CP: Citrus plantations, UR: High-to-medium density urban

897   areas.

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	1972	1977	1981	1986	1992	1996	2001	2006
UR	0	0	0	0	0	0	0	0
MG	106,02	105,39	55,98	47,52	27,45	13,86	25,29	12,87
AG	35,1	29,25	27,72	11,43	8,82	8,01	20,07	10,98
LF	305,37	299,88	288	341,37	448,56	451,35	463,32	538,83
DF	12,69	11,79	39,96	1,35	1,98	1,8	4,59	4,86
CP	135,72	136,8	179,28	199,44	125,73	137,16	99	50,4
SC	25,47	37,26	29,43	19,26	7,83	8,19	8,1	2,43

899   * values expressed in hectares.

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902 Appendix 2. Results of the invaded area expressed as a percentage of the initial area of each land cover category, to represent the magnitude of

903 changes relative to the spatial extension of each land cover in the study area. LF= *L. lucidum* forests. SMF: Subtropical montane forest, DF: Dry

904 forest or "Chaco forest", MG: Montane grassland, AG: Anthropogenic grassland and shrubland, SC: Sugar cane, CP: Citrus plantations, UR: High-

905 to-medium density urban areas.

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	1972 (ha)	LF (ha)	LF (%)	1977 (ha)	LF (ha)	LF (%)	1981 (ha)	LF (ha)	LF (%)	1986 (ha)	LF (ha)	LF (%)	1992 (ha)	LF (ha)	LF (%)
UR	3619,08	0	0,00	4884,4	0	0	5865,5	0	0	7263,9	0	0	7758,45	0	0
MG	5682,42	106,02	1,87	6226,1	105,39	1,6927	3985,1	55,98	1,4047	4146,57	47,52	1,14601	3723,03	27,45	0,7373
AG	6389,46	35,1	0,55	10559	29,25	0,277	10236	27,72	0,2708	10187,64	11,43	0,11219	12286,9	8,82	0,07178
SMF	45043,2	305,37	0,68	61863	299,88	0,4847	63759	288	0,4517	63525,78	341,37	0,53737	65033,6	448,56	0,68974
DF	5877,81	12,69	0,22	22858	11,79	0,0516	23043	39,96	0,1734	20275,74	1,35	0,00666	19141,1	1,98	0,01034
CP	15709,86	135,72	0,86	19183	136,8	0,7131	25924	179,28	0,6915	23889,33	199,44	0,83485	24669,3	125,73	0,50966
SC	36303,3	25,47	0,07	59384	37,26	0,0627	52144	29,43	0,0564	55668,78	19,26	0,0346	52345,4	7,83	0,01496
Others*	52189,65	73,26	0,14	97686	78,3	0,0802	91289	97,11	0,1064	93396,06	32,04	0,03431	91531,9	18,63	0,02035

907

	1996 (ha)	LF (ha)	LF (%)	2001 (ha)	LF (ha)	LF (%)	2006 (ha)	LF (ha)	LF (%)
UR	9044,28	0	0	10866,87	0	0	13983,84	0	0
MG	3380,94	13,86	0,409945	3192,75	25,29	0,792107	3326,31	12,87	0,386915
AG	10536,12	8,01	0,076024	11522,07	20,07	0,174187	12343,23	10,98	0,088956
SMF	64682,1	451,35	0,697797	65372,94	463,32	0,708734	67127,31	538,83	0,802699
DF	19408,32	1,8	0,009274	21561,66	4,59	0,021288	22085,19	4,86	0,022006
CP	22187,16	137,16	0,618195	24420,24	99	0,405401	29573,55	50,4	0,170423
SC	55718,82	8,19	0,014699	48021,21	8,1	0,016868	36518,31	2,43	0,006654
Others*	94707,54	18	0,019006	91971,81	32,76	0,03562	84930,57	18,27	0,021512

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909 * "Others" includes the sum of UR, DF, AG and SC
910