Landscape Ecol (2017) 32:2167–2185
DOI 10.1007/s10980-017-0563-2

RESEARCH ARTICLE

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

Lia Montti · Verónica Piriz Carrillo · Jorgelina Gutiérrez-Angonese · N. Ignacio Gasparri · Roxana Aragón · H. Ricardo Grau

Received: 4 October 2016 / Accepted: 18 August 2017 / Published online: 11 September 2017

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

---

Electronic supplementary material The online version of this article (doi:10.1007/s10980-017-0563-2) contains supplementary material, which is available to authorized users.

L. Montti (✉) · V. P. Carrillo · N. I. Gasparri · R. Aragón · H. R. Grau
Instituto de Ecología Regional-CONICET-Universidad Nacional de Tucumán, CC 34, (4107) Yerba Buena, Tucumán, Argentina
e-mail: liamontti@gmail.com

L. Montti
Instituto de Investigaciones Marinas y Costeras-CONICET, Instituto de Geología de Costas y del Cuaternario Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Mar del Plata, CC 722, Deán Funes 3350, (7600) Mar del Plata, Buenos Aires, Argentina

J. Gutiérrez-Angonese
Laboratorio de Socio-ecosistemas, Universidad Autónoma de Madrid, Madrid, Spain

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 socio-cultural 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 (Alston and Richardson 2006; Botham et al. 2009; Wang et al. 2011a, b). 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 and Richardson 2010; Hulme 2011; Pergl et al. 2016). Recent studies found that human population and wealth (Pyšek et al. 2010; Decker et al. 2012), as well as the historical legacy (Essl et al. 2011) are strong predictors of a wide range of invasive species distribution. Therefore, it is expected that cities and anthropogenic peri-urban landscapes play a key role in the introduction and spread of invasive species.

The capacity of a particular species to colonize areas depends on the interaction among propagule availability, dispersal capacity, population growth potential, and landscape heterogeneity (Vilá et al. 2008; O'Reilly-Nugent et al. 2016). In this sense, biological (e.g., intrinsic species attributes, life history traits) (Grotkopp and Rejmánek 2007; Leishman et al. 2007; Peñuelas et al. 2010) and environmental factors (climate, topography, hydrology) are important drivers that interact with human activities and determine the geographical extent of plant invaders in their novel distribution range (Rejmánek and Richardson 1996; Thuiller et al. 2006). For example, human disturbances can regulate resource availability (e.g., light, soil nutrients), affecting ecosystem invasibility and often enhancing the competitive ability of invasive species (Standish et al. 2008; Karalius and Alpert 2010). Furthermore, changes in landscape configuration (e.g., replacing forests by grasslands, increased of roads, etc.) can affect dispersal barriers and corridors and thus, the spread pattern (Miller et al. 2015). This results in higher invasion rates in fragmented landscapes than in continuous and unconnected areas (Vilá and Ibañez 2011). When the cultural landscape construction results in strongly modified environmental conditions, they can overwhelm the influence of climate and natural physical environment (e.g., soils, hydrology or topography) (Chiron et al. 2009; Sharma et al. 2010; Fuentes et al. 2015). Cities and peri-urban areas are characterized by distinctively intensive features of the cultural landscape. In addition to present-day landscape configuration, invasions are often associated with the historical changes in land-use (Mosher et al. 2009; Vilá and Ibañez 2011). Although biophysical factors and their interaction with city dynamic can be very relevant to understand biological invasion processes as side effects of cultural landscape development, they have been largely explored separately.

The cultural landscape construction in the subtropical humid forest of northwest Argentina, Yungas ecoregion, experienced a major change with the

Spanish arrival in the region in the sixteenth century. As a result of the territory reconfiguration implemented during colonial times, the main productive activities and population shifted from the highlands in the pre-Hispanic and early Hispanic period, to the forested humid flatlands of the foothills. Much of the lowland and lower montane forests with flat topography were deforested for agriculture and grazing, and the main urban centers were located nearby. These areas include the three province capital cities of the region: San Miguel de Tucumán, Salta, and San Salvador de Jujuy, with approximately 900,000, 600,000 and 300,000 inhabitants, respectively (INDEC 2010). During the past decades, several montane areas near these urban centers experienced abandonment or disintensification of agriculture and livestock grazing, which resulted in the expansion of secondary forests (Grau et al. 2008; Gutiérrez-Angonese and Grau 2014). Parts of these new forests are dominated by exotic tree species. A large proportion of them are originally from SW Asia, including *Ligustrum lucidum* W. T. Aiton (Oleaceae), the most aggressive and fast growing tree species in this area (Grau and Aragón 2000; Aragón and Morales 2003; Easdale et al. 2007). *L. lucidum* was possibly introduced primarily for urban shade, gardening, living fences and windbreaks. One of the first records in Argentina dates to c.1900 (Montti et al. 2016). The extent of *L. lucidum* forests and the drivers of the invasion are still not well documented. Here, we follow a multiscale approach to explore the dynamics of this invasion into cultural landscapes in NW Argentina, with particular emphasis on the role of cities and distant connections between native and novel ranges of distribution of this species. Specifically in this study, we pursued the following objectives: (1) to identify the potential area of invasion by *L. lucidum* in the Yungas ecoregion of Argentina using ecological niche distribution models, (2) to map, quantify and describe current invaded area in this ecoregion by using satellite images in three peri-urban focal zones, and (3) to quantitatively describe the spatial and temporal patterns of *L. lucidum* forest invasion at local scale, linking environmental and cultural landscape features in the largest peri-urban sector of the region: San Miguel de Tucumán and Sierra de San Javier (SSJ).

Methodology

Studied species

Ligustrum lucidum or Chinese glossy privet is an evergreen tree native of the south of the Yangtze River in China, where it grows in different climates and soil types between 0 and 2900 m.a.s.l., in full sunlight, as well as in shaded understory (Chang et al. 1996). *L. lucidum* has been extensively cultivated for different purposes (e.g., traditional medicine, culturing wax-insects to obtain white wax, furniture) for a long time in China. Because of its particular functional traits (e.g., fast growth rate, tolerance to air pollution), it is regarded as a great landscaping plant and it is used extensively as an ornamental in streets and gardens around the world (Guilhermetti et al. 2013). But it is also considered a successful global invader outside its native range (Panetta 2000; Aslan et al. 2012; Montti et al. 2016).

Study area

Our study focuses on Yungas ecoregion, the humid native forests of northwestern Argentina (−22.25° S to −27.95° S, −64.22° to −65.65° W; Fig. 1a). The climate is subtropical with a monsoon regime of precipitation (dry winters, rainy summers) (Brown et al. 2001). Temperature and precipitation are controlled by topography; the average annual temperature is high in the eastern piedmont (20 °C) and decreases with elevation. Precipitation exceeds 1100 mm per year (Bianchi 1981), 78% concentrated in the months of November to March. Additional supply of water, particularly during the dry season, comes from fog or horizontal rain (Hunzinger 1997). The native humid forest that *L. lucidum* replaces has a high proportion of evergreen and semi-deciduous tree species, with *Ocotea porphyria*, *Blepharocalyx salicifolius*, *Pisonia ambigua* and *Cedrela lilloi*, as dominant tree species (Brown et al. 2001; Grau et al. 2010; Blundo et al. 2012). For the purpose of this study, three spatial scales of analysis were considered: (1) regional: including all Yungas distribution in Argentina, c. 5.2 million ha, (2) sub-regional: three pre-selected focal zones or sectors where invasion was notorious covering 408,500 ha approx., and (3) local: that include the most affected sector by the invasion, near to

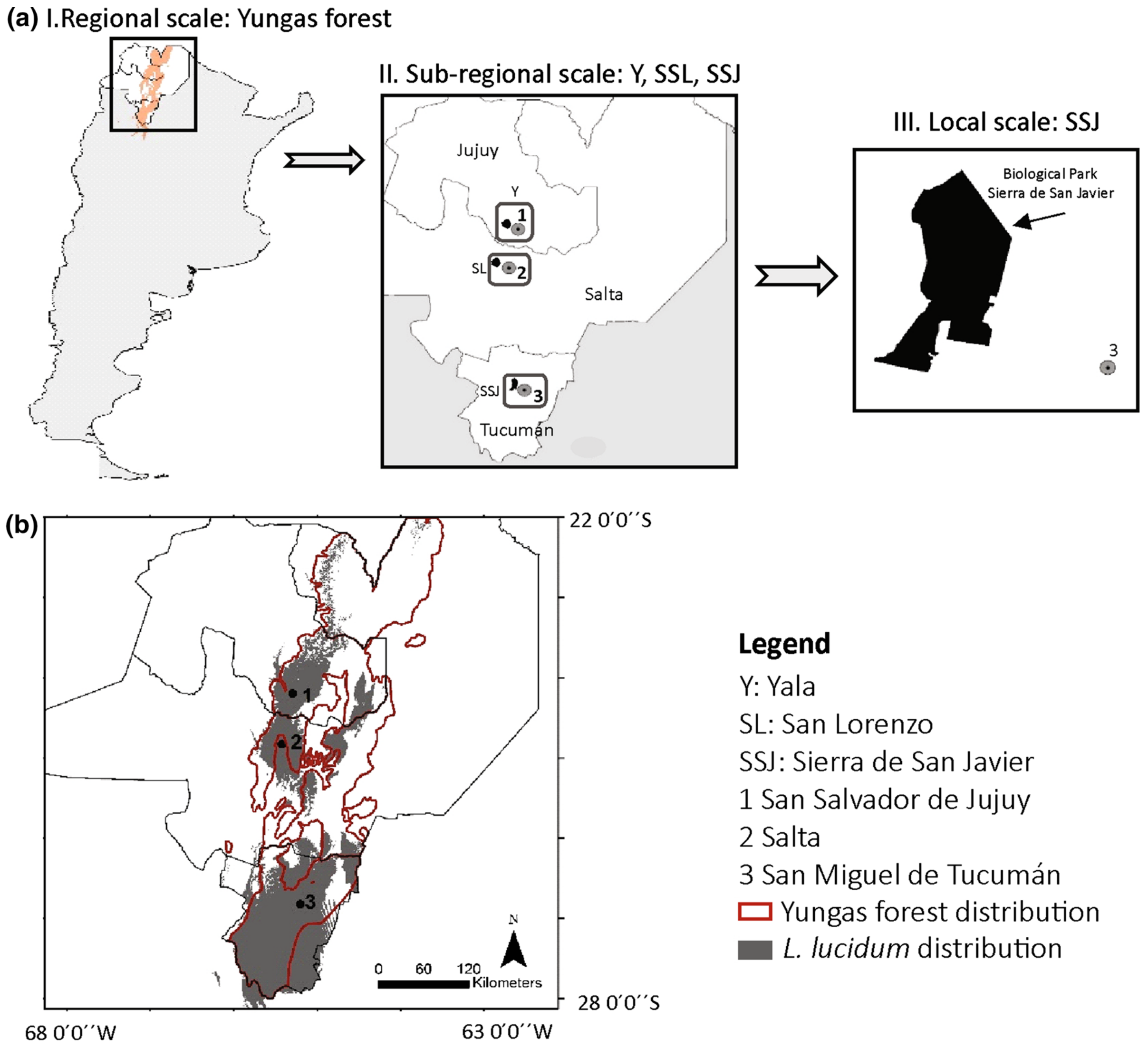

Fig. 1 **a** Location of the study area in Argentina at three different scales, **b** Original Yungas ecorregion (native forest) and map of potential *L. lucidum* distribution in NW Argentina

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

Potential distribution of *Ligustrum lucidum* at regional scale

We generated a potential distribution map at regional scale based on recently observed presence records, climatic variables and maximum entropy algorithm implemented in Maxent 3.3.1 (Phillips et al. 2006). This map represents the distribution of suitable climatic conditions for *L. lucidum* in our study area. Maxent has proven to produce more reliable results than other comparable methods such as Bioclim, Domain or Garp (Wisz et al. 2008). This reliability has been confirmed by its high capacity to predict novel presence for not so well-known species (Pearson et al. 2007) and to predict the outcome of introductions of invasive species outside the native range (Ficetola et al. 2007; Rödder et al. 2008; Rödder and Lötters 2009). We initially considered 127 presence records of *L. lucidum* collected from fieldwork (50%), national herbarium specimen data examined by the authors (35%) and well as other records reported in the literature throughout the study area (15%). Obviously erroneous occurrence points (e.g., coordinates outside the studied area under which they had been listed) and duplications resulting from the merger of records from the different sources were removed. In the case of invasive species, most records tend to be collected where high densities of people and researchers occurs. This sampling bias may influence the prediction of the model. Therefore, we removed randomly presence records that were geographically close together trying not to leave records in adjacent cells. As a result, not all presence records collected were used in model calibration (60 presences records).

First, we obtained an initial set of 10 models setting Maxent with hinge and quadratic features and cross-validation, using 90% of presence data to fit the model and the remaining 10% for model validation given the small number of presence points. In addition, we disaggregated potentially clustered/repeated presence records by randomly selecting one per grid cell. In order to characterize the "background" of environment available to the species, we restricted the area only to the study region (Merow et al. 2013). This initial set was used to identify variables with minimal or no contribution to overall model taking into account the predictive efficacy using the jackknife test of variable importance, variable response curves and percent contribution of each variable in the model. Only environmental variables with relatively low collinearity (i.e., Pearson correlation values lower than 0.7 considering only the cells with presence data) and greater biological significance were selected. The average training gain values of selected variables were examined once again and the variables showing the lowest decrease in gain values when omitted from the full model were removed. These variables correspond to a subset of 19 climatic variables from the WorldClim database (http://www.worldclim.org/; Hijamans et al. 2005), that were projected at a 30 arc second (approximately 1 km^2) spatial resolution.

The model's performance was evaluated using the area under the receiver operating characteristic curve (AUC). An AUC value of 0.5 indicates that the performance of the model is no better than random, while values closer to 1.0 indicate better model performance (Phillips et al. 2006). To obtain a model we ran Maxent with 100 replicate using the reduced set of variables and the same setting. Then the 10 models with greatest AUC values were selected and averaged to obtain the final model. Finally, to generate a binary prediction of occurrence it was necessary to choose a threshold. Because no single procedure is recommended to select thresholds, we used a *maximum training sensitivity plus logistic threshold* to cut-off. This criterion has been described as the most objective to identify optimal habitats when only presence data are available (Liu et al. 2013a, b). Pixels with a value higher than the selected threshold were considered presence data, meaning that they harbored the appropriate climate conditions for the species. We used ArcGis 10.1 and Spatial Analysis tool to construct the final model.

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

To evaluate and quantify the current distribution of *L. lucidum* forests we surveyed the whole Yungas ecoregion in Argentina and identified three focal zones where invasion was notorious (i.e., where several hectares of monodominant forest are present). These sectors included the peri-urban landscapes around the most important cities, centered in the localities of Yala (*Y*, Jujuy province), San Lorenzo (*SL*, Salta province) and Sierra de San Javier (*SSJ*, Tucumán province). These study sectors were included in two subsets of Landsat TM images: scene path 231/row 77 for *Y* and *SL* and scenes path 231/row 78 and 79 (mosaic) for *SSJ*. Four images were selected for each sector corresponding to January, July, August and December 2010 to maximize potential differences in phenology between native and exotic forest. Images were almost cloudless; the remaining few clouds (less than 10% in two images in one date) were masked. Landsat image proved an excellent alternative at low cost to mapping spread of *L. lucidum* forests and was previously used by Hoyos et al. (2010) and Gavier-Pizarro et al. (2012) in more seasonal forests of Argentina at higher latitude. The images have 30 × 30 m spatial resolution and were orthorectified and georeferenced using GPS points obtained in the field (geopositional error <10 m) and converted to the official coordinate system of Argentina (Gauss-Krügger POSGAR94 System, zone 3). The six multispectral bands of the Landsat images were combined into a single multi-temporal stack with resulting 24 bands for each study area. The stack of bands also included the normalized difference vegetation index

(NDVI) and the hill shade image, obtained from the digital elevation model resampled to match the spatial resolution to a 30 × 30 m pixel, which allows modelling the shadows caused by the topography. As a result, final staked images included 26 layers of information: 24 multispectral bands + NDVI + hill shade. Images were obtained from the *Instituto Nacional de Pesquisas Espaciais* (http://www.dgi.inpe.br/CDSR/). Lastly, multi-temporal images for the three sites were clipped to cover the interest sectors leaving a surface of 106,183 ha for *Y* and *SL* sector, and 248,305 ha for *SSJ*.

Land cover maps were derived using the non-parametric classifier support vector machine (SVM; Hsu et al. 2007). SVM defines a hyperplane that separates points corresponding to two different classes in a multidimensional space (Huang et al. 2002; Foody and Mathur 2004). In our case, land cover was classified into five classes: 1, forest (including Yungas and dry forest, but also a small proportion of tree plantations), 2, *L. lucidum* forest, 3, urban, 4, water, and 5, others (agriculture, grassland, mix agriculture, citrus and perennials plantation, cleared, roads and bare soil). *L. lucidum* forests differ substantially in structural and physical characteristics from native forest (Grau et al. 2010). *L. lucidum* canopies are evergreen and closed, resulting in higher absorption in the visible domain and higher reflection in the near-infrared domain and thus present high NDVI (Zamora Nazca et al. 2014). During fieldwork in 2010, we identified training areas used to parameterize a SVM classifier. This methodological approach was previously used to classify our study species in other region of Argentina by Gavier-Pizarro et al. (2012).

Ligustrum lucidum relationship invasion with environment and land-cover changes at sub-regional and local scale

Based on the current distribution map of the *L. lucidum* forests in the three focal sectors (see current distribution of *Ligustrum lucidum* forest at sub-regional scale section) the landscape structure of these invaded stands was analyzed using the FRAGSTATS software (McGarigal and Marks 1995) at sub-regional scale. The selection of metrics was based on their ability to characterize various aspects of fragmentation such as: class area (sum the area of all fragments per class), mean patch size (an index of fragmentation), number of patches (an indicator of several ecological processes and landscape heterogeneity), total edge length (indicator of patch complexity), average nearest-neighbor distance and mean proximity index. Additional information on these metrics and detailed mathematical description can be found in McGarigal and Cushman (2002). In addition, we used ArcGis 10.1 and Spatial Analysis tool to compute descriptive statistics and explore the relationship between geographic distribution of *L. lucidum* forest patches and variables such as slope, elevation, temperature, precipitation and distance to roads, rivers and urban areas. We also explored the relationship between *L. lucidum* forests per sector (*SSJ*, *SL* and *Y*), population and cities' features as time of foundation and size by fitting linear regression. Population data was extracted from official data of Censo Nacional de Población, Hogares y Viviendas 2010. INDEC-Instituto Geográfico Nacional (IGN, http://www.sig.indec.gov.ar/censo2010/). Additionally, to enrich the discussion we combined *Ligustrum* sub-regional map and urban data with the data from Córdoba City extracted from Gavier-Pizarro et al. (2012) where *L. lucidum* invasion has been reported.

To analyze the influence of past land-uses on forest invasion and to assess the invasion rate we worked at local scale in *SSJ* and San Miguel de Tucumán City, the most affected sector by the invasion. San Miguel de Tucumán is the largest political, economic and cultural urban center in NW Argentina. For this analysis, we used an additional set of land cover history data that we combined with our *L. lucidum* forests areas for 2010. The series of land cover maps previously made for *SSJ* by Gutiérrez-Angonese and Grau (2014) and Gutiérrez-Angonese (2015) were derived from Landsat MSS and TM images (30 × 30 m of spatial resolution) from 1972 to 2010, selecting early-spring cloud-free images with a temporal frequency of 4–5 years (1972, 1977, 1981, 1986, 1992, 1996, 2001, 2006 and 2010). All Landsat images were image-to-image spatially co-registered and atmospherically corrected using DOS method (Song et al. 2001). Images were classified by applying the machine learning algorithm Random Forest (Breiman 2001), using the Random Forest Package (Liaw and Wiener 2002) in the R statistical Software (R Development Core Team 2014). For this map land cover was classified into seven categories: 1, montane forest (SMF) that we called here Yungas forest, 2, dry forest or “Chaco” (DF), 3, montane grassland (MG), 4, anthropogenic grassland and shrubland (AG), 5, sugar cane (SC), 6, citrus plantations (CPs) and 7, high-to-medium density urban areas (UR). Final accuracy estimation OOB (out of bag) ranges from 8.8 to 12.6% of error in TM scenes and 12.9 to 18.8% in MSS scenes (Gutiérrez-Angonese and Grau 2014). To combine our data with the land cover history, we used our map of invaded areas by *L. lucidum* in 2010 as a reference. The set of data from Gutiérrez-Angonese and Grau (2014) and Gutiérrez-Angonese (2015) was used to estimate the temporal trajectory of the invasion and the previous land cover for the areas that end being *L. lucidum* forests in 2010. In the Gutiérrez-Angonese and Grau (2014) and Gutiérrez-Angonese (2015) data, different land covers were discriminated (see above), but *L. lucidum* forests were not discriminated from native forest (Yungas). Therefore, the map of *L. lucidum* forests in 2010 was used as a mask to extract the information from the history land cover maps and the invasion rate was estimated assuming that the class “SMF” in the Gutiérrez-Angonese and Grau data corresponds to *L. lucidum* forests.

Additionally, to investigate the factors that were associated with past invasion patterns of *L. lucidum*, we performed a multiple logistic regression using the presence of *L. lucidum* forests in 2010 as a binary dependent variable, and two sets of independent environmental and land use variables derived from the map of 1972 (Eastman 2016) (Table 2). A stratified sample (selecting 10% of the pixels) was applied to reduce the inherent spatial autocorrelation of spatial data (i.e., locations close to each other exhibit more similar values than those further apart). Model fit was evaluated through the pseudo-R^2 coefficient, ranging from 0 to 1 (values greater than 0.2 means a good fit, Eastman 2016), representing the percentage of variance explained in non-linear functions. Additionally, the contribution of each independent variable to explain the probability of occurrence of *L. lucidum* forests in 2010 was assessed by obtaining the standardized coefficients (b') of each variable, which allows comparing variables with one another, regardless of the unit of measurement for each variable. Standard coefficients were quantified using the formula proposed by Lesschen et al. (2005). The higher the ‘b’ value the more the corresponding variable contributes to explain the presence of *Ligustrum* forests in its current location.

Results

The model of potential *L. lucidum* distribution at regional scale (Fig. 1b) had a good overall accuracy with an AUC of 0.82 for independent data. Four variables were used in the setting of final model of the predictive map with different relative contribution: Bio 14: precipitation of the driest month (56%), Bio 1: annual mean temperature (25%), Bio 12: annual precipitation (12%) and Bio 6: minimum temperature of the coldest month (7%). The spatial model generated only by these environmental variables suggests that the study area presents a high climatic suitability, almost overlapping in some part with the distribution of Yungas ecoregion in Argentina (Fig. 1b). This is not surprising, given that *L. lucidum* tolerate a wide range of environmental conditions (Chang et al. 1996).

Despite its wide potential distribution range, *L. lucidum* forest patches were limited in 2010 to three “hotspots” of invasion in the peri-urban areas of the largest cities (Fig. 2). The *L. lucidum* forests covered approximately 700 ha in 2010, that represents 0.22% of the total forest area (324,000 ha) in these three sectors and was distributed in several patches (relatively discrete forest areas) with mean patch size of <0.6 ha (Table 1). Although the mean patch size was small, a high proportion of the invaded forests were distributed in large patches (between 2 and 38 ha, that represent more than 50% of the total invaded area). *SSJ* in Tucumán has the largest area of *L. lucidum* forests, and *Y* the smallest one. The spatial and spectral resolution of the Landsat TM images (30 m) did not allow us to detect young or mixed forest of *L. lucidum*, and only monodominant-invaded forest was detected, mapped and analyzed. Landscape indices appear related to the size of the total invaded area per sector. We observed an increase in mean patch size and a decrease in distance to nearest-neighbor from *Y* to *SSJ* (less to more invaded areas; Table 1); indicating a process of forest patch coalescence (inverse of fragmentation) as the area of *L. lucidum* forests increases.

At sub-regional scale, the current *L. lucidum* forests were located between 15 and 19 °C mean annual temperature and 600–900 annual precipitation and in

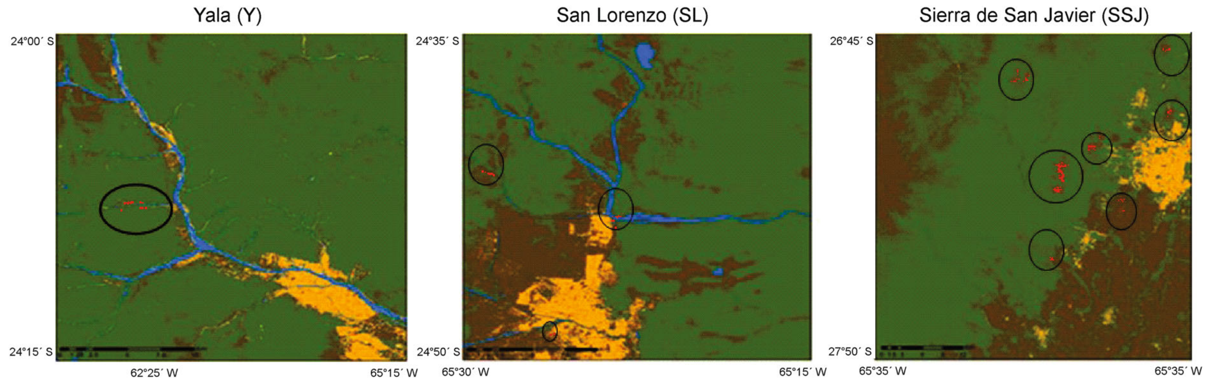

Fig. 2 *Ligustrum lucidum* forests current distribution and different land covers at sub-regional scale. *Blue squares* water† (lakes, lagoons, dams and rivers), *yellow* urban (cities, roads and others built-up areas), *green* forest (native perennial and deciduous forests and tree plantations), *red L. lucidum* forests (mono-specific and mature secondary forest) and *brown* 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* highlight areas with *L. lucidum* forests. (Color figure online)

Table 1 Spatial patterns of *L. lucidum* forests (LFs) and other land-cover classes around three study areas in NW Argentina at sub-regional scale

Variables	*Y*	*SL*	*SSJ*
Land-cover class (ha)			
Total study area	104,801	103,591	246,732
Urban	4796	5260	8333
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

Y Yala, *SL* San Lorenzo, *SSJ* Sierra de San Javier

areas with gentle slopes (Fig. 3a–c). However, a particular distribution pattern was observed when considering elevation: *L. lucidum* forests were concentrated in two distinct altitudinal ranges: low elevation foothills (around 500 m.a.s.l.) and mountain ridges and slopes (between 1000 and 1500 m.a.s.l.; Fig. 3d). Additionally, *L. lucidum* forest patches were less common as distance to roads and rivers increase (Fig. 3e, f). Along the three sectors, a sturdy relationship with variables associated to cities was observed: *L. lucidum* forests extent appeared to be influenced by different urban features such as age of city foundation, size, urban population and population density of the three more important cities located in the Yungas. This relationship holds when the data for the City of Córdoba is included (Fig. 4).

At local scale, patches of *L. lucidum* forest were distributed in seven clusters around San Miguel de Tucumán City and *SSJ*, mostly located at the top and bottom of the mountain range (Figs. 3d, 5). The distribution of *L. lucidum* forests cover in 2010 and the land-cover changes observed since 1972, indicate that the species doubled its area during this period from 306 to 620 ha. The invasion process apparently varied in intensity through time, with two main expansion pulses, during 1986–1992 and after 2001 (Fig. 6a). The expansion occurred mainly over CPs (43%, Fig. 6b) located at the foothills. Other anthropic uses

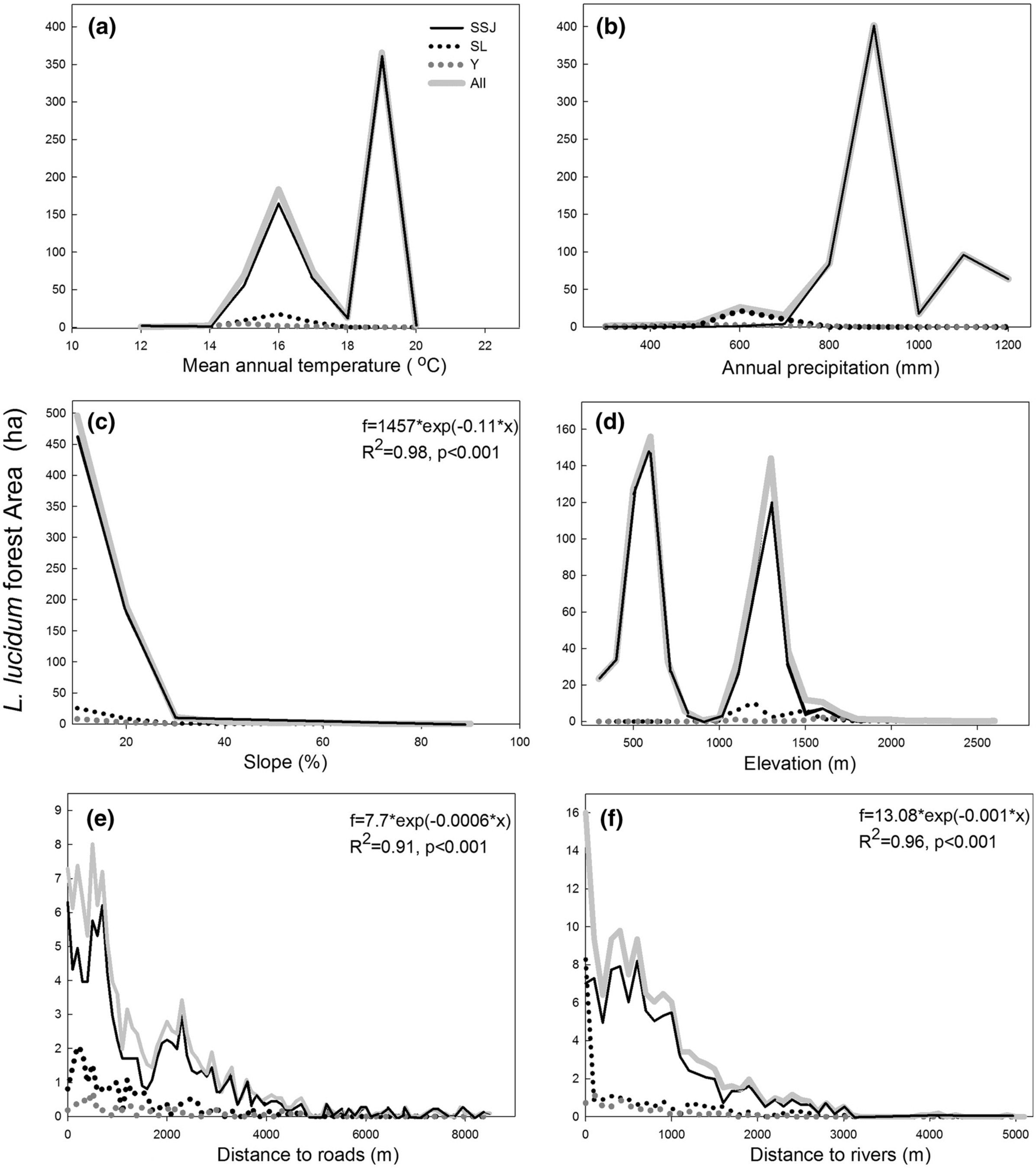

Fig. 3 *Ligustrum lucidum* forests (ha) and environmental or distance variables in the three peri-urban areas of NW Argentina (*Y* Yala, *SL* San Lorenzo, *SSJ* Sierra de San Javier) at sub-regional scale

such as AG or SC were comparatively less invaded by *L. lucidum* forests, representing 8 and 11% of net changes, respectively. Among natural ecosystems *L. lucidum* expansion occurred mainly over MG (approximately 34%) distributed at the top of *SSJ*.

At local scale, precipitation and elevation were the best environmental predictors to explain the presence of *L. lucidum* forests. In addition, at this spatial scale there was also a negative relationship between new *L. lucidum* forests and slope (pseudo-$R^2 = 0.66$,

Table 2). However, according to the logistic regression analysis, land cover variables were better predictors than environmental factors to explain the presence of *L. lucidum* forests in *SSJ* (Table 2, b′ coefficient). Among these variables, distance to *L. lucidum* forests in 1972 was the variable that better explained the probability of occurrence of *Ligustrum* forests in 2010. Many patches were close to the initial foci of invasion, irrespectively of whether these patches were previously occupied by other uses, showing that this species' spread involves a spatial "contagious" pattern. In addition, the invasion was enhanced in areas near to roads, CPs, DF, SC and UR, land covers mainly distributed in the piedmont of *SSJ*, and away from MG or AG (located at the top of SSJ) during the 1970s (Table 2).

Discussion

At the classical ecological or landscape scales, controls of plant succession can be categorized in three main groups of factors: (1) site availability, (2) differential species performance and (3) species availability (Pickett et al. 1987). Exotic plant invasions can be considered a particular component of plant succession, in which species availability plays a key role, and in turn, is regulated by mechanisms that

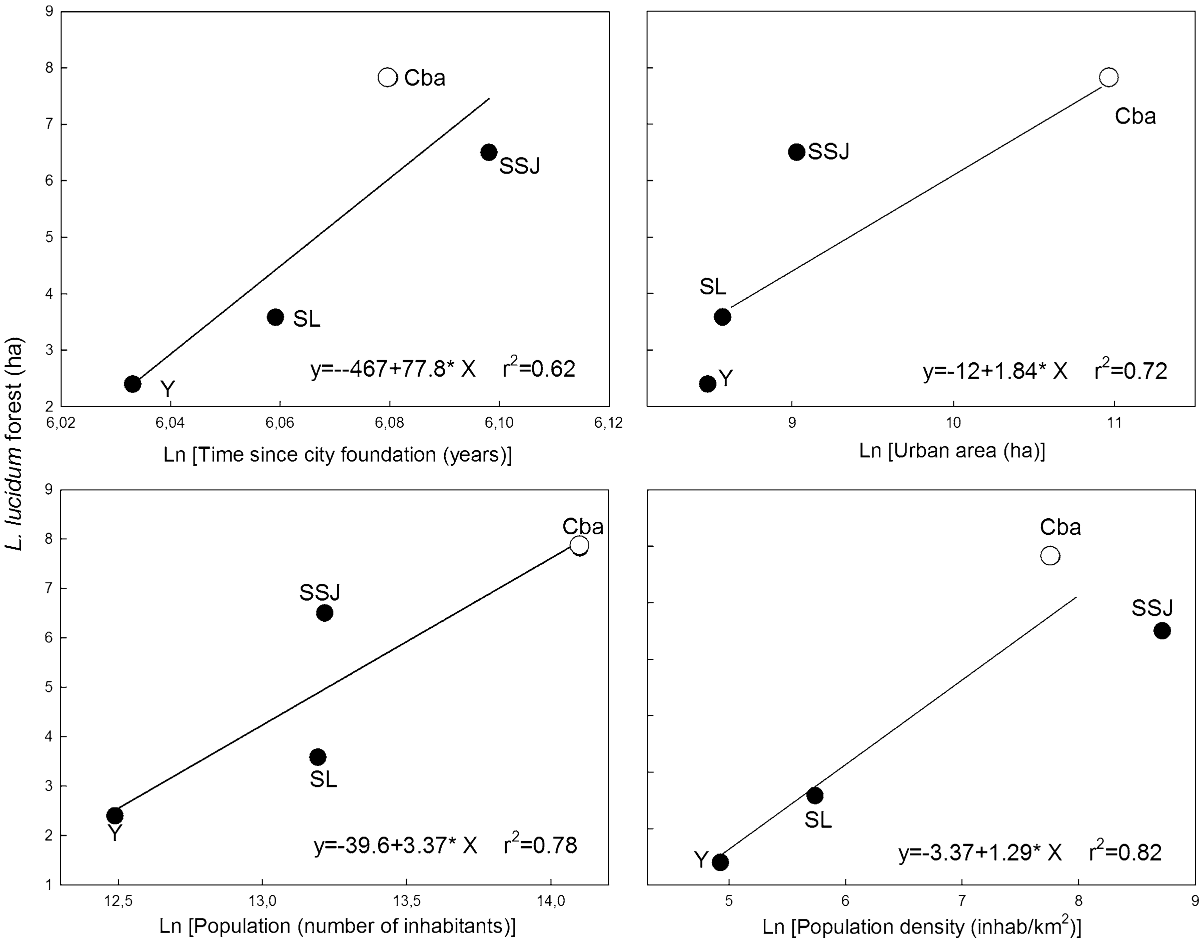

Fig. 4 Relationship between urban features and *Ligustrum lucidum* forests by in the three peri-urban areas of NW Argentina (*Y* Yala, *SL* San Lorenzo, *SSJ* Sierra de San Javier) and Córdoba City (Cba). Data presented was transformed to natural logarithm (LN) in all cases. Data for Córdoba was obtained from Gavier-Pizarro et al. (2012). Population data was extracted from official data of INDEC. Censo Nacional de Población, Hogares y Viviendas 2010. Instituto Geográfico Nacional (IGN). 2010. http://www.sig.indec.gov.ar/censo2010/

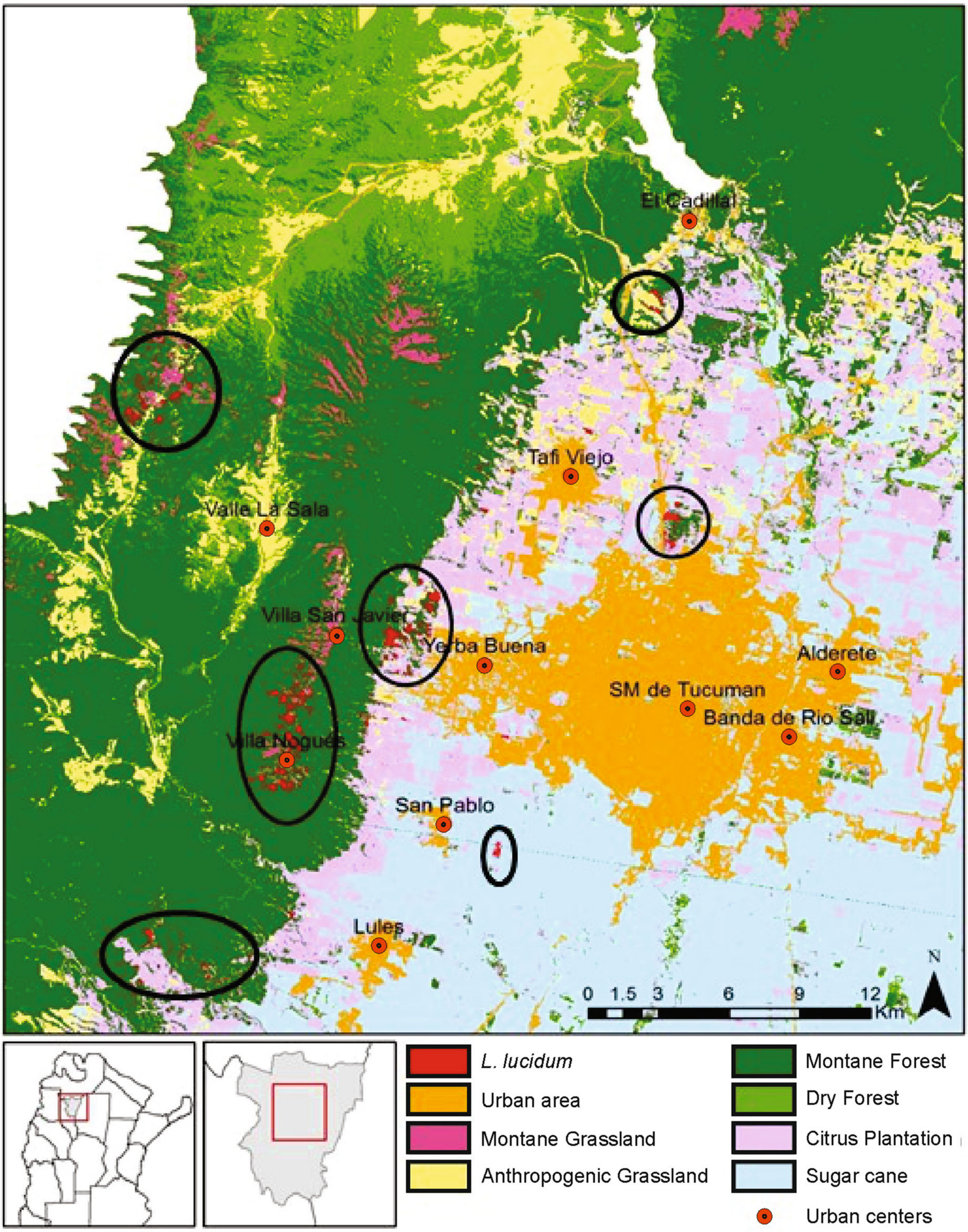

Fig. 5 Land cover type spatial distribution in 2010 at local scale. *Black circles* highlight areas that present *Ligustrum lucidum* forests. The small maps in the *lower left* corner shows the location of Tucumán province in Argentina and the location of surveyed area at local scale inside the province

operate at global scale and are dependent on socio-political variables in addition to biophysical ones. Thus, understanding plant invasion and its effects in framing emerging cultural landscapes, depends on the co-occurrence of factors that operate a different spatial scales, from global to local and that includes: (1) suitable environmental and climatic conditions, (2) human induced conditions/cultural landscape, and (3) human propagule introduction, “pressure”; and a posteriori landscape scale dispersal. In this study, we explored these different components as controls of the invasion of the Asian tree *L. lucidum* in the Argentinian Yungas ecoregion. Cities are a prominent and increasingly important cultural feature of landscapes and regions, since they regulate economic and political activities and concentrate human population that in turn has influential decisions over ecosystems. Our study point out the potential role of cities as key

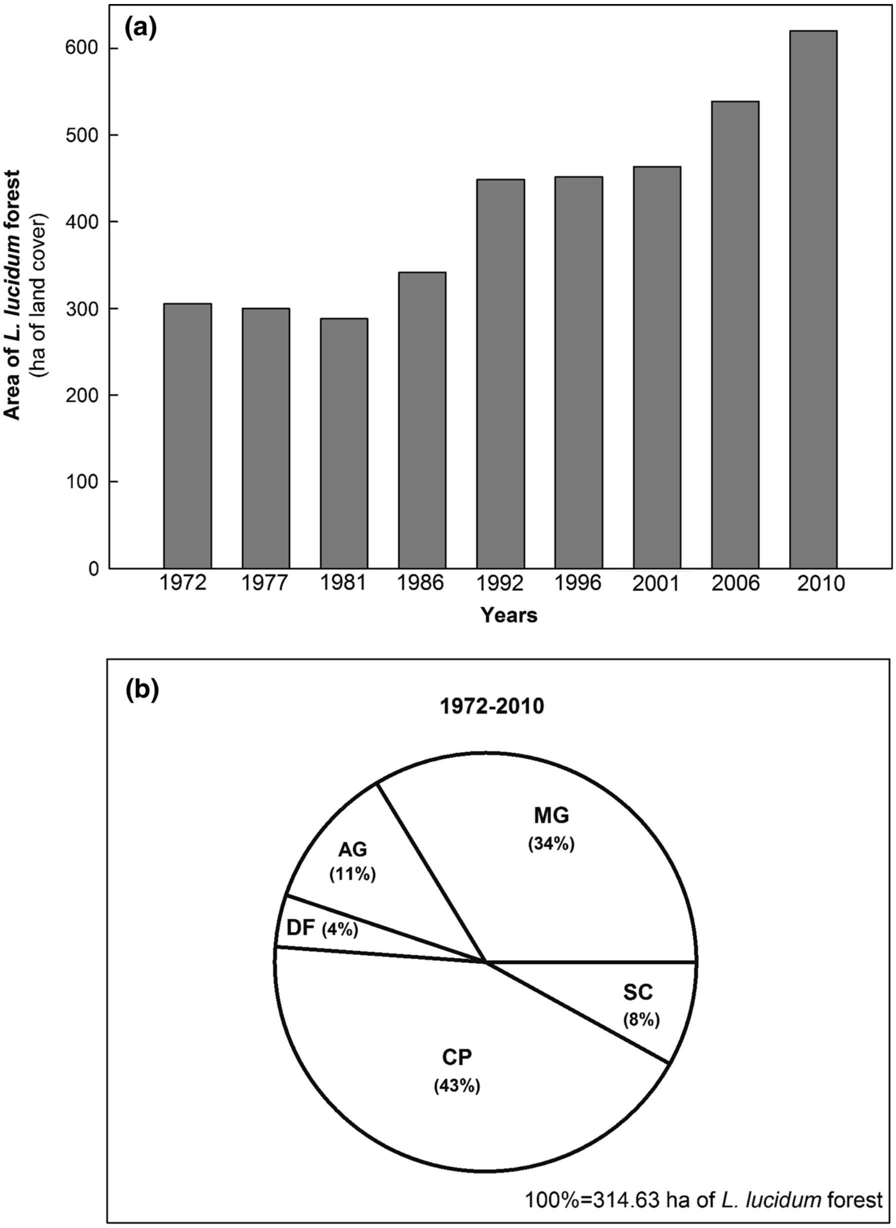

Fig. 6 Local scale study in Sierra de San Javier (*SSJ,* Tucumán). **a** Area invaded by *Ligustrum lucidum* in each date during the period 1972–2010. **b** Area of land cover classes replaced by *L. lucidum* forests during the period 1972–2010. The values express the relative percentage of each land cover over the total invaded area during the period. *MG* mountain grassland, *CPs* citrus plantations, *AG* anthropogenic grassland, *DF* dry forest, *SC* sugar cane

Table 2 Results of multiple logistic regression at local scale (dependent variable = presence of *L. lucidum* forests in 2010; independent variables = 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		

b′ (Standard coefficient) represent the contribution of each independent variable to explain the probability of occurrence of the dependent variable and was calculated according to Lesschen et al. (2005). Pseudo-R^2 = 1 indicates a perfect fit. Pseudo-R^2 greater than 0.2 is considered a relatively good fit

controls of the interaction between invasive species availability (largely anthropogenic) and landscape characteristics that control colonization and dispersal.

Suitable environmental and climatic conditions

The influence of environmental variables in invasive species distribution is well known (e.g., Gormley et al. 2011; Xu 2015). The results of our niche modelling (Fig. 1b) suggested that Yungas ecoregion in NW Argentina (mainly in Tucumán province) has suitable climatic conditions for the expansion of this species. *L. lucidum* forests current distribution, however, only occupies a minor and aggregated portion of this potential range, despite the species has been present in the region for more than a century. This could reflect the “lag phase” in biological invasions (Aikio et al. 2010). Although our understanding of causality is still limited, dispersal barriers coupled with the original location of seed sources rather than climatic conditions appear to be the main restriction to a widespread distribution. In its native range, *L. lucidum* experiences more extreme climatic conditions than in subtropical Argentina (from wet-warm to temperate) and grows up to 2500 m.a.s.l. (Chang et al. 1996). As a result, and according with niche conservationism (Peterson 2003; Thuiller et al. 2005), it is possible that this species presents advantageous adaptations to diverse environmental conditions. Furthermore, it has been documented that exotic species can broaden their native-range ecological niche during the process of invasion (e.g., Broennimann et al. 2007; Essl et al. 2009; Fitzpatrick et al. 2012). If this is the case of *L. lucidum*, we could expect major expansions of the current distribution area into the Argentinian Yungas, but also in other ecosystems such as dry forest or natural grasslands. The potential capacity of *L. lucidum* to invade places under different and contrasting environmental and vegetation conditions is supported by examples of invasions in other places of Argentina including sectors of dry forest in Córdoba (Gavier-Pizarro et al. 2012), grasslands in Buenos Aires (Ghersa et al. 2002) and riparian forest in Entre Rios (Torresin et al. 2013). In this work, we only sampled a subset of *L. lucidum*’s large geographic range. Thus, other environmental and climatic predictors may be important to explain the distribution at bigger scale studies (i.e., country, continental or global).

Human induced conditions/cultural landscape

We identified three hotspots of invasion in the Argentinian Yungas, with *SSJ* as the one experiencing the most advanced invasion (with more than 600 ha of homogeneous monodominant *L. lucidum* forest) and *Y* the least. Although this represents only 0.22% of the studied Yungas forest cover, there are many potential sources of invasion along this ecoregion. Landsat images provided an excellent data source to map *L. lucidum* invasion in dry seasonal forests (Hoyos et al. 2010; Gavier-Pizarro et al. 2012), but in partially evergreen mountain ecosystems, it showed limitations for mapping young or mixed stands, which could not be reliably discriminated from native forests. Previous works using remote sensing in *SSJ* showed the same limitation (Grau et al. 2008). In addition, small patches (<0.5 ha), even those highly dominated by *L. lucidum* were not detected due to the medium-spatial resolution of Landsat images. However, based on our extensive field knowledge, we are confident that our map captures the main patterns of *L. lucidum* invasion, showing the largest invaded forest patches.

In *SSJ* particularly, CPs (in the foothills) and MG (mainly distributed close to the mountain top) were the land cover types over which *Ligustrum* forests expanded more aggressively. Expansion occurred at a higher rate between 1986 and 1992 and after 2001 (Fig. 6). During the 1940s, a small touristic village was developed in *SSJ*, and in 1948 the National Government, legally expropriated nearly 10,000 ha to create a university project and a Natural Reserve. As a consequence, 36 private owners abandoned their agricultural land. However, the development failed to materialize; this history of land use may have produced the initial introduction of seed sources and availability of potentially colonized fields. Then, during 1973 through a Resolution of the National University of Tucumán, the Biological Park *SSJ*, a protected area that belonged to the University was created, and many areas were abandoned (Gutiérrez-Angonese and Grau 2014), creating opportunities for the second pulse of invasion. Although we do not have strong evidence to link directly the first and second pulses of invasion, our interpretation of the observed pattern is that political conservation decisions taken several years before invasion pulse could have unintentionally promoted the spread of *L. lucidum* by creating adequate local environmental conditions and encouraging the abandonment of agriculture and grazing fields. A similar pattern was found in another area by Gavier-Pizarro et al. (2012). In addition to formal conservation practices, the combination of abandonment of marginal agriculture and the expansion of sub-urban residential areas after the rapid economic growth during the beginning of the twenty first century may have favored the second expansion pulse.

Ligustrum lucidum monodominant forests close to peri-urban areas of large urban centers, present a strong spatial association with roads and rivers and with urban areas of larger size and higher population density (Figs. 3, 4; Table 1). Roads and rivers often act as corridors along which invasive species can spread (Wang et al. 2011a, b) and cities as reservoir of seed sources. Large urban areas of the Yungas ecoregion, appeared to have favored *L. lucidum* invasion likely by hosting large seed sources since the species is intensively used for urban forestry and vegetated fences near recently disturbed areas (e.g., in association to urban development), or recently abandoned agriculture lands (as agriculture becomes non-competitive in comparison to urban land uses) (Davis et al. 2000; Theoharides and Dukes 2007; Hufbauer et al. 2012). Importantly, the relationship between *L. lucidum* invaded area and cities size is consistent with the scaling attribute of cities (Bettencourt 2013), that explains several properties of urban systems considering variables such as green areas, transport infrastructure, human interaction, among others. This pattern is more evident if we combine our data with the *L. lucidum* cover around Córdoba City described by Gavier-Pizarro et al. (2012) (see Fig. 4). This relationship confirms that *L. lucidum* responds to the scaling rule proposed for city systems and could be considered as a side effect linked with the urban centers dynamics and functioning. It is also worth noting that even though *L. lucidum* showed strong association with peri-urban forest transition and land abandonment, and that the urban areas grew during the last decades, the expansion of new forest has slowed down in recent times (Gutiérrez-Angonese 2015); probably because newly abandoned agriculture areas are becoming scarce. However, our results should be considered a conservative estimate of the present invaded forests. Recent field data shows that *L. lucidum* is expanding into mature native forest (Malizia et al. 2017), revealing that invasion could occur by other ways unable to be detected by standard remote sensing methods.

Propagule pressure and dispersal

Our results suggest that humans and their activities are the main control of landscape features influencing *L. lucidum* distribution pattern. Urban areas play an important role as *L. lucidum* propagule sources, and roads and rivers enhance dispersion and increase propagule pressure into sites suitable for invasion, such as abandoned fields. The invasion across the cultural landscape followed a contagious pattern, with a strong decrease of invasion probability with distance from pre-existing *Ligustrum* stands. Consistently, previous studies suggested this pattern also could be consequence of propagule pressure conditions and seed dispersal mechanism at a micro local scale (Aragón and Morales 2003; Powell et al. unpublished work). In others words, urban and peri-urban areas present a relatively high abundance of *L. lucidum* as a result of widespread cultivation by humans in gardens and streets, and the availability of invasion prone sites. *L. lucidum* invasion into areas nearby seed sources, can later achieve persistence by two mechanisms. First, this species has a high growth rate and effective vegetative reproduction (Grau and Aragón 2000; Aragón and Groom 2003), which helps competitively displacing native species (Malizia et al. 2017). Second, *L. lucidum* produces massive fruit crops that fall and germinate underneath the parental tree (Aragón and Groom 2003). In addition, *L. lucidum* produces fruits during the winter (when native fruit offer is scarce) and its seeds are frequently eaten and dispersed by birds (Aragón and Groom 2003). *Turdus rufiventris* a medium-sized passerine, which is the most abundant fruit-eating bird species in the southern Argentinian Yungas, disperses seeds beyond canopy proximity, using native trees or abandoned CPs as perches (Blendinger et al. 2012; Ayup et al. 2014). Also as Powell et al. (unpublished work) confirmed recently, seeds dispersed by birds presented different spatial patterns depending on their handling technique and the tree density influenced the number of seeds and their dispersal distance. The combination and relative contribution of these factors to control invasion spread needs to be better understood in order to refine models of invasion and develop future scenarios.

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

Several studies described the biological traits that confer advantages to *L. lucidum* over the native species (Aragón and Groom 2003; Aragón and Morales 2003; Tecco et al. 2006; Easdale et al. 2007; Ferreras et al. 2008). Here, we showed that, human activities are also key factors controlling its expansion in Argentinian Yungas. As different studies revealed, human-assisted propagule movements and disturbances related to the development of cultural landscapes could be more important in shaping the invasion process than the invasive species' traits themselves (Chytrý et al. 2008a, b). This suggests that tree invasion should be tackled from a multidisciplinary focus that includes the human dimension view and the dynamic processes associated with it (i.e., social, economic, geographic, historic and landscape ecology), in order to develop a comprehensive theoretical framework on how these factors operate during the invasion process at different stages and spatio-temporal scales.

Based in our multiscale analysis we argue that invasions have a strong interaction with "telecoupled cultural landscapes". The concept of "telecouplings" has been recently developed to study the links between distant socio-environmental systems and the environmental modifications related with distant drivers (Liu et al. 2013a, b). The concept is used to study land use change processes (e.g., Gasparri and le Polain de Waroux 2014) and urban–rural interactions (Deines et al. 2016); it was proposed as potentially important to explain species invasions (Liu et al. 2013a, b). In the telecoupling frame, cities are crucial elements to articulate the interaction between the telecoupled systems (Seto et al. 2012). Cities concentrate the main fluxes of information, energy and materials, as well as the most powerful decisions. Therefore cities and peri-urban zones are particularly prone to result into "telecoupled cultural landscapes" where invasive plants such as *L. lucidum* could play the role of incorporating biological features from distant locations and creating novel ecosystems. In this scenario, peri-urban areas are expected to be the first ones affected.

Under this framework, to better understand why *L. lucidum* became a successful invasive species in Argentina it is advisable to consider the long and intermittent telecouplings operating between China and Americas, and particularly Argentina. Since the 1600s, sociocultural and economic telecoupling between Asia and the Americas has been intensive, especially related with the interchange of natural resources. For example, American silver enhanced Chinese economy particularly on final of Ming and beginning of Qing Dynasties (Flynn and Giráldez 2002; Flynn et al. 2003); and American crops species (maize, potato, sweet potato) helped mitigating human famine and changed human population dynamic (mainly in eighteenth century). In addition, sugar cane from SE Asia influenced socioeconomic organization and food habits in America (Mann 2006). Nowadays, both areas continue with some relationships that not only favor international trade of material resources (i.e., China is the main soybean importer from Argentina), but also important flows of people, information and cultural aspects (as garden diversity composition, type of food, natural medicine, etc.). Three of the cities described here, in which the surrounds are being invaded by *L. lucidum* forests (Salta, San Miguel de Tucumán and Córdoba), have more than 1% of their population composed by Asian people (INDEC 2010). Also, these cities and San Salvador de Jujuy, were important nodes of the trade route known as the ‘‘Hispanic American china silk route" used to commerce different goods from Asia during the colonial times (Bonialian 2014). Essl et al. (2011) emphasizes that the impact of human activities and socio economy legacy on species invasion can often exhibit a considerable time lag. For these reasons, we argue that historical flows and connections between native (China) and novel ranges (Argentina) need to be studied as relevant drivers of cultural landscape change and *L. lucidum* invasion.

Conclusions

Two main conclusions emerge from this study: first, a multiscale approach is necessary to explain invasive species distributions. Second, the interaction at multiple-scale between biophysical variables and factors involved in the development of cultural landscapes is crucial to explain invasive species success. As a corollary, we suggest that a better developed inclusion of cultural aspects into the theory of invasion is a priority.

Our results suggest that at regional scale, Yungas ecoregion of NW Argentina presents climatic conditions adequate for *L. lucidum* expansion. However, for the invasion to develop it is necessary the co-occurrence of other factors. In the studied area invaded ranges are clustered around the regional major cities and according to scale rules (i.e., the bigger the city, the larger the invaded area), thus suggesting that major urban centers in the Yungas ecoregion could create particular conditions in their surrounding areas that increase invasibility. The 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 Anthropocene.

Acknowledgements This study was supported by Argentinian National Council of Scientific and Technological Research (CONICET) and by Rufford Small Grant. We thank N. Diaz and MJ Orofino for the permanent help with English, our colleagues from IER who helped us in fieldwork and from Nanjing Forestry University (China) who facilitated us information about *L. lucidum* in native range and to Dr. T Kuemmerle and the anonymous reviewers for their useful comments.

References

Aikio S, Duncan RP, Hulme PE (2010) Lag-phases in alien plant invasions: separating the facts from the artefacts. Oikos 119(2):370–378

Alston KP, Richardson DM (2006) The roles of habitat features, disturbance, and distance from putative source populations in structuring alien plant invasions at the urban/wildland interface on the Cape Peninsula, South Africa. Biol Conserv 132(2):183–198

Aragón R, Groom M (2003) Invasion by *Ligustrum lucidum* (Oleaceae) in NW Argentina: early stage characteristics in different habitat types. Rev Biol Trop 51:59–70

Aragón R, Morales JM (2003) Species composition and invasion in NW Argentinean secondary forests: effects of land use history, environment and landscape. J Veg Sci 14:195–204

Aslan CE, Rejmánek M, Klinger R (2012) Combining efficient methods to detect spread of woody invaders in urban–rural matrix landscapes: an exploration using two species of Oleaceae. J Appl Ecol 49:331–338

Ayup M, Montti L, Aragón R, Grau HR (2014) Invasion of *Ligustrum lucidum* (Oleaceae) in the Southern Yungas. Changes in habitat properties and decline in bird diversity. Acta Oecol 54:72–81

Bellard C, Thuiller W, Leroy B, Genovesi P, Bakkenes M, Courchamp F (2013) Will climate change promote future invasions? Glob Change Biol 19:3740–3748

Bettencourt LM (2013) The origins of scaling in cities. Science 80(340):1438–1441

Bianchi AR (1981) Las precipitaciones en el Noroeste argentino. INTA. Estación Experimental Regional agropecuaria Salta

Blendinger PG, Ruggera RA, Núñez Montellano MG, Macchi L, Zelaya PV, Álvarez MV, Martín E, Orsinaga Acosta O, Sánchez R, Haedo F (2012) Fine-tuning the fruit-tracking hypothesis: spatiotemporal links between fruit availability and fruit consumption by birds in Andean mountain forests. J Anim Ecol 81(6):1298–1310

Blundo C, Malizia L, Blake JG, Brown AD (2012) Tree species distribution in Andean forests: influence of regional and local factors. J Trop Ecol 28:83–95

Bonialian M (2014) China en la America Colonial. Bienes, Mercados, Comercio y cultura del consumo desde Mexico hasta Buenos Aires. México, Mora-Biblos

Botham MS, Rothery P, Hulme PE, Hill MO, Preston CD, Roy DB (2009) Do urban areas act as foci for the spread of alien plant species? An assessment of temporal trends in the UK. Divers Distrib 15:338–345

Breiman L (2001) Random forests. Mach Learn 45:5–32

Broennimann O, Treier UA, Muller-Scharer H, Thuiller W, Peterson AT, Guisan A (2007) Evidence of climatic niche shift during biological invasion. Ecol Lett 10:701–709

Brown AD, Grau HR, Malizia LR, Grau A (2001) Argentina. In: Kappelle M, Brown AD (eds) Bosques nublados del Neotrópico. Instituto Nacional de Biodiversidad, San José, pp 623–659

Chang MC, Qiu LQ, Green PS (1996) Oleaceae. Flora China 15:272–319

Chiron F, Shirley S, Kark S (2009) Human-related processes drive the richness of exotic birds in Europe. Proc R Soc B 276:47–53

Chytrý M, Jarosik V, Pyšek P, Hájek O, Knollová I, Tichý L, Danihelka J (2008a) Separating habitat invasibility by alien plants from the actual level of invasion. Ecology 89:1541–1553

Chytrý M, Maskell LC, Pino J, Pyšek P, Vilá M, Font X, Smart SM (2008b) Habitat invasions by alien plants: a quantitative comparison among Mediterranean, subcontinental and oceanic regions of Europe. J Appl Ecol 45:448–458

Davis MA, Grime JP, Thompson K (2000) Fluctuating resources in plant communities: a general theory of invasibility. J Ecol 88:528–534

Decker KL, Allen CR, Acosta L, Hellman ML, Jorgensen CF, Stutzman RJ, Unstad KM, Williams A, Yans M (2012) Land use, landscapes and biological invasions. Invasive Plant Sci Manag 5:108–116

Deines JM, Liu X, Liu J (2016) Telecoupling in urban water systems: an examination of Beijing's imported water supply. Water Int 41(2):251–270

Easdale TA, Healey JR, Grau HR, Malizia A (2007) Tree life histories in a montane subtropical forest: species differ independently by shade-tolerance, turnover rate and substrate preference. J Ecol 95:1234–1239

Eastman JR (2016) TerrSet. Geospatial monitoring and modeling system. Clark Labs, Clark University, Worcester

Essl F, Dullinger S, Kleinbauer I (2009) Changes in the spatiotemporal patterns and habitat preferences of *Ambrosia artemisiifolia* during the invasion of Austria. Preslia 81:119–133

Essl F, Dullinger S, Rabitsch W, Hulme PE, Hülber K, Jarošík V, Kleinbauer I, Krausmann F, Kühn I, Nentwig W, Vilà M, Genovesi P, Gherardi F, Desprez-Loustau ML, Roques A, Pyšek P (2011) Socioeconomic legacy yields an invasion debt. Proc Natl Acad Sci USA 108:203–207

Ferreras AE, Torres C, Galetto L (2008) Fruit removal of an invasive exotic species (*Ligustrum lucidum*) in a fragmented landscape. J Arid Environ 72:1573–1580

Ficetola GF, Thuiller W, Miaud C (2007) Prediction and validation of the potential global distribution of a problematic alien invasive species—the American bullfrog. Divers Distrib 13(4):476–485

Fitzpatrick MC, Preisser EL, Porter A, Elkinton J, Ellison AM (2012) Modeling range dynamics in heterogeneous landscapes: invasion of the hemlock woolly adelgid in eastern North America. Ecol Appl 22(2):472–486

Flynn DO, Giráldez A (2002) Cycles of silver: global economic unity through the mid-eighteenth century. J World Hist 13(2):391–427

Flynn DO, Giráldez A, Von Glahn R (2003) Global connections and monetary history, 1470–1800. Ashgate, Aldershot, pp 1–34

Foody GM, Mathur A (2004) Toward intelligent training of supervised image classifications: directing training data acquisition for SVM classification. Remote Sens Environ 93(1):107–117

Fuentes N, Saldaña A, Kühn I, Klotz S (2015) Climatic and socio-economic factors determine the level of invasion by alien plants in Chile. Plant Ecol Divers 30:609–628

Gasparri NI, le Polain de Waroux Y (2014) The coupling of South American soybean and cattle production frontiers: new challenges for conservation policy and land change science. Conserv Lett 8(4):290–298

Gavier-Pizarro GI, Kuemmerle T, Hoyos LE, Stewart SI, Huebner CD, Keuler NS, Radeloff VC (2012) Monitoring the invasion of an exotic tree (*Ligustrum lucidum*) from 1983 to 2006 with Landsat TM/ETM? Satellite data and support vector machines in Córdoba, Argentina. Remote Sens Environ 122:134–145

Ghersa CM, de la Fuente E, Suarez S, Leon RJC (2002) Woody species invasion in the Rolling Pampas grasslands, Argentina. Agric Ecosyst Environ 88:271–278

Gormley AM, Forsyth DM, Griffioen P, Lindeman M, Ramsey DSL, Scroggie MP, Woodford L (2011) Using presence-only and presence–absence data to estimate the current and potential distributions of established invasive species. J Appl Ecol 48:25–34

Grau HR, Aragón R (2000) Ecología de los árboles invasores de la Sierra de San Javier. In: Grau HR, Aragón R (eds) Arboles exóticos de las Yungas Argentinas. LIEY-UNT, Tucumán, pp 5–20

Grau HR, Hernández ME, Gutierrez J, Gasparri NI, Paolini L (2008) A peri-urban forest neotropical forest transition and its consequences for environmental services. Ecol Soc 13(1):35

Grau HR, Paolini L, Malizia A, Carilla J (2010) Distribución, estructura y dinámica de los bosques de la sierra de San Javier (Tucumán, Argentina). In: Grau HR (ed) Ecología de una interfase natural urbana. La sierra de San Javier y el Gran San Miguel de Tucumán. EDUNT, Tucumán, pp 33–50

Grotkopp E, Rejmánek M (2007) High seedling relative growth rate and specific leaf area are traits of invasive species: phylogenetically independent contrasts of woody angiosperms. Am J Bot 94(4):526–532

Guilhermetti GC, Vogel GF, Martinkoski L, Mokochinski FM (2013) Aspectos da distribuicão de *Ligustrum lucidum* W.T.Ainton em diferentes ecossistemas: revisão bibliográfica (aspects of the distribution *Ligustrum lucidum* W.T.Ainton in different ecosystems: literature review). Rev Verde Agroecol Desenvolv Sustent 8:171–176

Gutiérrez-Angonese J (2015) Historia de uso del territorio en el área peri-urbana de la Sierra de San Javier y el Gran San Miguel de Tucumán, Argentina (1972–2010). Dissertation, Universidad Nacional de Córdoba, Argentina

Gutiérrez-Angonese J, Grau HR (2014) Assessment of swaps and persistence in land cover changes in a subtropical periurban region, NW Argentina. Landsc Urban Plan 127:83–93

Hijamans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated climate surface for global land areas. Int J Climatol 25:1965–1978

Hoyos LE, Gavier-Pizarro GI, Kuemmerle T, Bucher EH, Radeloff VC, Tecco PA (2010) Invasion of glossy privet (*Ligustrum lucidum*) and native forest loss in the Sierras Chicas of Córdoba, Argentina. Biol Invasions 12:3261–3275

Hsu CW, Chang, CC, Lin, CJ (2007) A practical guide to support vector classification. National Taiwan University. http://ntu.csie.org/~cjlin/papers/guide.pdf

Huang C, Davis LS, Townshend JRG (2002) An assessment of support vector machines for land cover classification. Int J Remote Sens 23:725–749

Hufbauer RA, Facon B, Ravigne V, Turgeon J, Foucaud J, Lee CE, Rey O, Estoup A (2012) Anthropogenically induced adaptation to invade (AIAI): contemporary adaptation to human-altered habitats within the native range can promote invasions. Evol Appl 5(1):89–101

Hulme PE (2009) Trade, transport and trouble: managing invasive species pathways in an era of globalization. J Appl Ecol 46:10–18

Hulme PE (2011) Addressing the threat to biodiversity from botanic gardens. Trends Ecol Evol 26:168–174

Hulme PE, Bacher S, Kenis M, S. Klotz, Kühn I, Minchin D, Nentwig W, Olenin S, Panov V, Pergl J, Pyšek P, Roques A, Sol D, Solarz W, Vilà M (2008) Grasping at the routes of biological invasions: a framework for integrating pathways into policy. J Appl Ecol 45:403–414

Hunzinger H (1997) Hydrology of montane forests in the Sierra de San Javier, Tucumán, Argentina. Mt Res Dev 17:299–308

INDEC (2010) Censo Nacional de Población, Hogares y Viviendas 2010. Instituto Geográfico Nacional (IGN). http://www.sig.indec.gov.ar/censo2010/

Karalius T, Alpert P (2010) High abundance of introduced plants on ancient Native American middens. Biol Invasions 12:1125–1132

Leishman MR, Haslehurst T, Ares A, Baruch Z (2007) Leaf trait relationships of native and invasive plants: community- and global-scale comparisons. N Phytol 176:635–643

Lesschen JP, Verburg PH, Staal, SJ (2005) Statistical methods for analysing the spatial dimension of changes in land use and farming systems. International Livestock Research Institute

Liaw A, Wiener M (2002) Classification and regression by random forest. R News 2(3):18–22

Liu J, Hull V, Batistella M, DeFries R, Dietz T, Fu F, Hertel TW, Izaurralde RC, Lambin EF, Li S, Martinelli LA, McConnell WJ, Moran EF, Naylor R, Ouyang Z, Polenske KR, Reenberg A, de Miranda Rocha G, Simmons CS, Verburg PH, Vitousek PM, Zhang F, Zhu C (2013a) Framing sustainability in a telecoupled world. Ecol Soc 18:26

Liu C, White M, Newell G (2013b) Selecting thresholds for the prediction of species occurrence with presence-only data. J Biogeogr 40(4):778–789

Mack RN (2000) Cultivation fosters plant naturalization by reducing environmental stochasticity. Biol Invasion 2:111–122

Malizia A, Osinaga-Acosta O, Powell P, Aragón R (2017) Invasion of *Ligustrum lucidum* (Oleaceae) in subtropical secondary forests of NW Argentina: declining growth rates of abundant native tree species. J Veg Sci. Accepted Author Manuscript. doi:10.1111/jvs.12572

Mann CC (2006) 1493 Una nueva historia del mundo después de Colón. Ed. Clave Intelectual, Madrid

McGarigal KY, Cushman SA (2002) Comparative evaluation of experimental approaches to the study of habitat fragmentation effects. Ecol Appl 12(2):335–345

McGarigal KY, Marks B (1995) FRAGSTATS: spatial pattern analysis program for quantifying landscape structure. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station

Merow C, Smith MJ, Silander JA (2013) A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. Ecography 6(10):1058–1069

Miller AL, Wiser SK, Sullivan JJ, Duncan RP (2015) Creek habitats as sources for the spread of an invasive herb in a New Zealand mountain landscape. NZ J Ecol 39(1):71

Montti L, Ayup MM, Aragón R, Qi W, Ruan H, Fernández R, Casertano S, Zou X (2016) Herbivory and the success of *Ligustrum lucidum*: evidence from a comparison between native and novel ranges. Aust J Bot 64(3):181–192

Mosher ES, Silander J, Andrew ML (2009) The role of land-use history in major invasion by woody plant species in the northeastern North American landscape. Biol Invasions 11:2317–2328

O'Reilly-Nugent A, Palit R, Lopez-Aldana A, Medina-Romero M, Wandrag E, Duncan RP (2016) Landscape effects on the spread of invasive species. Curr Landsc Ecol Rep 1(3):107–114

Panetta FD (2000) Fates of fruits and seeds of *Ligustrum lucidum* W.T.Ait. and *L. sinense* Lour. maintained under natural rainfall or irrigation. Aust J Bot 48:701–706

Pearson RG, Raxworthy CJ, Nakamura M, Townsend Peterson A (2007) Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. J Biogeogr 34(1):102–117

Peñuelas J, Sardans J, Llusia Owen S, Carnicer J, Giambelluca TW, Rezende EL, Waite M, Niinemets Ü (2010) Faster returns on leaf economics and different biogeochemical niche in invasive compared with native plant species. Glob Change Biol 16:2171–2185

Pergl J, Sádlo J, Petřík P, Danihelka J, Chrtek Jr J, Hejda M, Lenka M, Perglová I, Štajerová K, Pyšek P (2016) Dark side of the fence: ornamental plants as a source of wild-growing flora in the Czech Republic. Preslia 88(2):163–184

Peterson AT (2003) Predicting the geography of species invasions via ecological niche modeling. Q Rev Biol 78:419–433

Phillips SJ, Anderson RP, Schapire RE (2006) Maximum entropy modelling of species geographic distributions. Ecol Model 190:231–259

Pickett STA, Collins SL, Armesto JJ (1987) Models, mechanisms and pathways of succession. Bot Rev 53:335–371

Pyšek P, Richardson DM (2010) Invasive species, environmental change and management, and health. Annu Rev Environ Res 35:25–55

Pyšek P, Jarošík V, Hulme PE, Kühn I, Wild J, Arianoutsou M, Bacher S, Chiron F, Didžiulis V, Essl F, Genovesi, Gherardi F, Hejdaa M, Kark S, Lambdon PW, Desprez-Loustau ML, Nentwig W, Pergl J, Poboljšaj K, Rabitsch W, Roques A, Roy DB, Shirley S, Solarz W, Vilà M, Winter M (2010) Disentangling the role of environmental and human pressures on biological invasions across Europe. Proc Natl Acad Sci USA 107(27):12157–12162

R Development Core Team (2014) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. http://www.r-project.org/

Rejmánek M, Richardson DM (1996) What attributes make some plant species more invasive? Ecology 77:1655–1661

Rödder D, Lötters S (2009) Niche shift versus niche conservatism? Climatic characteristics of the native and invasive ranges of the Mediterranean house gecko (*Hemidactylus turcicus*). Glob Ecol Biogeogr 18(6):674–687

Rödder D, Solé M, Böhme W (2008) Predicting the potential distributions of two alien invasive house geckos (Gekkonidae: *Hemidactylus frenatus*, *Hemidactylus mabouia*). Northwest J Zool 4(2):236–246

Sadori L, Mercuri AM, Mariotti Lippi M (2010) Reconstructing past cultural landscape and human impact using pollen and plant macroremains. Plant Biosyst 144(4):940–951

Seto KC, Reenberg A, Boone CG, Fragkias M, Haase D, Langanke T, Marcotullio P, Munroe DK, Olah B, Simon D (2012) Urban land teleconnections and sustainability. Proc Natl Acad Sci USA 109(20):7687–7692

Sharma GP, Esler KJ, Blignaut JN (2010) Determining the relationship between invasive alien species density and a country's socio-economic status. S Afr J Sci 106:38–43

Song C, Woodcock CE, Seto KC, Lenney MP, Macomber SA (2001) Classification and change detection using Landsat TM data when and how to correct atmospheric effects? Remote Sens Environ 75(2):230–244

Standish RJ, Cramer VA, Hobbs RJ (2008) Land-use legacy and the persistence of invasive *Avena barbata* on abandoned farmland. J Appl Ecol 45:1576–1583

Tecco PA, Gurvich DE, Díaz S, Pérez-Harguindeguy N, Cabido M (2006) Positive interaction between invasive plants: the influence of *Pyracantha angustifolia* on the recruitment of native and exotic woody species. Austral Ecol 31:293–300

Theoharides KA, Dukes JS (2007) Plant invasion across space and time: factors affecting nonindigenous species success during four stages of invasion. N Phytol 176(2):256–273

Thuiller W, Richardson DM, Rouget M, Proches S, Wilson JRU (2006) Interactions between environment, species traits and human uses describe patterns of plant invasions. Ecology 87:1755–1769

Thuiller W, Richardson DM, Pysek P, Midgley GF, Hughes GO, Rouget M (2005) Niche-based modelling as a tool for predicting the risk of alien plant invasions at a global scale. Glob Change Biol 11:2234–2250

Torresin JA, Zamboni LP, Sione WF, Rodriguez E, Aceñolaza PG (2013) Modelado de la distribución espacial de árboles exóticos invasores (AEI) en el Parque Nacional Pre-Delta (Entre Ríos Argentina). Multequina 22:2013

Vilá M, Ibañez I (2011) Plant invasions in the landscape. Landscape Ecol 26:461–472

Vilá M, Valladares F, Traveset A, Santamaría L, Castro P (2008) Invasiones biológicas. Consejo Superior de Investigaciones Científicas, Madrid

Vitousek PM, D'Antonio CM, Loope LL, Westbrooks R (1996) Biological invasions as global environmental change. Am Sci 84:218–228

Wang HF, Lopez-Pujol J, Meyerson L, Qiu JX, Wang XK, Ouyang ZY (2011a) Biological invasions in rapidly urbanizing areas: a case study of Beijing, China. Biodivers Conserv 20:2483–2509

Wang R, Wang JF, Qiu ZJ, Meng B, Wan FH, Wang YZ (2011b) Multiple mechanisms underlie rapid expansion of an invasive alien plant. N Phytol 191(3):828–839

Wisz MS, Hijmans RJ, Li J, Peterson AT, Graham CH, Guisan A (2008) Effects of sample size on the performance of species distribution models. Divers Distrib 14(5):763–773

Xu Z (2015) Potential distribution of invasive alien species in the Upper Ili River basin: determination and mechanism of bioclimatic variables under climate change. Environ Earth Sci 73(2):779–786

Zamora Nazca LB, Montti L, Grau HR, Paolini L (2014) Efectos de la invasión del ligustro, *Ligustrum lucidum*, en la dinámica hídrica de las Yungas del noroeste Argentino. Bosque 35(2):195–205