



Invasion of *Ligustrum lucidum* (Oleaceae) in subtropical secondary forests of NW Argentina: declining growth rates of abundant native tree species

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Nomenclature

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Introduction

Biological invasions, together with changes in land use, are two major components of global change affecting biodiversity worldwide (Vitousek et al. 1997; Vila & Ibáñez 2011). Habitat loss and fragmentation reduce population viability (Fischer & Lindenmayer 2007), causing the

Abstract

Aims: *Ligustrum lucidum*, native to China, is one of the dominant exotic and invasive tree species in secondary forests in Argentina. (1) We assessed its invasion during 20 yr in post-agricultural secondary forests dominated by native tree species, and (2) evaluated tree demographic rates of native individuals under and away from *L. lucidum* trees that invaded these forests.

Locations: Four 1-ha permanent plots of secondary forests, subtropical Andes of Tucumán, Argentina.

Methods: We quantified the invasion of *L. lucidum* individuals (≥ 10 -cm diameter) from 1991 to 2011 within four 1-ha plots of secondary forests and analysed annual growth and mortality rates of native tree individuals (≥ 10 -cm diameter) under and away from *L. lucidum* trees. For this, we compared tree demographic rates of all native individuals together (community level) under and away from individuals of *L. lucidum*, referred to as *exotic* and *native neighbourhoods*, respectively. Then, we described the relative growth rate of native tree species in *exotic*/*native neighbourhoods* (species level) and related them to their demographic life histories and morpho-physiological traits.

Results: Both density and basal area of *L. lucidum* increased from 0.1% to 4% between 1991 and 2011. Native tree individuals grew 65% less in *exotic neighbourhoods* compared to *native neighborhoods*. Relative growth rate showed negative values under *L. lucidum* individuals for the abundant species *Ocotea porphyria*, *Parapitadenia excelsa*, *Juglans australis* and *Allophylus edulis*, indicating competition; while less abundant species *Terminalia triflora*, *Cupania vernalis* and *Blepharocalix salicifolius* showed positive growth values under *L. lucidum*, suggesting a facilitation process. Thus, *L. lucidum* competes efficiently with some native tree species, particularly with those abundant species that dominate the canopy.

Conclusions: *Ligustrum lucidum* is invading post-agricultural secondary forests dominated by native tree species. While invading, *L. lucidum* competes with native abundant tree species that dominate the main structure of the forest canopy. As this invasive trend will likely increase in the near future, *L. lucidum* may alter forest structure, composition and dynamics, as well ecosystem functioning.

extinction of native species (Sala et al. 2000) while enhancing terrestrial biological invasions, which, in turn, may alter the landscape (Vila & Ibáñez 2011). Many factors affect ecosystem vulnerability to invasions at different spatial scales and in a hierarchical way (Milbau et al. 2009). Climate can be considered the dominant factor at continental scale, while at regional and landscape scales

topography, land cover and land use become increasingly important (Milbau et al. 2009). Invasive processes, including establishment, population growth and population spread, take place at the landscape scale (Theoharides & Dukes 2007). Changes in land cover and land use, such as clearing for pasture or agriculture, logging, field abandonment and urbanization, generate the conditions for new colonizations (Vila & Ibáñez 2011).

In South America, one of the current trends of land-use and cover-change is the abandonment of marginal agricultural lands (Waggoner & Ausubel 2001) where forest recovery occurs in association with human and socio-economic development (Aide & Grau 2004; Grau et al. 2007; Grau & Aide 2008; Redo et al. 2012). Proximity of these abandoned areas to native forests promotes rapid recovery, which depends heavily on seed dispersal (Chazdon 2003). However if these lands, where successional processes are occurring, are close to suburban areas opportunities arise for the spread of exotic and invasive plant species, such as ornamentals or cultivars (Vila & Ibáñez 2011; Gavier-Pizarro et al. 2012). If non-native species do not couple with the typical successional pattern, i.e. site colonization, canopy closure, recovery of species richness, increases in basal area, and convergence in species composition to old-growth conditions (Guariguata & Ostertag 2001), forest succession may be altered. Following the general theory of invasion ecology, establishment and invasion success of an exotic tree species should be higher in these early successional communities with high resource availability and low species richness and diversity, as well as low functional diversity (Shea & Chesson 2002; Fridley et al. 2007; MacDougall et al. 2009). This may be due to the fact that these exotic and invasive species may have no natural herbivores, and/or they can make use of natural resources more efficiently than native species (Crawley 1987; Cannas et al. 2004). As a result, these successional forests may differ from the original ones in their floristic composition and structural characteristics. In addition, these forests may have important ecological implications by affecting ecosystems at the individual, population and community levels (Parker et al. 1999), as well as forest dynamics, biodiversity and ecosystem functioning (Hobbs 2000; Lugo & Helmer 2004; Ayup et al. 2013).

A common tree invader in numerous regions of the world is *Ligustrum lucidum* (Oleaceaceae), a native of South-east Asia (Cronk & Fuller 1995). It has been reported as an aggressive and invasive tree in Australia, New Zealand and in the US (Panetta 2000). In Argentina, it was introduced at the beginning of the 20th century (Río & Achával 1904) for ornamental purposes (Panetta 2000) and it became invasive in various areas of the country, such as the Chaco region in Córdoba and the riparian forests in Buenos Aires (Montaldo 2000; Aragón y Morales 2003; Gavier-Pizarro

et al. 2012). In particular, *L. lucidum* became invasive in the northwestern subtropical mountain secondary forests of Sierra San Javier in Tucumán, where forest area has increased by 1000 ha between 1949 and 2006, mainly on marginal and abandoned agricultural areas and pastures (Grau et al. 2008). This species establishes monospecific stands (Grau & Aragón 2000; Aragón & Morales 2003; Lichstein et al. 2004; Grau et al. 2007, 2008) but also invades native successional forests. Previous studies indicate that adult individuals of *L. lucidum* (i.e. >10-cm diameter) have the highest growth and recruitment rates, and the lowest mortality rates, compared to most common native tree species in these secondary forests of Sierra de San Javier (Easdale et al. 2007). Its competitive ability may not only depend on its intrinsic demographic characteristics but also on the demographic life histories and morpho-physiological traits of native species (Goldberg 1996). Easdale et al. (2007) indicate the importance of *L. lucidum* in these successional forests, although the ecological consequences on forest dynamics have not yet been evaluated.

In this study, we describe the successional trajectories of post-agricultural secondary forests in the subtropical Andes of Argentina over 20 yr, assessing *L. lucidum* invasion and evaluating native tree growth and mortality rates under and away from *L. lucidum* individuals. Specifically, we (1) quantified the invasion of *L. lucidum* individuals (≥ 10 -cm diameter) from 1991 to 2011 within four 1-ha permanent plots of secondary forests, and (2) analysed annual growth and mortality rates of native tree individuals (≥ 10 -cm diameter) under and away from *L. lucidum* trees. We first compared tree demographic rates of all native individuals together (community level), under and away from the trees of *L. lucidum*, referred to as *exotic* (i.e. under *L. lucidum*) and *native* (i.e. under native species) *neighbourhoods*, respectively. Then, we examined and described the relative growth rate of native species in *exotic/native neighbourhoods* (species level); and related them to their demographic life histories and morpho-physiologies. For this, we relied on previous demographic (Easdale et al. 2007) and plant trait (Easdale & Healey 2009) measurements for common tree species of the studied subtropical forests. We hypothesized that the proximity of these post-agricultural secondary forests to urban areas – where *L. lucidum* is abundant as ornamental tree – may favour its potential for invasion, interfering in the recovery of natural ecosystems where it may become dominant, altering forest succession (Grau et al. 2007). We expected that after 20 yr, both tree density and basal area of *L. lucidum* would increase in these secondary forests and that native tree species would show lower annual growth rates and higher annual mortality rates under individuals of *L. lucidum*.

Methods

Study area and background information

The study was carried out in the protected area, Parque Sierra de San Javier (26°45' S, 65°19' W), Tucumán, Argentina (Fig. 1). The vegetation is typical of subtropical mountain forests (also known as *Yungas*), corresponding to the lower elevation belt known as Montane Forest (Brown et al. 2001). Annual rainfall ranges from 1300 to 1500 mm and is distributed in a monsoonal regime with dry winters and wet summers (Hunzinger 1997). The rainy season occurs from Oct to Mar and concentrates 80–90% of the annual rainfall, while the dry season extends from April to September. Mean annual temperature is 18 °C, with frosts from June to August. Parque Sierra de San Javier is a nature reserve of semi-deciduous forests with an uneven canopy reflecting natural disturbances (e.g. tree-fall gaps). A large percentage of the area was deforested during the first half of the 20th century, and planted with annual crops and fruit orchards, mostly citrus. Subsequently, soil fertility declined and lands were abandoned and progressively re-forested. The inclusion of the study area into a reserve in 1976 facilitated forest recovery. Consequently, the landscape is currently a mosaic of different successional stages of both native (Grau et al. 1997) and *L. lucidum*-dominated forests.

This study is based on 20 yr of four 1-ha permanent sample plots in closed-canopy, post-agricultural secondary forests at ca. 700 m a.s.l. (Grau et al. 2010), which are part of a major permanent plot database monitored through time by the Instituto de Ecología Regional (IER-CONICET). These plots were established in 1991 in forests that were

11–12, 20–25 and 45–50 yr old, and three of them are located on sites with slopes <15%. The fourth plot, also 45–50-yr-old forest, is located on a steeper slope (40–55%) (Table 1; Grau et al. 1997). During the establishment of the plots all trees ≥ 10 cm in DBH were marked with aluminium tags nailed at breast height, mapped and identified to species. After that, all trees were re-measured (or recorded as dead) four times in 5-yr intervals between 1991 and 2011 (1996, 2001, 2006 and 2011).

Data analysis

To describe successional trajectories of the four 1-ha permanent sample plots between 1991 and 2011 we performed a NMDS (Kruskal & Wish 1978) based on a Bray-Curtis distance matrix (Legendre & Legendre 1998) between forest plots in each census (1991, 1996, 2001, 2006 and 2011; $n = 20$) where the main matrix was tree density (individuals-ha⁻¹). Before running the ordination we discarded tree species that were represented by a single individual or were not identified to species level (i.e. we used 34 tree species out of 40). We considered a two-dimensional configuration because the final stress was 12.88 (a value below 20 is acceptable for ecological community data sets) and was significantly different from chance (Monte Carlo: 250 runs with randomized matrix, $P < 0.001$). In addition, we estimated Shannon's diversity index and Evenness (Shannon & Weaver 1949). Shannon's diversity index was calculated as $H = -\sum (P_i \times \ln(P_i))$ where P_i represents the relative abundance of each tree species, and Evenness was calculated as $E = H/\ln(\text{richness})$. In addition, for each tree species we estimated their percentage population change in 20 yr as well as annual growth rates (Condit et al. 2006).

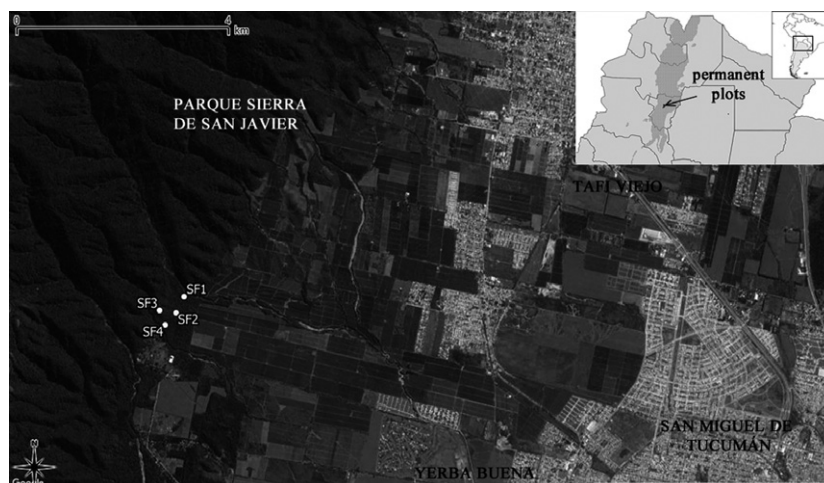


Fig. 1. Location of secondary forest plots. Location of four 1-ha permanent sample plots of secondary forest (SF1, SF2, SF3 and SF4) in Parque Sierra de San Javier, Tucumán, Argentina. Nearby urban areas are shown.

Table 1. Description of four 1-ha permanent sample plots of secondary forest located at Parque Sierra de San Javier, Tucumán, Argentina. Descriptive data were taken from Grau et al. (1997) and Easdale et al. (2007). Density, basal area, biomass and species richness were estimated from the year of plot establishment in 1991. Species richness included all species with at least one individual. For biomass estimation we used the formula of Chave et al. (2005) for moist forest stands.

	SF1	SF2	SF3	SF4
Labels in Grau et al. (1997)	f1	f2	f3	f4
Vernacular Name	Guarán	Mora	Nogal	Cebil
Previous Land Use	Herbaceous crop	Citrus orchard	Herbaceous crop	Herbaceous crop
Age at Time of Establishment	11–12	20–25	45–50	45–50
Slope (%)	<15	<15	<15	45–50
Elevation (m a.s.l.)	741	740	751	805
Density (Trees \geq 10 cm DBH·ha ⁻¹)	582	416	349	359
Basal Area (m ² ·ha ⁻¹)	11.94	16.44	17.04	18.12
Biomass (t·ha ⁻¹)	60.94	128.17	151.25	201.04
Species Tree Richness (Species with Trees \geq 10 cm DBH·ha ⁻¹)	17	20	19	24

To quantify *L. lucidum* invasion from 1991 to 2011 we recorded the total number of individuals of *L. lucidum* \geq 10 cm DBH in all censuses. Then, we estimated tree density (individuals·ha⁻¹) and basal area (m²·ha⁻¹) for each census, and performed ANOVA and *post-hoc* Fisher test to check for temporal changes in 20 yr. For this, we log-transformed the response variables to achieve normality and homoscedasticity.

To compare tree demographic rates of all native individuals together (community level) under individuals of *L. lucidum* and under native trees, we identified all trees of *L. lucidum* that recruited (\geq 10 cm DBH) between 1991 and 2006 in all four sample plots. Then, we selected a buffer area of 5-m radius around each tree (i.e. 10-m diameter, *exotic neighbourhood*) where all individual trees of native species (\geq 10 cm DBH) were recorded. In each of these *exotic neighbourhoods* we estimated tree demographic rates for all native individuals during the last re-measurement period 2006–2011. We considered tree annual growth rates as the increment in diameter of native tree stems during the last re-measurement (2006–2011) expressed in mm·yr⁻¹ ($G = \ln(\text{dap}_{2011}) - \ln(\text{dap}_{2006})/t$, where dap_{2006} and dap_{2011} are the DBH in 2006 and 2011, respectively; and t is time in years). We considered annual tree mortality rates as the proportion of dead stems during the last re-measurement period ($M = \ln(N_{2006}) - \ln(N_{2011})/t$, where N_{2006} is the number of stems counted in 2006 and N_{2011} is the number of stems that survived in 2011; and t is time in yr; Condit et al. 2006). As a control, we randomly selected individuals of native canopy tree species showing similar size to *L. lucidum* individuals that recruited between 1991 and 2006. For these trees, we selected a buffer area of 5-m radius (*native neighbourhoods*) where all native individuals (\geq 10 cm DBH) were recorded and where we estimated both annual growth and mortality rates for the period 2006–2011. To evaluate differences in annual growth and mortality rates of all native individuals together (regardless

of species) between *exotic* and *native neighbourhoods* we performed *t*-tests. We log-transformed the response variables to achieve normality and homoscedasticity.

To examine and describe the relative growth of native tree species in *exotic/native neighbourhoods* (species level), we used a log response ratio. We calculated this response ratio for each species as $\ln(G \text{ in } \textit{exotic neighbourhoods} / G \text{ in } \textit{native neighbourhoods})$ and we used it as an indicator of the interaction strength between *L. lucidum* and each native species. We interpreted positive (>0) values as facilitation and negative (<0) values as competition. Relative growth rate (RGR) was calculated only for species that had, at least, two stems in each type of neighbourhood (only 11 species out of 40 met this condition).

To relate the RGR of native tree species to their life histories and morpho-physiological traits, we relied on previous studies about demographic (Easdale et al. 2007) and plant trait (Easdale & Healey 2009) measurements carried out for common tree species of Parque Sierra de San Javier (same study area as this study, but also including old growth forests nearby). Easdale et al. (2007) interpreted three dimensions of life-history variation: (1) (PC1 dem) A light-demand and growth potential axis showed that species with high growth rates tend to have well exposed crowns and have high density of trees in secondary forest. (2) (PC2 dem) A population turnover (r-K) axis revealed that species with low rates of tree survivorship and short-lived individuals have high rates of recruitment, lower basal area and few large individuals in old-growth forest. (3) (PC3 dem) A third axis indicated species that recruited on landslides and had low recruitment in old-field successions (Appendix S1). Easdale & Healey (2009) interpreted two dimensions of variation for these same species: (1) (PC1 mor) A 'resource capture' axis separated species with large and thin leaf laminae, high leaf K, P and N concentrations from species with opposite attributes, and (2) (PC2 mor) a 'physiognomic' axis separated species with

compound leaves, high leaf/above-ground mass ratio from species with opposite attributes (Appendix S2). We performed Spearman correlations between the RGR of native species and the scores of these species in these five dimensions, and between the RGR of native species and their total abundance in 2011. Since the variable RGR was not normally distributed we used non-parametric correlations.

Repeated ANOVA, *post-hoc* Fisher test, *t*-tests and Spearman correlations were performed with the R statistical package (v 3.1.2; R Foundation for Statistical Computing, Vienna, AT), while NMDS was performed with PcOrd for Windows (v 5.0; MjM Software Design, Gleneden Beach, OR, US).

Results

Between 1991 and 2001 all four 1-ha permanent plots of secondary forests showed similar successional trends, moving towards the negative side of axes 1 and 2 in the ordination diagram (Fig. 2). These changes illustrate strong ($\geq 50\%$) abundance change of particular taxa (Appendix S3). Shade-tolerant canopy tree species such as *Blepharocalyx salicifolius*, *Juglans australis*, *Ocotea porphyria* and *Terminalia triflora* increased in all plots as well as the sub-canopy species *Allophylus edulis*, *Piper tucumanum* and *Urera caracasana* (Table 2). Other tolerant canopy species such as *Cedrela angustifolia*, *Cupania vernalis* and *Myrsine laetevirens* increased particularly in SF1 and SF2. At the same time, individuals of pioneer species such as *Heliocarpus popayanensis*, *Tecoma stans* and *Solanum riparium* tended

to decrease in all plots (Appendix S3). Both diversity and evenness increased over 20 yr (Table 2). During the 20-yr period, forests maintained tree density but gained basal area, particularly between 1991 and 2006 ($F_{4,12} = 38.3$, $P < 0.01$; Fig. 3a).

Importantly, between 1991 and 2011, there was a consistent increase in *L. lucidum* density (individuals·ha⁻¹; $F_{4,12} = 7.64$, $P < 0.01$) and basal area ($F_{4,12} = 7.01$, $P < 0.01$; Fig. 3b). Indeed, *L. lucidum* increased over 3000% in 20 yr (Appendix S3). The increase by periods was 400% during 1991–1996, 300% during 1996–2001, 175% in 2001–2006 and 160% during 2006–2011. By 2011, *L. lucidum* represented 4.18% (range = 0.22–9.76%) of the tree density and 3.86% (range = 0.03–9.10%) of the total basal area of each plot (m²·ha⁻¹). Moreover, *L. lucidum* showed the highest growth rate among all tree species (0.69 mm·yr⁻¹; Appendix S3).

Annual growth rate (mm·yr⁻¹) of native tree individuals was lower in *exotic neighbourhoods* (i.e. under individuals of *L. lucidum*) than in *native neighbourhoods* (0.015 ± 0.003 and 0.022 ± 0.002 in *exotic* and *native neighbourhoods*, respectively; $t = -2.00$, $df = 59$, $P = 0.05$). Annual mortality rates (proportion of dead stems) did not differ between *exotic* and *native neighbourhoods* ($t = 0.53$, $P = 0.60$).

Relative growth rate (RGR = $\ln(G \text{ in } exotic/G \text{ in } native \text{ neighbourhoods})$) differed among species (Fig. 4). The most abundant species *Myrsine laetevirens*, *Ocotea porphyria*, *Parapitadenia excelsa*, *Juglans australis* and *Allophylus edulis*, showed negative values indicating competition with *L. lucidum* (Spearman $R = -0.59$, $P = 0.05$; Fig. 5,

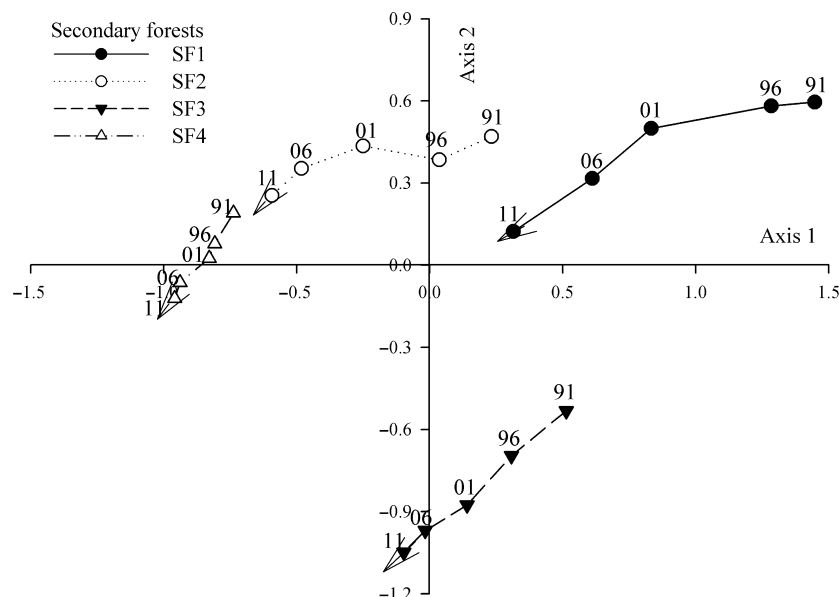


Fig. 2. Successional trajectories of secondary forest plots in 20 yr. NMDS ordination diagram of four 1-ha permanent sample plots of secondary forests (SF1, SF2, SF3, SF4) based on tree species composition. Points refer to five censuses between 1991 and 2011.

Table 2. Average of Shannon's diversity index and evenness estimated for four 1-ha secondary forest permanent sample plots (SF1, SF2, SF3 and SF4) at Parque Sierra de San Javier, Tucumán, Argentina, in five censuses between 1991 and 2011.

Census	Evenness	Diversity
1991	0.62	1.84
1996	0.65	1.98
2001	0.71	2.19
2006	0.75	2.34
2011	0.77	2.41

Appendix S3); while *Terminalia triflora*, *Heliocarpus popayanensis*, *Cupania vernalis* and *Blepharocalyx salicifolius* showed positive values implying facilitation (Figs 4 and 5). When taking into account life histories and morpho-physiologies of native tree species, RGR showed a negative correlation with the first dimensions of life-history variation (PC1 dem; Table 3). Native tree species with characteristics such as exposed crowns and with higher abundance in secondary forests tended to compete with *L. lucidum* and showed lower RGR under *L. lucidum* individuals. We found no relationship with other life histories (PC2 dem: population turnover, PC3 dem: substrate requirements for establishment), or with morpho-physiological traits of native tree species (PC1 mor: efficiency in resource capture, PC2 mor: physiognomic features; Table 3).

Discussion

Secondary forests in the subtropical Andes of Argentina changed between 1991 and 2011, showing similar successional trends among them, although younger stands changed faster (SF1) than older woodlands (i.e. SF4). Apparently, the typical successional patterns are occurring

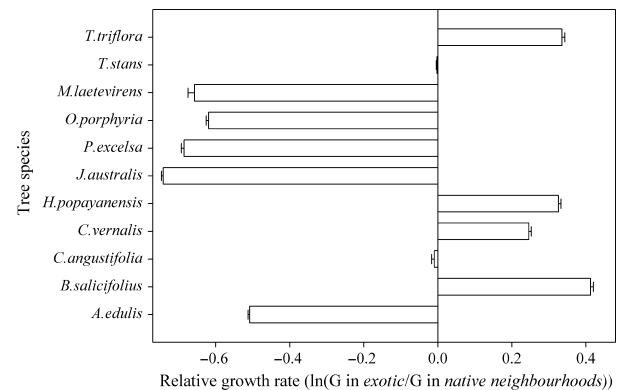


Fig. 4. Differences in RGR for native species. RGR = $(\ln(G \text{ in exotic neighbourhoods}/G \text{ in native neighbourhoods}))$ of native tree species: positive values imply facilitation while negative values imply competition under *L. lucidum* individuals. For each species, data correspond to the ratio of its average growth rate in the *exotic neighbourhoods* divided by its average growth rate in the *native neighbourhoods*. Error bars correspond to the average of the SE estimated in *exotic* and *native neighbourhoods*. Species are ordered alphabetically. Full species names are provided in Table 2.

in these plots where forests are recovering species richness, diversity and evenness (Guariguata & Ostertag 2001). In particular, shade-tolerant canopy and sub-canopy species such as *Blepharocalyx salicifolius*, *Juglans australis*, *Ocotea porphyria*, *Terminalia triflora*, *Allophylus edulis*, *Piper tucumanum* and *Urera caracasana* are increasing in all forest plots; while typical species of early successional stages such as *Heliocarpus popayanensis*, *Tecoma stans* and *Solanum riparium* are decreasing. These floristic changes are also reflected in structural changes. Although forests did not lose individuals, they tended to increase in basal area due to the natural growth of trees in the successional process. These changes may imply that species composition and structure of these

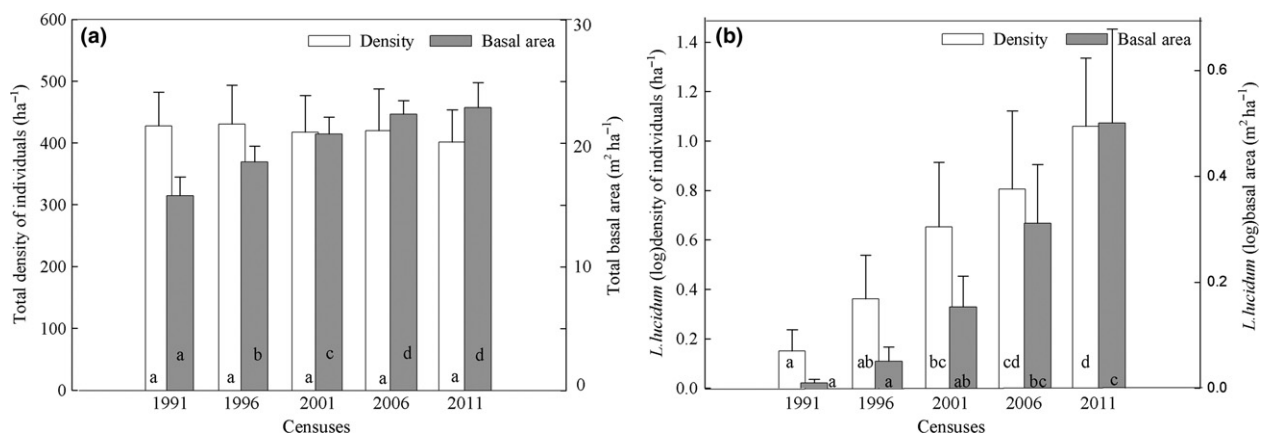


Fig. 3. Changes in density and basal area for all individuals and for *L. lucidum* in 20 yr. Changes in density (white) and basal area (grey) for (a) all tree individuals, and (b) *L. lucidum* in five censuses between 1991 and 2011. Letters identify different groups from repeated ANOVA and *post-hoc* Fisher test at significant level ($P < 0.01$). Error bars correspond to SE. Data are the per hectare average in four 1-ha permanent plots (SF1, SF2, SF3, SF4).

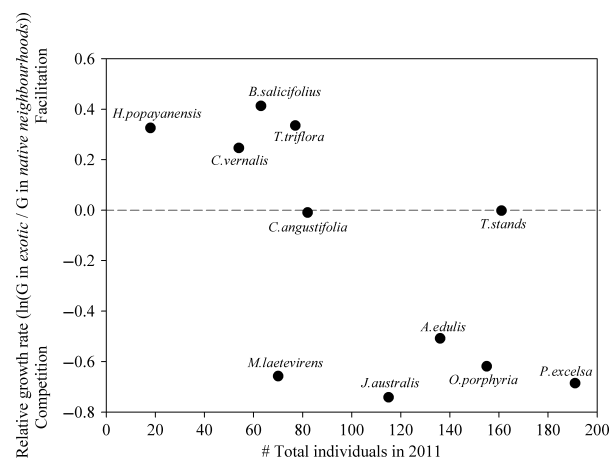


Fig. 5. Relationship between RGR and total individuals in 2011. RGR = $(\ln(G \text{ in exotic neighbourhoods}) / G \text{ in native neighbourhoods})$ of native tree species and their total number of individuals in 2011.

Table 3. Spearman correlation coefficients (*R*) between relative growth rate (RGR = $(\ln(G \text{ in exotic neighbourhoods}) / G \text{ in native neighbourhoods})$) and demographic and morphological dimensions.

Morphological and Demographic Dimensions	Spearman <i>R</i>	<i>P</i> -Level
Light Demand and Growth Potential (PC1 dem)	-0.74	0.01
Population Turnover (PC2 dem)	-0.18	ns
Substrate Requirements for Establishment (PC3 dem)	0.02	ns
Resource Capture and Conservation (PC1 mor)	-0.04	ns
Physiognomic Features (PC2 mor)	-0.29	ns

Bold numbers indicated significant values.

secondary forest plots are moving towards old-growth forest conditions (Guariguata & Ostertag 2001).

However, our results revealed that *L. lucidum* is successfully invading native secondary forests as it experienced a major increase in density and basal area between 1991 and 2011. This highlights that, within our study area, *L. lucidum* not only dominated agricultural land abandoned in the 1950s, where it tends to form monospecific stands (i.e. secondary forests dominated by *L. lucidum*; Grau & Aragón 2000; Grau et al. 2007, 2008), but it is also invading secondary forests where native successional processes are taking place. In 1991, when these permanent plots were established, only two individuals of *L. lucidum* with ≥ 10 cm DBH were recorded in SF2 and SF3; while zero individuals equal or larger than this size were recorded in SF1 and SF4. Twenty years later, *L. lucidum* has reached, on average, almost 4% of the total density and basal area per hectare. Guariguata & Ostertag (2001) state that the usual successional process begins with site colonization, then canopy closure, recovery of species richness, increases in basal area and biomass, and ends

with a convergence in species composition similar to old-growth forests (i.e. 400–500 yr). But the new plant communities may diverge from the original ones, especially if exotic and invasive species such as *L. lucidum*, which show some demographic advantages over native tree species (i.e. higher growth and recruitment rates, and lower mortality rates; Easdale et al. 2007), colonize during early stages of forest succession.

When colonizing, *L. lucidum* reproduction and expansion occurs mainly in two ways, through vegetative sprout regeneration (Grau & Aragón 2000) and through seed dispersal by birds during the winter season (cold and dry) when most native tree species do not produce fruit (Aragón & Groom 2003). In addition, *L. lucidum* is able to germinate from fallen fruits without passing through the digestive tract of birds (Aragón & Groom 2003). When studied in the same study area but within monospecific stands at seed and seedling stages, Aragón & Groom (2003) found that *L. lucidum* is capable of germinating and surviving in a broad range of forest habitats, including both tree-fall gaps and shady forest interior. Moreover, once established, *L. lucidum* saplings grew better than saplings of common native tree species (Aragón & Groom 2003). Given the plant traits and demographic characteristics shown at early stages in this monospecific stands, we expect that the increasing trend of *L. lucidum* within post-agricultural native secondary forests will continue in the near future. Similarly, in other forests of Argentina, such as in the Chaco region and riparian forests, *L. lucidum* has become a widespread invader and dominates forest regeneration in native successional forests which are located adjacent or close to monospecific stands of this species (Montaldo 2000; Hoyos et al. 2010; Gavier-Pizarro et al. 2012).

A key issue in invasion dynamics is whether or not exotic species become more dominant late in the successional processes. When individuals of *L. lucidum* become adults (i.e. larger than 10 cm DBH) competition at individual level with native tree species for water and other below-ground resources may become an important factor affecting the demography of native tree species. For example, Zamora Nasca et al. (2014) suggested that secondary forests dominated by *L. lucidum* (i.e. monospecific stands) consumed more water compared to native secondary forests, especially during the dry season (winter–spring); indeed soil water content in secondary forests dominated by *L. lucidum* was ca. 28% lower than in native secondary forests. This may result, in part, from the maintained green foliage throughout the year in contrast to native forests, which are partially deciduous (Zamora Nasca et al. 2014), and from the extremely dense root system of *L. lucidum* (pers. obs.). Within the native secondary forests, we found that native individuals (regardless of identity of the species;

community level) were at apparent disadvantage when growing under the invading individuals of *L. lucidum*. On average, native individuals grew ca. 65% less in *exotic neighbourhoods* when compared to native ones. We did not find native trees showing higher annual mortality rates under *L. lucidum* individuals, but we believe that once invasion becomes more spread out (i.e. more and larger individuals with deeper and denser roots), it may interfere with the mortality rates of native trees.

At species level, we were able to identify particular species that showed competition or facilitation processes in *exotic neighborhoods* in relation to native ones. On the one hand, some of the most abundant canopy native species such as *Myrsine laetevirens*, *Ocotea porphyria*, *Parapatadenia excelsa* and *Juglans australis* were in apparent disadvantage when growing under *L. lucidum* individuals. In addition, the sub-canopy species *Allophylus edulis* showed a negative interaction (i.e. competition). On the other hand, less abundant species such as *Terminalia triflora*, *Heliocarpus popayanensis*, *Cupania vernalis* and *Blepharocalix salicifolius* showed positive interactions (i.e. facilitation). Based on their different life histories and morpho-physiological traits, the species competing with *L. lucidum* tended to have exposed crowns and were more abundant in secondary forests (PC1 dem; Easdale et al. 2007). Taking these results together, *L. lucidum* was able to compete with some native tree species efficiently, particularly with those species that are very abundant and compose the main structure of the forest canopy. In Argentina, several studies have monitored the expansion of *L. lucidum* in different forest regions (Hoyos et al. 2010; Gavier-Pizarro et al. 2012), including subtropical forests (Montti pers. comm.), but none of these has evaluated its impact on an individual basis at community or species level.

It is likely that once *L. lucidum* achieves a considerable density within these native secondary forests in the near future, the ecological consequences may lead to major changes in successional trajectories, composition and structure, simplifying the forest interior (Ayup et al. 2013), decreasing biodiversity of different non-structural groups such as lianas (Ceballos et al. 2015) and modifying processes that occur during succession. For example, secondary forests dominated by *L. lucidum* may enhance biomass accumulation and C sequestration as a result of its demographic characteristics (i.e. highest growth and recruitment rates, and lowest mortality rates compared to most native tree species common in these secondary forests in Sierra de San Javier; Easdale et al. 2007). However, at the same time, its dominance may alter biodiversity of animals, such as bird communities (Ayup et al. 2013), and ecosystem functioning processes (i.e. productivity and water dynamics; Zamora Nasca et al. 2014). This idea is

consistent with the results of Hoyos et al. (2010) for forests in the Chaco region (Argentina) where *L. lucidum*, is already changing the patterns of vertical structure and diversity in native forests.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

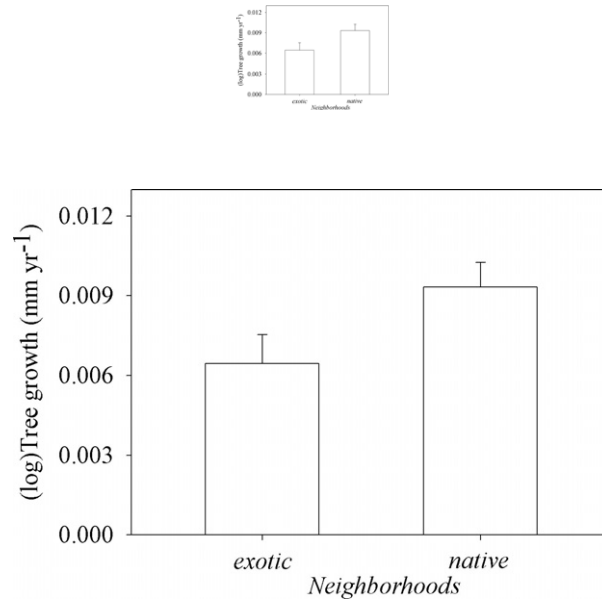
Appendix S1. Summary of demographic variables reported for 29 tree species at Parque Sierra de San Javier, Argentina.

Appendix S2. Summary of plant morphological traits reported for 29 tree species at Parque Sierra de San Javier, Argentina.

Appendix S3. Abundances of all tree species ≥ 10 cm DBH recorded at Parque Sierra de San San Javier in four 1-ha secondary forest permanent sample plots throughout first (1991) and final censuses (2011).

Graphical Abstract

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Ligustrum lucidum is invading post-agricultural native secondary forests. On average, native tree individuals grew 65% less in *exotic neighborhoods* (under *L. lucidum* trees) compared to *native neighborhoods* (under native trees). While invading, *L. lucidum* competed with native abundant tree species that compose the main structure of the forest canopy. In the future, *L. lucidum* may alter forest dynamics and ecosystem functioning.