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Reproductive performance of the invasive tree *Ligustrum lucidum* in a subtropical dry forest: does habitat fragmentation boost or limit invasion?

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Abstract The spread of non-native invasive plants is closely linked to land use changes imposed by human activities such as the expansion of urbanizations and agricultural activities that result in the loss and fragmentation of native forests. While the conditions generated in fragmented forests may provide suitable new habitat for the arrival and establishment of invasive plant propagules, we know little about the reproductive performance of established invasive populations growing in fragmented conditions. We assess sexual reproduction of *Ligustrum lucidum* in continuous and fragmented forests across 2 years. We also measure soil quality parameters in 1 year to determine their relative influence in shaping its reproduction in both landscape conditions. We observed a strong decrease in reproductive success at the population level in fragmented habitats. However, reproduction at the individual level showed no differences in seed production per tree between landscape conditions, implying no changes in pollination

service. Simultaneously, soils of continuous forests had higher water content, total nitrogen, organic matter and carbon. These soil quality parameters were positively correlated with seed production and seedling number per plot within the same year. Thus, reproductive failure in fragmented forests would not be the result of Allee effects but the consequence of less favorable abiotic soil conditions. In current dynamic and changing climatic scenarios imposed by human activities, water and nutrient demanding invasive plants like *L. lucidum* might be as likely as or even more susceptible to these changes than native ones. Climatic shifts acting in concert with land use changes may either ameliorate invasion spread in abiotically eroded fragmented habitats or boost invasion into novel environments, resulting in new distribution spread patterns.

Keywords Glossy privet · Soil quality · Reproductive success · Seedling · Seed germination · Progeny vigor

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Introduction

Land use changes resulting from human activities are often closely linked to terrestrial biological invasions, shaping their success and distribution patterns in novel environments (Hobbs and Huenneke 1992; Mosher et al. 2009; Vila and Ibáñez 2011; Decker et al. 2012). The spread of non-native invasive plants in particular,

can be especially promoted by the settlement and growth of urbanization in suburban areas, and by the expansion and intensification of agricultural activities (Hobbs and Huenneke 1992; With 2002; González-Moreno et al. 2012; Aikio et al. 2012). Suburban human settlements outside big cities offer opportunities for bringing new non-native plant species as ornamental or cultivars in the area, facilitating their spread to the adjacent native forests (Duguay et al. 2007; Vila and Ibáñez 2011; Gavier-Pizarro et al. 2012; Decker et al. 2012). Native forest remnants embedded within agricultural matrices in the rural landscape are highly susceptible to invasion (With 2002). Modified landscape structure following fragmentation can enhance spread by boosting specific stages of the invasion process (i.e., dispersal vs. population growth; With 2002). Fragmented forests provide increased forest edge exposure favoring pioneering non-native invasive species through increased light availability (Mosher et al. 2009; Gavier-Pizarro et al. 2012; González-Moreno et al. 2012). In addition, habitat fragmentation often involves a reduction of native population sizes and an increase in their degree of isolation, which may reduce competition and facilitate the establishment and growth of non-native invasive populations (With 2002; Eschtruth and Battles 2009; Vila and Ibáñez 2011).

While the conditions generated in fragmented forests may provide suitable new habitat for the arrival and establishment of invasive plant species propagules, we know little about the reproductive performance of established invasive populations growing in fragmented conditions. Sexual reproduction of non-native invasive plants represents a key aspect for determining the success of invasion, as it provides the source of propagules to increase population size and to colonize new sites via dispersion of genetically unique progeny (Barrett et al. 2008; Simberloff 2009). In this regard, the effects of habitat fragmentation on reproduction have been widely studied in native plant populations. Recent quantitative literature reviews have shown that habitat fragmentation significantly decreases pollination and sexual reproduction of remaining native populations (Aguilar et al. 2006; Leimu et al. 2006). Such reduced reproductive success in native plants has been mostly ascribed to decreased pollination service as a consequence of decreased pollinator richness and

abundance in fragmented habitats (e.g., Winfree et al. 2009) that result from direct anthropogenic effects on the pollinator fauna (e.g., Wilcock and Neiland 2002) and also from the lower population size and increased isolation of plant populations (i.e., “Allee effects”), which especially affects highly outcrossing species (Aguilar et al. 2006; Leimu et al. 2006). Moreover, changes in abiotic conditions due to habitat fragmentation, especially soil nutrient content and other microenvironmental properties have also been responsible of decreased reproductive output in native plant populations (Vergeer et al. 2003; Winter et al. 2008; Matezans et al. 2009; Tsaliki and Diekmann 2010). After the land is cleared, remnant vegetation patches embedded in anthropogenic matrices are subjected to changes in the physical environment (Saunders et al. 1991; Lindenmayer and Fischer 2006). Such changes often imply increased solar radiation, affecting nutrient cycling processes, soil microorganisms and soil moisture retention. Increased exposure to winds can also be common, raising evapotranspiration and desiccation in plants growing in forest patches (Saunders et al. 1991 and references therein; Lindenmayer and Fischer 2006). Despite the substantial evidence of fragmentation effects (either biotic or abiotic) on native plant species, we do not yet know whether sexual reproduction of non-native invasive populations growing in fragmented forests is similarly affected as native populations.

The Chaco Serrano forest in the Sierras Chicas of Córdoba, Argentina, has experienced an unprecedented growth and expansion in both, its suburban settlements and agricultural activities, resulting in widespread landscape change (Gavier and Bucher 2004; Gavier-Pizarro et al. 2012). Over the period of 1970–1997 the loss of native forest reached 40 %, with an increasing deforestation rate that was among the highest worldwide (2.8 % per year), accompanied by a strong process of forest fragmentation (Gavier and Bucher 2004).

Throughout this period, there was a parallel expansion of woody non-native invasive trees. Today, the Asian tree glossy privet (*Ligustrum lucidum* W.T. Aiton) is, by far, the most successful invader in the Sierras Chicas of Córdoba (Hoyos et al. 2010; Gavier-Pizarro et al. 2012). Glossy privet was introduced around 1900 as an ornamental plant (Rio and Achaval 1904) and has abruptly expanded its distribution and aggressively invaded vast regions of this

forest as well as other regions in the northwestern hills and eastern plains of Argentina (Grau and Aragón 2000; Gavier-Pizarro et al. 2012). Recent studies using Landsat satellite images to determine and map the patterns of glossy privet expansion from 1983 to 2006 in the Sierras Chicas have shown astonishing results. Within this 23-year period studied, glossy privet area increased 50 times (from 50 to 2,500 ha), dominating 20 % of all remaining native forest within the Chaco Serrano (Hoyos et al. 2010; Gavier-Pizarro et al. 2012).

Glossy privet has several advantages over native trees. It is a fast-growing, self-compatible, hermaphrodite tree that offers a massive yield of fleshy fruits in late autumn and throughout the winter (Montaldo 1993; Aragón and Morales 2003; Tecco et al. 2006; Ferreras et al. 2008); a period when native fruit production for birds significantly decreases. Also, seedlings can grow under both shaded and full light conditions, so the species can thrive in relatively undisturbed native forest (Aragón and Groom 2003). Thus, once it reaches the canopy, it creates low luminosity conditions outcompeting most native species and hampering their regeneration. This situation implies changes in vertical structure and composition due to the loss of native tree species and the drastic reduction in the herbaceous and shrubby cover strata, eventually resulting in complete glossy privet dominance (Grau and Aragón 2000; Hoyos et al. 2010).

In this study we assess the effects of habitat fragmentation on sexual reproduction, seed germination, seedling survival in the greenhouse, and seedling establishment in the field of non-native invasive populations of *L. lucidum*. Because the species is self-compatible with massive flowering, we hypothesize that reproductive success at the individual level is similar in both fragmented and continuous forests (Aguilar et al. 2006; Eckert et al. 2009). Moreover, such selfing capability implies that any change in mating patterns due to forest fragmentation should not significantly affect progeny performance (Aguilar et al. 2008; Angeloni et al. 2011). Also, because the species is particularly drought-intolerant (Panetta 2000; Aragón and Groom 2003; Aslan et al. 2012), we assess several soil quality parameters in fragmented and continuous forests to evaluate whether any abiotic microenvironmental differences affect the reproductive performance of these invasive populations (Milbau et al. 2009; Quiroz et al. 2011). In this

regard, we hypothesize that soil properties such as moisture, organic matter and nutrients are decreased or under-optimal in fragmented forests (Saunders et al. 1991; Lindenmayer and Fischer 2006), which may negatively affect the reproductive performance of maternal trees and/or the establishment of seedlings in the field (Panetta 2000; Vergeer et al. 2003; Winter et al. 2008; Tsaliki and Diekmann 2010).

Materials and methods

Study area and background information

The study was conducted in the Sierras Chicas, in the surroundings of the small city of Rio Ceballos, located at 36 km north of Córdoba city, central Argentina. The sampling sites were located in a total area of ca. 26 km², comprising contrasting zones of relatively continuous forests and highly fragmented forests (Fig. 1). The study area corresponds to the Chaco Serrano phytogeographical region, a subtropical dry forest with dominant montane woodland vegetation (Luti et al. 1979). The elevation ranges from 400 to 1,300 m a.s.l., and the average maximum and minimum annual temperatures range between 26 °C and −10 °C, respectively (Luti et al. 1979). Rains concentrate in the warm season (October–April). The mean annual rainfall of the last 50 years in the region is 944 mm; which is considered the highest precipitation volume recorded within the province (Cordoba Airport Meteorological Observatory).

As part of an ongoing long-term study aimed to assess the demographic dynamics of *L. lucidum* in contrasting landscape conditions, we established 16 permanent field plots of 20 × 50 m each (1,000 m²) in May 2010, across fragmented and continuous forests ranging from 400 to 700 m a.s.l. in altitude. Because of our primary demographic interest in building projection matrix models, the selection criterion for establishing each plot was to find *L. lucidum* populations with enough number of individuals representing pre-determined discrete classes of its life cycle (N = 30–50 individuals per class): seedlings, saplings, juveniles, and reproductive adults. These classes were defined previously to establishing the plots, and were based on a combination of stage (seedlings) and size classes (from saplings to adults). Size classes were determined by height and diameter

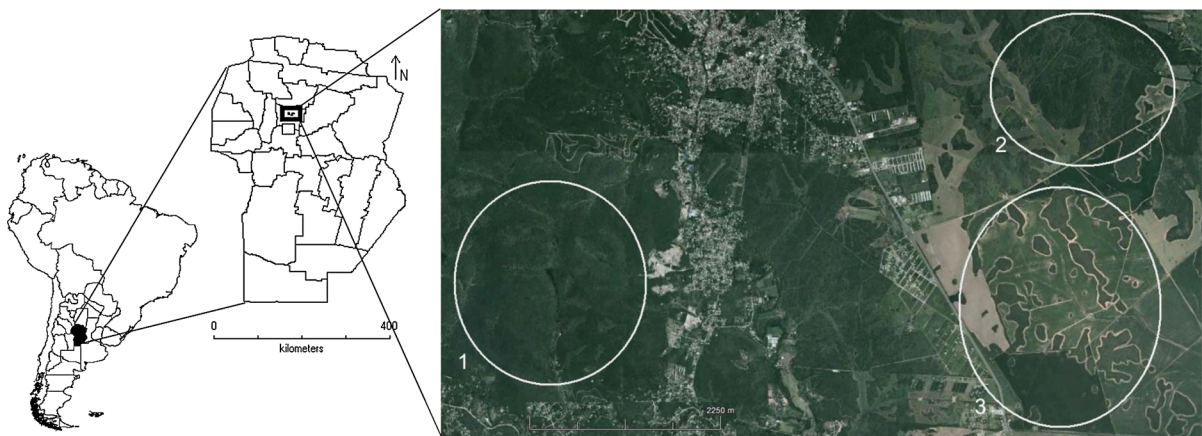


Fig. 1 Spatial location of studied sites in the Chaco Serrano Forest of Central Argentina. Landscape conditions: continuous (1, 2) and fragmented forests (3)

at breast height (DBH) of each individual (Morris and Doak 2002). Such selection criterion implies that all plots are comparable in their population size, structure, and degree of invasiveness, thus all share similar native surroundings within each plot and none of them are completely invaded (i.e., monotypic). Eight plots were located in an area of 9 km² of highly fragmented forest. Within this area, many forest fragments of varied sizes remain surrounded by a highly modified agricultural matrix dominated by wheat in winter and maize or soybean in summer. Another eight plots of identical size were distributed within two continuous forest tracts near the fragmented forest sites in an area of 10 km² (Fig. 1). The main change imposed by fragmentation in glossy privet populations imply the presence of agricultural matrix that creates edges and isolates populations growing in forest fragments (Fig. 1).

Study species

Ligustrum lucidum W.T.Aiton (Oleaceae) is an ever-green tree native to China and Korea. It has a dense canopy of glossy green leaves and reaches heights of 14 m. Small, cream-colored and strongly scented hermaphrodite flowers are produced in large clusters. Although it can reproduce via vegetative propagation, reproduction is mainly achieved through sexually-produced seeds (Montaldo 1993). The species has a mixed mating system, where the combination of self-compatibility with massive flowering production facultatively assures reproduction via autogamous and

geitonogamous crosses (Montaldo 1993). Besides Argentina, glossy privet has also been reported to be an aggressive invasive tree in Australia, New Zealand, and USA (Panetta 2000; Aslan et al. 2012).

Sexual reproduction

From observations conducted in 2009 in both continuous and fragmented forests, we determined that individual trees with DBH of at least 6.40 cm were sexually mature. Thus, in each plot, we tagged and followed all potentially sexually mature trees (i.e., >6.40 cm) of *L. lucidum* (N total = 738 trees). We assessed the fertility of each of these mature trees in each plot through two consecutive years (2010 and 2011). Moreover, we determined whether minimum DBH to flowering was held similar in each landscape condition and estimated the proportion of fruiting trees correcting for minimum DBH in each condition in each of the 2 years. Sexual reproduction was measured as the total amount of seeds produced per mature tree. Because trees can produce very large amounts of fruits, we obtained estimations of total fruit number per tree in both conditions. First, we randomly took 5 infructescences per tree and counted fruit number on each one of them. Then, we divided the canopy into 4–8 equally-sized quadrants, depending on the size of the canopy. In two of these quadrants, we counted the total number of infructescences and calculated an average number of infructescences per quadrant, which was then multiplied by the number of quadrants

to obtain the total number of infructescences per tree. Finally, total fruit production per tree was estimated by multiplying total number of infructescences by the mean number of fruits per infructescence. In trees with heterogeneous infructescence size we categorized infructescences in three classes: small (<20 fruits), medium (20–100 fruits) and large (>100 fruits). Thus we could correct quadrants by the size of the infructescences to obtain a better estimation. To further reduce the error estimation, field observations were conducted by a single observer throughout all plots. The majority of fruits (80 %) contain one seed but some fruits (20 %) can contain two seeds (Montaldo 1993). We corroborated these results when obtaining an average of 1.2 seeds per fruit after quantifying seed number in 100 fruits from trees in each landscape condition. Thus, total seed number per tree was finally calculated by multiplying fruit number by 1.2.

Seed germination, seedling mortality in greenhouse and seedling number in the field

As most bird-dispersed species, glossy privet seeds without the exocarp are significantly more likely to germinate (Montaldo 1993), so we manually removed the pulp of fruits before the germination trials. We obtained 20 seeds from each of 20 and 21 maternal trees from continuous and fragmented conditions (2–3 trees per plot), respectively ($N = 820$ seeds). These seeds were subjected to a 12/12 h daily photoperiod. Seeds were placed on filter paper in Petri dishes ($N = 20$ from the same maternal tree per Petri dish), in a germinating chamber at 25 °C, and watered every two days. Germination, assessed as radicle emergence, was also registered every two days until the last seed germinated. Germination percentage was calculated as: $(\text{Number of germinated seeds} / \text{Number of seeds sown}) \times 100$. We also assessed germination speed (GS) as: $GS = (\text{germinated seeds} / \text{days to first count} + \text{germinated seeds} / \text{days to } n \text{ count} + \text{germinated seeds} / \text{days to final count})$ (Maguire 1962). Groups of 50 germinated seeds were placed in common pots (30 × 70 × 20 cm depth) to assess seedling survival in the greenhouse for 120 days. Seedlings were watered once a week. Finally, we searched for newly emergent seedlings (1–3 cm height) in each of the 16 plots across both landscape conditions. The search was conducted in November

2011, after the rainy season had begun, thus seedling found in the field are likely to belong to the previous reproductive season of 2010. Because each plot is visibly delimited with thin rope every 100 m², we were able to cover the entire plot in detail to search for emergent seedlings.

Soil properties

In November 2011 we collected soil samples in all plots across continuous and fragmented forests, each soil sample was a composite of 3 subsamples (0–10 cm depth) taken randomly. Samples were stored in a portable Styrofoam cooler in the field and immediately taken to the Soil Laboratory of the Faculty of Agronomic Sciences, National University of Córdoba. Gravimetric soil moisture was determined immediately and the remaining sample were air-dried and ground to pass through a 2 mm mesh. Soil was analyzed for organic carbon (C), total nitrogen (N), nitrates (NO³⁻), extractable phosphorous (P), pH, electrical conductivity (EC), and exchangeable cations (Ca²⁺, Mg²⁺, Na⁺ and K⁺). The following analyses were carried out according to the procedures described in Sparks et al. (1993) and Raveh (1973): organic C by the Walkley–Black wet digestion method, total N by semi-micro Kjeldahl, nitrates using ion selective electrodes, extractable P by the Bray–Kurtz method, pH in water (1:1, soil:water ratio), electrical conductivity (1:1, soil:water ratio), and exchangeable cations in 1M NH₄OAc extracts by atomic absorption spectrometry. Soil organic carbon data were multiplied by a factor of 1.72 to give soil organic matter values (Howard and Howard 1990). Soil depth (cm) was measured with an iron bar hammered into the soil until the rock substrate was reached; we took fifteen measures per plot.

Data analysis

Analyses were performed in R environment (R Development Core Team 2009). We used linear mixed effects model (*lme* function from the *nlme* package, Pinheiro et al. 2009) for the quantitative response variable (germination speed) and generalized linear mixed effect models (*lmer* function from the *lme4* package, Bates and Maechler 2009), for binomial-distributed (germination percentage, seedling mortality) and Poisson-distributed variables (seed production

per tree, seedling number). In the case of seed production per tree we included the DBH of each tree as a covariate within the model (i.e., ANCOVA for count data; Crawley 2007). We also assessed whether the binary response of fruiting versus non-fruiting trees was determined by landscape condition simultaneously including each tree's DBH as a covariate within the model (i.e., ANCOVA for binary data; Crawley 2007). We used landscape condition as the fixed main effect with two levels (continuous and fragmented forests), and plots as a random effect ($N = 16$). Significance of fixed effect was assessed with t tests in linear mixed models and with Wald-Z in generalized linear mixed models. Model parameters were estimated with restricted maximum likelihood methods and Laplace approximation for *lme* and *lmer* functions, respectively. Soil nutrient variables were obtained at the plot level, thus we tested for differences between the two landscape conditions with t tests and Wilcoxon tests for variables with non-normal error distributions. Such multiple pair wise comparisons of soil nutrient parameters can inflate the probability of committing type I error, thus we adjusted p values following Holm method (Crawley 2007). Because we were able to assess soil properties only in 2011, we tested for relationships between log-transformed seed production during 2011 and soil nutrient characteristics with Pearson correlation coefficients. Additionally, we run the same test between seedlings found in 2011 within the same parcels with soil property parameters, as a means to link them with the sexual reproductive event of 2010.

Results

Sexual reproduction

Flowering of *L. lucidum* in the studied area takes place synchronously across both landscape conditions from mid December until mid January. Flowering trees produce vast numbers of flowers that are assiduously visited by many insects from different taxonomic orders (Diptera, Himenoptera, Coleoptera, and Lepidoptera; Personal observation). Fruits are fully matured in June offering fruit resources to many bird species throughout the winter and beginning of spring. The minimum stage class for sexual maturity, based on diameter at breast height (DBH), was held similar

in both reproductive seasons only in continuous forest (6.40–6.43 cm). However, the minimum DBH threshold for sexual maturity in trees growing in fragmented forest was 10.63 and 24.70 cm for 2010 and 2011, respectively. Thus, estimations of reproductive success at the population level were taken from different numbers of potentially mature individuals. Specifically, from an original sample of 366 and 372 potential mature trees (DBH ranging 6.40–68.3 cm) growing in continuous and fragmented forests, respectively, we reduced the potential mature individuals in fragmented conditions to 241 mature trees (i.e., $DBH > 10.63$ cm) in 2010 and 26 mature trees (i.e., $DBH > 24.70$ cm) in 2011. By individually tagging and following the same trees across the two flowering seasons, we were able to identify which trees changed reproductive patterns from one season to the other. From the total number of trees that produced fruits during the first season only 44 and 5 % of them consistently produced fruits in the following season, in continuous and fragmented forests, respectively. Alternatively, 20 % of the trees that produced no fruits in the first season yielded fruits the second year but only in continuous forest. In fragmented forest, all trees without fruits in the first year remained fruitless the following year.

The proportion of fruit-producing trees in continuous forest was overwhelmingly larger than in fragmented forest throughout the two reproductive seasons (Fig. 2). In both landscape conditions, however, there was a parallel strong decrease of fruit-producing trees from 2010 to 2011. The lower proportion of fruiting

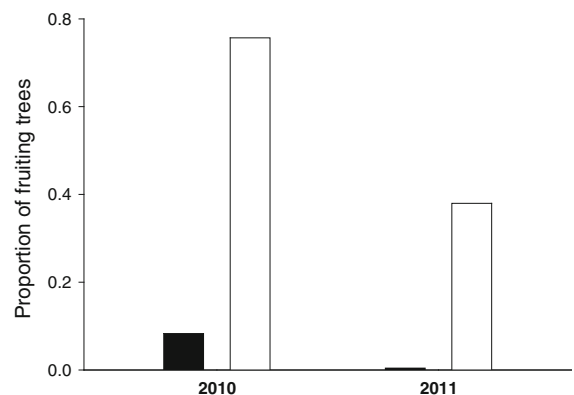


Fig. 2 Proportion of fruiting trees of *L. lucidum* across two consecutive reproductive years in two contrasting landscape conditions: continuous (white bars) and fragmented forests (black bars)

trees growing in fragmented forest was dramatically exacerbated in 2011, where only a single tree produced fruits (Fig. 2). The ANCOVA on the binary response of fruiting vs non-fruiting trees statistically confirms the significant differences of higher number of fruiting trees in continuous forest for 2010 ($Z = 5.96$; $p < 0.0001$) and 2011 ($Z = 3.44$; $p < 0.001$), with no significant influence of DBH on this response ($Z < 0.95$; $p > 0.188$), and no significant interaction of DBH and landscape conditions ($Z < 0.39$; $p > 0.690$) in both years (i.e., equivalent slopes between conditions). These results indicate that in absolute terms at the landscape level, the larger number of fruiting trees in continuous forest implies a significantly overall greater propagule pressure coming from continuous forest in both years.

We then compared seed production per tree between conditions through an ANCOVA for count data with DBH as the covariate. We were able to do this for the first reproductive year, as only a single tree yielded fruits in fragmented condition in the second year. Interestingly, when comparing only fruiting trees, seed production per tree was not significantly different between landscape conditions ($Z = 1.01$; $p = 0.311$), while DBH significantly explained seed production variation among trees ($Z = 4.94$; $p < 0.0001$); i.e., larger trees produced more seeds (Fig. 3). The interaction term between landscape condition and DBH remained non-significant

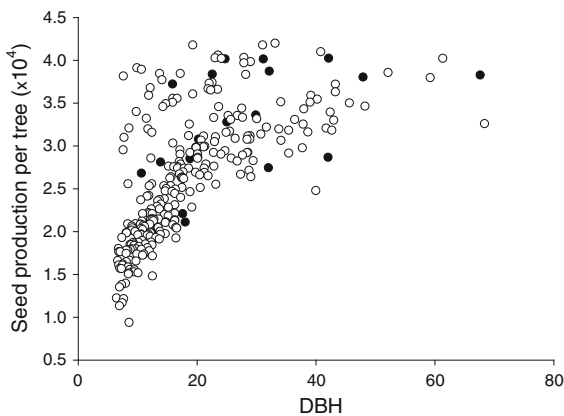


Fig. 3 Relationship between DBH and seed production per individual tree of *L. lucidum* growing in two contrasting landscape conditions: continuous (white circles) and fragmented forests (black circles). The relationship is positive and statistically significant ($r = 0.67$; $p < 0.0001$). On average, seed production per tree was similar between landscape conditions

($Z = 0.912$; $p = 0.362$), indicating that slopes of DBH and seed production are homogeneous across landscape conditions. Because data were strongly unbalanced, we further repeated the ANCOVA taking a random sample of fruiting trees from continuous forest that matched the total number of fruiting trees in fragmented condition. This balanced comparison produced the same outcome: the fewer fruit-producing trees in fragmented condition produced on average similar quantities of seeds as trees in continuous forest ($Z = 0.81$; $p = 0.549$), with DBH explaining most of seed production variation among trees ($Z = 2.29$; $p < 0.01$).

Seed germination, seedling mortality in greenhouse and seedling number in the field

Seeds without the exocarp started germinating 10–14 days after sowing and continued germinating throughout 87 days. By this day, we were able to visually determine that remaining seeds were dead (moldy and rotten) and thus unable to germinate. The percentage of seed germination was slightly higher in seeds from trees growing in continuous forest but this difference was not statistically significant (Table 1). Germination speed was similar between landscape conditions (Table 1). Seedling mortality was also comparable, nearly half of the planted seedlings survived for 120 days in controlled conditions in the greenhouse (Table 1). Seedling emergence in the field was observed after the rainy season began

Table 1 Seed germination, germination speed, seedling mortality, and seedling number per plot of *L. lucidum* in two contrasting landscape conditions

	Forest condition		Statistical tests
	Continuous	Fragmented	
Seed germination (%)	82.0 ± 5.94	70.5 ± 5.80	$Z = 1.86$; $p = 0.063$
Germination speed	0.43 ± 0.04	0.43 ± 0.06	$t = 0.007$; $p = 0.994$
Seedling mortality (%) in the greenhouse	46.0 ± 6.00	59.0 ± 4.20	$Z = 0.789$; $p = 0.430$
Seedling number per plot in the field	36.6 ± 5.96	16.1 ± 6.18	$Z = 3.37$; $p = 0.0006$

Values are the mean ± standard error

(September–November). Thus, seedlings found in November 2011 belong to the previous reproductive event (December 2010). We found a significantly larger number of seedlings in plots located in continuous forest (Table 1). With similar seed germination potential and seedling mortality probabilities between conditions, the larger seedling recruitment found in continuous forest is likely the result of massive seed production in such forest condition.

Soil properties

We found significant differences in soil water, organic carbon, organic matter and total nitrogen content

Table 2 Soil depth and soil nutrient parameters of permanent plots of *L. lucidum* in two contrasting forest conditions

	Forest condition		Statistical tests
	Continuous	Fragmented	
Depth (cm)	23.05 ± 1.37	25.33 ± 1.79	$t = 0.782$; $p = 0.451$
Water content (%)	23.62 ± 1.66	18.62 ± 0.52	$W = 9$; $p = 0.012$
Organic matter (%)	7.97 ± 1.09	5.51 ± 0.11	$W = 8$; $p = 0.042$
Organic carbon (%)	4.64 ± 0.64	3.20 ± 0.06	$W = 8$; $p = 0.041$
Total nitrogen (%)	0.37 ± 0.04	0.26 ± 0.03	$W = 6.5$; $p = 0.015$
C:N ratio	12.26 ± 0.34	12.36 ± 0.15	$t = -0.272$; $p = 0.79$
Nitrates (ppm)	22.57 ± 2.07	18.68 ± 2.14	$t = 1.302$; $p = 0.217$
Phosphorous (ppm)	18.5 ± 9.61	9.02 ± 1.97	$t = 0.965$; $p = 0.367$
pH	6.93 ± 0.11	6.92 ± 0.10	$t = 0.082$; $p = 0.947$
Electric conductivity (dS/m)	0.90 ± 0.08	0.81 ± 0.09	$t = 0.679$; $p = 0.510$
Ca ²⁺	30.81 ± 3.61	25.80 ± 2.98	$t = 1.066$; $p = 0.305$
Mg ²⁺	0.50 ± 0.0	0.75 ± 0.16	$t = -1.528$; $p = 0.154$
Na ⁺	0.25 ± 0.01	0.30 ± 0.0	$t = -1.154$; $p = 0.155$
K ⁺	1.06 ± 0.14	1.30 ± 0.06	$t = -1.584$; $p = 0.140$

Values are the mean ± standard error. To prevent increased chance of type I error, p values were adjusted following Holm method

between landscape conditions: plots in continuous forest had consistently larger mean values of these parameters than plots in fragmented forest (Table 2). Also Nitrates and Phosphorous had larger values in continuous forest but they were not statistically different (Table 2). The rest of the other soil properties, including soil depth, showed comparable values between landscape conditions. We then run correlations to determine whether there was a link between these four soil parameters that were significantly affected by habitat fragmentation and the reproductive success of *L. lucidum*. Because water content, organic carbon, organic matter and total nitrogen are highly correlated among them (here with Pearson's r ranging 0.79–0.98) we avoided running individual correlation analyses. Instead, we used a new variable that integrates these four soil quality variables, which were equally expressed in percentage. For obtaining such integrated soil quality variable we run a principal component analysis among these four variables across the 16 plots and used the coefficients generated in the first axis (i.e., PC1), which explained 93 % of the variation among them (Jolliffe 2002). We then used this integrated soil quality variable (log-transformed) to run correlations with seed production (log-transformed) and with seedling number in 2011 (Fig. 4). Both correlations were overall positive and statistically significant (Fig. 4a, b), indicating that increased soil water, organic carbon and matter, and total nitrogen is related with increased seed production per plot and increased seedling number per plot. It should be noticed that because seed production in fragmented conditions during 2011 was almost nil, such relation is mostly evidenced and validated by parcels within continuous forest condition (Fig. 4b).

Discussion

In this work we observed a strong decrease in reproductive success at the population level in fragmented habitats across two consecutive years. Simultaneously, at the same plot level, we found significant higher water content, total nitrogen, organic matter and carbon in soils of continuous forests, and these soil nutrient parameters were positively correlated with seed production and seedling number per plot within the same year. At the individual tree level, however, seed production was similar between landscape

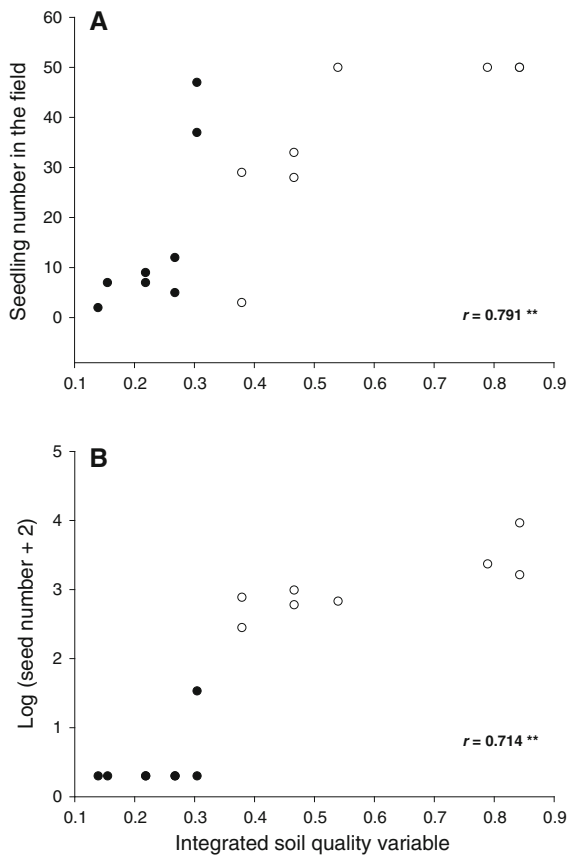


Fig. 4 Relationships of the average seedling number per plot (a) and the average seed number (Log transformed) per plot (b) in continuous (white circles) and fragmented (black circles) conditions with the integrated soil quality variable (log transformed). Such integrated variable was obtained from coefficients generated from a principal component analysis (see text) among soil water content, organic carbon, organic matter, and total nitrogen. Pearson correlation coefficients are given in each graph. ** denotes $p < 0.001$. Each data point is the average value of seedlings, seed production, and soil quality parameters per plot of *L. lucidum* ($N = 16$) measured in November 2011; in certain cases identical values overlap data points

conditions, implying no changes in pollination efficiency. These results suggest that reproductive failure of the invasive glossy privet populations in fragmented forests would not be the result of Allee effects imposed by higher isolation and less flowering conspecific but the result of less favorable abiotic soil conditions in highly fragmented forest.

Sexual seed production is an essential process for the long-term sustainability of flowering plant populations as it provides an independent dispersal phase, an opportunity for increasing genetic diversity, and the

potential to adapt to new environments (Wilcock and Neiland 2002). In non-native invasive plant populations in particular, their successful establishment and spread is strongly influenced by the production, dispersal, and genetic constitution of propagules (Barrett et al. 2008; Jesse et al. 2010). Specifically, distinctive reproductive traits that allow for reproductive assurance via uniparental reproduction (self-compatible hermaphroditism/monoecious and/or asexual reproduction by clonal propagation or apomixis) are common features in many invasive plant species as recently observed across very different phylogenetic groups (Rambuda and Johnson 2004; Harmon-Threatt et al. 2009; Hao et al. 2011; Petanidou et al. 2012). Such traits not only facilitate establishment after dispersal when invasive founder groups are small, which may expose them to “Allee effects” in newly introduced populations (Drake and Lodge 2006; Barrett et al. 2008; Hao et al. 2011), but are also advantageous reproductive traits for any given plant species surviving in isolated and fragmented habitat remnants (i.e., long-term Allee effects; Aguilar et al. 2006; Leimu et al. 2006; Eckert et al. 2009). Thus, any plant species (invasive or not) with such reproductive attributes will have an advantage to successfully thrive in highly fragmented anthropogenic habitats (i.e., Baker’s rule; Baker 1955). Such expectation has been generalized for native plant species (Aguilar et al. 2006; Aguilar et al. 2008) but not for invasive plant species simply because there is not enough accumulated evidence yet. Only a few studies have evaluated Allee effects on reproduction of invasive plants in the wild (e.g., Cappuccino 2004; van Kleunen and Johnson 2005; Firestone and Jasieniuk 2012) but none in explicit anthropogenic fragmented habitats. Habitat fragmentation implies a more complex phenomenon than simply reduced population sizes or density. While population size and/or density may or not decrease in fragmented habitats, edge effects, isolation from other populations, and changes in biotic and abiotic interactions are often pervasive (Aguilar et al. 2006; Lindenmayer and Fischer 2006). Hence, it is still uncertain to what extent forest fragmentation affects the reproductive performance of invasive plant populations, either with or without advantageous reproductive assurance mechanisms.

Interestingly, we observed here that glossy privet populations growing in fragmented conditions showed a strong decrease in reproductive success at the

population level because a significantly larger number of trees flowered and set fruits in continuous forests, thus providing an overwhelming larger source of propagules compared to populations in fragmented habitats. Nevertheless, when analyzing the reproductive output at the individual level the response pattern is changed and no differences are found between conditions. Thus, the significantly fewer trees that flowered in fragmented conditions produced similar quantities of seeds per tree as those in continuous forest, and most variation in seed production per tree was equally explained by DBH in both landscape conditions. Such results, and the fact that *L. lucidum* is able to self-pollinate via autogamous crosses (Montaldo 1993, personal observation), imply that reproductive failure in fragmented populations of glossy privet is very unlikely to be the consequence of decreased pollination service (i.e., pollen/pollinator limitation), as has been observed for native plant populations (Aguilar et al. 2006) and for the few self-incompatible invasive plants tested for Allee effects (Elam et al. 2007; Firestone and Jasieniuk 2012). Our results agree with the expectation that advantageous reproductive traits (here self-compatibility and pollination-generalist) do ensure sexual reproduction in fragmented conditions because all trees that attained flowering yielded massive fruiting. Moreover, due to the same reasons, any changes in mating patterns (i.e., pollination quality) at the individual level did not result in differences in early progeny vigor, measured as seed germinating capability and speed as well as seedling mortality in the greenhouse, from maternal trees growing in both landscape conditions (Aguilar et al. 2008; Angeloni et al. 2011).

We also found here that soil water content, organic carbon, organic matter, and total nitrogen were on average significantly lower in parcels of *L. lucidum* growing in fragmented conditions. These four soil nutrient parameters were positively correlated among them, evidencing their inherent interdependence (e.g. Karlen et al. 2008). For example, organic matter and organic carbon are intimately related, and both are well known to influence water dynamics in soils (Hudson 1994; Karlen et al. 2008). Thus, at equal precipitation regime in both landscape conditions, the less soil organic matter and carbon content observed in forest fragments may result in reduced soil water retention (e.g., Hudson 1994; Karlen et al. 2008; Matezans et al. 2009). Soil organic matter also serves

as an important source of plant nutrients released through mineralization (Weil and Magdoff 2004). Although we only observed significant differences in total nitrogen content between fragments and continuous forest, total nitrogen was closely related with nitrates content ($r = 0.78$; $p < 0.05$). As we initially hypothesized, changes observed in these soil nutrient parameters can be triggered by the loss and fragmentation of habitats through changes in the physical environment. Forest remnants increase edge-to-area ratios and often suffer from increased solar radiation and exposure to winds coming from the surrounding agricultural matrix (Saunders et al. 1991; Lindenmayer and Fischer 2006). Also, the hydrological system can be much less buffered by the surrounding matrix, increasing run-off events. All these changes can alter nutrient cycling processes and moisture retention, and decrease soil microorganism activity (Saunders et al. 1991; Lindenmayer and Fischer 2006), as observed elsewhere (Kolb 2005; Winter et al. 2008; Matezans et al. 2009; Tsaliki and Diekmann 2010). While the potential causality of fragmented conditions per se on soil nutrient parameters represents a valid explanation, we cannot preclude the influence of other factors. Landscape fragmentation is frequently a non-random process and, at least within the studied area, intimately related to the agricultural potential of the land. Here, the few continuous forests left are located nearby the piedmont, thus there may be other intrinsic reasons guiding the abiotic microenvironmental differences we observed. Independently of the concomitant events of habitat fragmentation and reduced soil properties, our results suggest that significant impoverishment in soil nutrients within parcels of *L. lucidum* located in highly fragmented forests may be closely linked to the marked decrease in sexual reproductive output at the population level also observed in the same parcels. Such an assertion can be sustained from the significant positive correlations observed between both seed production and seedling number with the integrated soil nutrient variable that included the four correlated soil nutrient variables.

Correlated responses between reproductive success and certain soil nutrient parameters have been detected in other fragmented and human-disturbed contexts elsewhere for native (Vergeer et al. 2003; Winter et al. 2008; Matezans et al. 2009; Tsaliki and Diekmann 2010) and invasive plant species (Leishman and Thomson 2005; Quiroz et al. 2011; Jauni and

Hyvönen 2012). It has been determined in several species that decreased soil water content (e.g., Breen and Richards 2008; Lambretch et al. 2011; von Euler et al. 2012) and/or soil chemical properties such as organic carbon/matter and nitrogen can negatively affect sexual plant reproduction (e.g., Wagner et al. 2001; de Vere et al. 2009; Matezans et al. 2009) and seedling survival (e.g., Walters and Reich 2000; Breen and Richards 2008). Especially in perennial water-demanding species, such as glossy privet, soil water content may be of key importance. For example, floral water balance is essential for flower opening and expansion, pollen viability, and nectar production (Galen 2005). High water use of flowers might limit future flowering and reproductive success during dry years (Lambretch et al. 2011; von Euler et al. 2012). In fact, susceptibility to water stress in glossy privet has been previously observed within its native distribution range, where adult individuals rapidly lose hydraulic conductivity after experimental drought treatments (Li et al. 2006). Nutrient uptake is also related to water availability; high soil water content reduces tortuosity and allows efficient transport of nutrients whereas reduced soil water content negatively affects nutrient uptake (Blank et al. 2002). In agreement with these arguments and our findings, glossy privet populations in Australia subjected to experimental low levels of soil water content significantly decreased seedling abundance (Panetta 2000), and also abundant recruitment have been observed in irrigated areas of Sacramento Valley in California (Aslan et al. 2012), both regions where it is also an aggressive invasive tree. Taken all together, we suggest that glossy privet's high demand of water and nutrients for successful flowering and fruiting may represent the "Achilles heel" of invasive populations growing in highly fragmented forests, where such abiotic parameters can be significantly reduced. As a potential mechanism, we may argue that glossy privet needs a minimum threshold of water and soil nutrient content to trigger flowering, below which only the largest trees with deeper roots, or the ones located in better microhabitat conditions within the plot, will be the only ones to successfully flower and set fruits. However, we cannot be fully conclusive in our assertions because our data presents only indirect evidence of these relationships. While our results do

suggest that fragmented populations are not pollen-limited, we cannot exclude the role of other external factors shaping the strong decrease in reproductive success observed in fragmented parcels. For example, different grazing or fire history between landscape conditions may have effects on today's adult reproductive success. No fire has been recorded in the last decades within the study sites, but cattle presence is almost ubiquitous across continuous and fragmented forests in the area. Although sites were comparable in this regard, we did observe that trees growing in fragmented plots had significantly larger numbers of branches or regrowth from the base of the trunk, potentially indicating a stronger grazing history in the past. Such historical grazing pattern could be potentially aggravating the reproductive limitations observed in the adult glossy privets growing in fragmented parcels.

In conclusion, our results show that while changes in landscape patterns imposed by habitat loss and fragmentation resulting from the expansion of urban and agricultural boundaries may favor the establishment of invasive plants (e.g., With 2002, Gavier-Pizarro et al. 2012; González-Moreno et al. 2012), they do not necessarily promote their potential to act as continued sources of propagules for spreading to new invasive frontiers. Moreover, decreased reproduction of glossy privet in fragmented forests would not be the result of reduced pollination, but the result of less favorable abiotic soil conditions. No study has yet reported such an abiotic effect on maternal fitness of an invasive tree. Any climatic shifts, affecting rainfall regimes or soil nutrient cycling processes through increased atmospheric CO₂ (e.g., Six et al. 2001; Kelly and Goulden 2008), may have stronger effects in water and nutrient demanding invasive plants like glossy privet. In current dynamic and changing abiotic scenarios imposed by human activities, established invasive plant populations might be as likely as or even more susceptible to these changes than native ones. Depending on the direction of such changes, the invasibility susceptibility of local communities and ecosystems may also change, acting synergistically or detrimentally on the invasiveness capacity of non-native invasive plants. Thus, climatic changes acting in concert with land use changes may either ameliorate invasion spread, as we observed for *L. lucidum* in highly anthropogenic fragmented habitats, or boost invasion spread to novel changing

environments resulting in new distribution spread patterns. While much research has been advocated to predicting the impacts of climate change on the distribution of native plant species (e.g., Kelly and Goulden 2008) it would be important also to make the same effort with non-native invasive plants. The ability to detect key limiting factors for the successful reproduction and spread of aggressive plant invaders should help generating applied knowledge and appropriate management tools for their control and eventual eradication.

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