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Disentangling the invasion process of subtropical native forests of Uruguay by the exotic tree *Ligustrum lucidum*: establishment and dominance determinants

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Abstract

Background What factors, processes and mechanisms regulate invasive processes and their effects? This is one of the main questions addressed by the ecology of biological invasions. *Ligustrum lucidum*, a tree species native to East Asia, became an aggressive invader of subtropical and temperate forests around the world. We analyzed here the *L. lucidum* invasion in Uruguayan forests to determine the factors controlling two stages of the invasive process, the establishment, and the dominance. Establishment was assessed by the occurrence, measured in 1525, 1 × 1 km-cells, and dominance by remotely measuring the *L. lucidum* coverage at the forest canopy in 5554, 1 × 1 km-cells. The occurrence and dominance were modeled using Generalized Linear Models in function of independent environmental and geographic variables.

Results *Ligustrum lucidum* has become established in 13.4% of the Uruguayan forests and has dominated the forest canopy in 1.2%. Our models explained 45% and 35% of the occurrence and dominance spatial variance respectively and detected in both cases strong diffusion patterns from the S-SW region to rest of Uruguay. Occurrence increased mainly in function of urban areas, and with the proximity to towns, probably because *L. lucidum* trees planted in gardens are seed sources, and near railways and highways, that could function as biological corridors. Occurrence also increased in loamy soils and near rivers, suggesting moisture conditions are favorable for establishment. Dominance increased with reduced forest area, in high productive soils and at higher altitudes. Moreover, dominance increased near urban areas, roads, and railways, as well as in highly afforested landscapes, and in loamy and low-rockiness soils.

Conclusions The invasion of Uruguayan forests by *L. lucidum* is in the spread and impact stages, currently in expansion from the invasion focus on the S-SW region, where the oldest urbanizations are settled, towards the rest of the country. The geographic proximity to the invasion focus is currently the main predictor of both *L. lucidum* establishment and dominance. Additionally, whereas establishment is mainly facilitated by human infrastructures improving propagule pressure and dispersion, dominance is enhanced in small or fragmented forest patches, in rich-nutrient soils, and at higher altitudes, suggesting ecosystem resistance is also operating.

Keywords Glossy privet, Tree invasion, Occurrence model, Dominance model

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Background

The invasions of exotic species constitute a serious environmental problem at a global level, capable of generating strong ecological, economic, and social impacts (e.g., Vitousek et al. 1996; MEA 2005; IPBES 2019; Pyšek et al. 2020b). The relevance of this problem has encouraged the development of an ecology of invasions around a great central question, what factors, processes, and mechanisms regulate invasive processes and their effects? (Davis 2009).

For a species to become an invasive alien, it must be transported from its region of origin, introduced to a new region, and there, be able to establish itself (becoming alien, or exotic), and ultimately become an invader if it is able to spread and dominate the receiving communities, generating impacts (Davis 2009). In addition to this traditional view, other perspectives have been proposed, such as the neutral framework of Colautti and MacIsaac (2004), in which the impacts of nonindigenous species (NIS) are not used to define invasion processes. They argued several subjective problems in using impact criteria and recommended using only biogeographic criteria to evaluate invasion processes, such as distribution range (localized to widespread) and abundance level (rare to dominant). According with such scheme, invasive populations are those that reach high abundance (dominant), either with localized (local) or widespread (regional) distribution.

The invasion success can be broadly defined as the successful establishment, spread, or proliferation of alien (or NIS) in novel regions, and basically depends on two opposite factors, propagule pressure that promotes invasion, and ecosystem resistance, that limits or reduces it. Propagule pressure is defined as the number of individuals (or any organism parts capable to become an individual, like plant seeds or animal eggs), introduced to a new location and is given by the number of introduction events and the number of individuals per event (Williamson 1996; Lockwood et al. 2009). Ecosystem resistance defines the ecosystem susceptibility to a given alien invader, i.e., to its establishment and proliferation, what is known as invasibility (Williamson 1996; Lonsdale 1999; Colautti et al. 2006). The ability of species to establish in, spread to, or become abundant in novel communities, what is known as invasiveness (Williamson 1996; Colautti et al. 2006), is another key factor in the invasion process.

To achieve a comprehensive explanation of invasive processes, we must understand the factors and mechanisms operating during the different phases of the process, from colonization and establishment to dispersal and community dominance. Multiple hypotheses have been proposed to explain plant invasion patterns, but accordingly with the PAB framework proposed by

Catford et al. (2008), they could be structured around four main effects: propagule pressure (P), abiotic characteristics of the new site (A) and biotic characteristics (B) of both the new site and of the exotic organisms, with the additional influence of humans (H) on P, A and B. Recently, Pyšek et al. (2020a) proposed the macroecological framework for invasive aliens (MAFIA), that explains the invasion phenomenon using three interacting classes of factors: alien species traits (Species), location characteristics (Location), and factors related to introduction events (Event), and explicitly maps these interactions onto the invasion sequence from transport to naturalization to invasion. Event related factors include propagule pressure and other human factors (e.g., pathways, and date of introduction that determines the residence time), but also, for example, the season during which the species is introduced (summer, winter).

These theoretical frameworks, PAB, and MAFIA, although using different logics, somehow integrate all types of factors that can account for an invasive process, both with very relevant contributions. For its part, the PAB framework allows discriminating anthropic effects through their actions on propagule pressure (P), abiotic (A) or biotic (B) characteristics of the system. The MAFIA framework, in the factors related to the event, incorporates several factors mediated by the anthropic action (e.g., propagule pressure), with the novelty of emphasizing the introduction time, a factor that defines the residence time of the exotic species, of great relevance to understand invasive processes.

In this paper we study the invasion of the native forest of Uruguay by the exotic tree *Ligustrum lucidum* (W. T. Aiton, Oleaceae) –glossy privet–, focusing on the factors that control two key stages of the process, the establishment, and the dominance. *Ligustrum lucidum* is native to China and became an aggressive invader of temperate and subtropical forests after its introduction since the eighteenth century for ornamental purposes, in numerous countries around the world (Fernandez et al. 2020). Nowadays is present on all continents except Antarctica (Fernandez et al. 2020), has expanded its invasion range towards wet tropical areas (Dreyer et al. 2019), and has a potential distribution around the globe of 14,201,846 km², an area slightly smaller than the size of South America (Montti et al. 2021). This tree species presents life history traits that enhance the invasion success (Zamora et al. 2014), as the large production of seeds (Aguirre-Acosta et al. 2014), having attractive fruits for birds that enhance seed dispersion (Aragón and Groom 2003), and rapid grow, both in the shade and in direct sun (Montaldo 2000). In advanced stages of invasion, this evergreen species forms almost monospecific patches, covering the canopy and generating low light conditions

in the understory hampering the establishment and growth of most species of trees, shrubs, lianas, and epiphytes, ultimately resulting in the privet dominance and the exclusion of several native plant species (Grau and Aragón 2000; Hoyos et al. 2010; Ceballos et al. 2015; Malizia et al. 2017; Franco et al. 2018). Furthermore, because privet dominate primary production and change the vegetation structure in highly invaded forests, the invasion could also affect animal biodiversity via altering the habitat quality and food supply for some animal species, as was observed in soil invertebrates and birds (i.e., alteration in species abundance and composition), although the effects were highly variable (Fernández et al. 2020). The invasion could also alter some ecosystem services, for example, altering water cycle and thus affecting water supply, as was documented in the Yungas region, Argentina (Whitworth-Hulse et al. 2023).

According to global climatic models, almost all Uruguayan territory is suitable for *L. lucidum* (Montti et al. 2021). However, the National Forest Inventory (2009–2016) detected the presence of privet only in 12% of the forest plots ($n=1467$) surveyed throughout Uruguay (Brazeiro et al. 2021), putting in evidence an important discrepancy between the potential, and the actual coverage of *L. lucidum* in Uruguayan forests. We propose two non-exclusive hypotheses to explain such discrepancy: (1) The invasion process of Uruguayan forests is in the initial stage, far from the equilibrium yet, because the time since introduction has not been largely enough. *Ligustrum lucidum* has been observed in Uruguay since the end of the nineteenth century, when was introduced as an ornamental species (Nebel and Porcile 2006), but invasion spread in trees is generally low (<1 km per year, Davis 2009); and (2) There are factors operating at the landscape and local levels that significantly restrict the invasion process, reducing propagule dispersal and promoting ecosystem resistance. Conversely, we expect *L. lucidum* invasion to be successful mainly where anthropic activities and infrastructures promote propagules pressure and dispersion and reduce ecosystem resistance. Thus, our aim is to determine the main anthropic and environmental drivers of propagule pressure (P) and forest invasibility (B) that control the establishment and subsequent dominance of *L. lucidum* in Uruguayan forests.

Methods

Study area

The study area covered the entire native forested surface of Uruguay (835,349 ha; 4.7% of the territory) (REDD+Uruguay 2018). Despite the low coverage, forests are distributed throughout the entire country and covering the complete climatic range, from

the south with the lower temperature (16.6 °C) and precipitation (1000 mm yr⁻¹), to the north and northeast with the higher temperature (19.8 °C) and precipitation (1300 mm yr⁻¹) respectively. The climate is humid subtropical (Cfa, sensu Köppen-Geiger), with a strongly seasonal temperature, while rainfall is evenly distributed during the year, but very variable between years (Instituto Uruguayo de Meteorología 2023). Uruguayan forests are subtropical, seasonal, broad-leaved, and semideciduous (Brazeiro et al. 2020). Several forests ecosystem types have been identified depending on physiognomy and site conditions, being the riparian forests and savannas (wooded and palm groves savannas) of lowlands, and the hillside forests, the principal ones (Brazeiro et al. 2020).

Assessing invasion processes: privet establishment and dominance

We analyzed two invasion stages of *L. lucidum* in Uruguayan forests, the establishment, and the dominance. In the context of biological invasions, a successful establishment occur when the exotic organism persists long enough in the new environment to reproduce, what means the organism was able to: (1) tolerate the abiotic conditions; (2) find the resources necessary to its maintenance, growth, and reproduction; (3) find a mate to reproduce (for out-crossing species); and (4) avoid the pre-reproductive mortality (Davis 2009). Therefore, we decided to assess the establishment through the occurrence of adult individuals. The establishment was evaluated by modeling the probability of privet occurrence in forests (i.e., binary response variable), with a resolution of 1 km², using presence/absence data in 1525 locations (1×1 km cells) surveyed in the field between 2009 and 2020. The occurrence data were obtained from two sources, the National Forest Inventory (DGF 2019) ($n=1491$; plots of 200 m²) and field samplings carried out by our research group ($n=64$, plots of 400–1000 m²). The 1555 forest plots were mapped over a 1×1 km-grid covering the Uruguayan territory, to obtain a total of 1525, 1×1 km-cells with presence/absence data, because some plots were in the same cell. We marked presences (1) in those cells where adults and/or saplings privets were registered in any plot, absence (0) in those cells where no adults nor saplings privet were detected within the surveyed plots, and the cells without sampling information were not used to adjust the occurrence model.

To assess the dominance stage, we used as the response variable the privet coverage in the forest canopy. This response variable was expressed as proportion of the forest cover, assuming values in the standard unit interval (0, 1), and was measured in 5,554 1×1 km-cells, covering the complete native forests distribution of Uruguay. The privet coverage in the forest canopy was estimated

through a supervised classification of satellite images using the Random Forest algorithm. This classification was based on the combination of multispectral and radar data (Sentinel-1 and Sentinel-2 images acquired in spring–summer of 2020–2021), and the calculation of several vegetation indices from their bands. The forest stands that were highly invaded by *L. lucidum* (i.e., coverage >60%) have a denser and more persistent canopy than non-invaded native forests, allowing their discrimination through remote sensing (Olivera and Riaño 2022). The analyses were implemented on the Google Earth Engine (GEE) platform. The overall accuracy of the privet coverage map was very good (87.5%), which was estimated by comparing the map predictions with a sample of field photos taken with a drone, during the privet flowering season, to facilitate the detection. The remote sensing detection of forest stands invaded by *L. lucidum* was done in the frame of a master thesis (Olivera 2023), that will be published in detail in another article (in preparation).

Modeling approach

To model the effects of environmental variables on *L. lucidum* establishment and dominance in Uruguayan forests, we first created a set of 42 potential predictors (Additional file 1: Table S1), including environmental (climatic, edaphic, habitat, hydrographic, topographic), anthropogenic (e.g., distance to towns, roads, cattle load), and spatial variables. These variables were previously digitalized over the same grid of 1×1 km cells in QGIS software. The existence of collinearity between numerical covariates was explored by assessing pairwise correlations between variables and variance inflation factor (VIF). For this, the variables were separated among main groups (i.e., climatic, edaphic, hydrographic, etc.) and then they were analyzed together. Finally, a group of 28 environmental variables without high correlations among them ($R^2 < 0.70$) and $VIF < 2$, was retained (Dormann et al. 2013) (Table 1). The correlations among the selected variables are shown in Additional file 1: Tables S2 and S3. Numerical variables were centered and standardized before models fitting.

Analyzing spatial data in ecological studies is very challenging, due to the problem of the spatial dependence of the response variables (this point will be addressed later), and due to the problem of discriminating between environmental (usually spatially autocorrelated) and pure spatial effects (e.g., historical effects or spatial ecological processes) (Dormann et al. 2007). Spatial processes are key to understanding invasion processes, and especially during the expansion

phase. To address pure spatial effects, we used a polynomial trend-surface analysis (TSA), integrating latitude (X), longitude (Y), and a quadratic and cube effect of X and Y and interactions between them, to predict the respond variables (Legendre 1993). Using stepwise logistic regressions, the non-significant spatial terms were eliminated, to generate spatial linear combinations that were included in modeling procedure as another potential predictor (TSA in Table 1) (Details of TSA results in Additional file 1: Table S4).

We used Generalized Linear Models (GLM) to fit logistic regressions with binomial distributions and logit link functions (i.e., $\ln(p/1-p)$), to assess the effects of the filtered predictors on the *L. lucidum* establishment. Stepwise selection method based on the Akaike Information Criterion (AIC) was used to select the best models, incorporating the predictors in both directions. Those models with the lowest AIC were selected. The R function StepAIC from the {MASS} package (Venables and Ripley 2002) was used; residuals were evaluated using QQ plot, through {DHARMA} package (Hartig 2019). To assess the dominance of *L. lucidum* in forest canopy, a Beta Regression model (Cribari-Neto and Zeileis 2010) was fitted using the {betareg} package. The model was simplified using the 'StepBeta' function of the {StepBeta} package, according to AIC.

After verifying with semivariograms, correlograms, and Moran Index (Legendre 1993), the existence of strong spatial autocorrelation in the residuals of both final models, we incorporate autocovariates (autocovi) into the models (Fletcher and Fortin 2018). Autocorrelated residuals violate the assumption of data independence, increasing Type I errors in the models and altering the regression coefficients of the models (Bini et al. 2009). We constructed the autocovariates from the residuals of the final models, to avoid masking the effects of other environmental predictors, then, they were incorporated into the final GLM models as additional predictors (Cruse et al. 2012).

To evaluate the performance of the occurrence final model, a stratified random partition of the data was performed, 50 times iteratively, in (I) 2/3 of the data for the training sample; and (II) 1/3 of the data for the sample test. In each iteration, the model was adjusted with sample I and predictions were generated on sample II, obtaining the accuracy (i.e., overall correct classification rate), sensitivity (i.e., rate of true presence correctly classified), area under the curve (AUC) and pseudo- R^2 (pseudo- $R^2 = (\text{null deviation} - \text{deviation residual}) / \text{null deviation}$). The performance of the dominance model was evaluated using pseudo- R^2 .

Table 1 Description of the variables used in the statistical modeling of two stages of the invasion process of *Ligustrum lucidum* in native forests of Uruguay, establishment, and dominance

Code	Variable description	Hypothesis
<i>Response variables</i>		
Establishment	Y1 Occurrence of <i>L. lucidum</i> : presence (1) or absence (0). <i>N</i> = 1525	
Domination	Y2 Domination degree of <i>L. lucidum</i> in canopy coverage (0–1). <i>N</i> = 5554	
<i>Anthropic factors</i>		
AfforArea	Area occupied by afforestation (hectares)	A, P
AreaTown	Area occupied by towns (km ²)	P
DistTown	Distance to the nearest town (km)	P
Population	Estimated population by 2010 (N° of inhabitants)	P
Livestock	Mean cattle and sheep load during 2000–2017 (livestock units/km ²)	B _C
Fire	Accumulated fires in the period 2000–2009 (#)	A
RailDens	Railway density (km of railways/km ²)	P
RailDist	Distance to the nearest railways (km)	P
RoadDens	Roads and routes density (km of roads and routes/km ²)	P
RoadDist	Distance to the nearest road or route (km)	P
<i>Climatic factors</i>		
BIO-6	Mean daily minimum air temperature of the coldest month (°C)	A
BIO-7	Annual range of air temperature (°C)	A
BIO-8	Mean daily mean air temperatures of the wettest quarter (°C)	A
BIO-14	Precipitation amounts of the driest month (kg/m ²)	A
BIO-16	Mean monthly precipitation amount of the wettest quarter (kg/m ²)	A
BIO-18	Mean monthly precipitation amount of the warmest quarter (kg/m ²)	A
<i>Edaphic factors</i>		
SoilProd	CONEAT index, proxy of soil productivity	A
SoilDepth	Soil depth category (cm): 1) Superficial (≤ 25); 2) Medium (> 25 to ≤ 80); 3) Deep (> 80)	A
SoilRock	Rockiness category (%): 1) Low-Null (≤ 2); 2) Medium (> 2 to ≤ 25); 3) High (> 25)	A
Ph	Soil pH category: 1) Very acid (≤ 5,4); 2) Neutral (> 5,4 to ≤ 8,4); 3) Alkaline (> 8,4)	A
Text	Soil texture category: 1) Sandy soils; 2) Loamy soils; 3) Clay soils	A
SoilDrain	Soil drainage—1: Null; 2: Slow; 3: Moderate; 4: Fast; 5: Excessive	A
<i>Hydrographic factors</i>		
RiverDens	River density (km/km ²)	A
RiverDist	Distance to the nearest river (km)	A
<i>Habitat factors</i>		
NatForest	Area occupied by native forests (hectares)	B _C
<i>Topographic factors</i>		
Altitude	Mean altitude (m)	A
Drain	Average runoff estimated from digital terrain model	A
Insola	Orientation category, as proxy of insolation time (IT): 1) S (very low IT); 2) SE-SW (low IT); 3) E-W (medium IT); 4) NE-NW (high IT); 5) N (very high IT)	A
<i>Spatial factors</i>		
TSA	Trend Surface Analysis vector (0–1)	P
Acov	Autocovariate	P

Variables are grouped by category (anthropic, climatic, edaphic, topographic, habitat, spatial), and the connection with the main hypothesis tested here are indicated. The hypotheses referred to the main invasion drivers involved, i.e., dispersal and propagule pressure (P), abiotic ecosystem resistance (A) and biotic ecosystem resistance (B_C). The information sources of the variables are shown in Additional file 1: Table S1



Fig. 1 Occurrence (presence and absence) of *Ligustrum lucidum* in 1,525 surveyed forest stands of Uruguay. The native forest cover of 2016 is shown. In the inserted boxes are presented the map of the main urban areas (cities and towns) of Uruguay (upper right) and the location of Uruguay in South America (down right)

Results

Ligustrum lucidum establishment in Uruguayan forests

There were 205 presences and 1,320 absences of privet in the 1,525 surveyed forest stands (Fig. 1), suggesting an incidence of 13.4% nationwide. The presences were mainly concentrated in the S and SW of the country (Fig. 1). The best GLM model adjusted explained the 44% of the occurrence variability of *L. lucidum* in Uruguayan forests, with a good predictive performance

(AUC = 0.74 ± 0.02 ; Accuracy = 90.03 ± 1.03 ; Sensitivity = 51.7 ± 4.9), and account for the spatial autocorrelation of the residuals (Additional file 1: Fig. S2). The modeling revealed the occurrence probability of *L. lucidum* was in part explained by a combination of spatial trend and environment factors linked with propagule pressure and ecosystem resistance (Table 2).

The spatial trend explained about 30% of the occurrence variance, through a polynomial that included significant effects of the latitude (negative effect, i.e.,

Table 2 Summary of the best GLM model adjusted to evaluate the probability of occurrence (establishment) of *L. lucidum* in Uruguayan forests

Model performance: $R^2 = 0.44$; AIC: 713.8
AUC = 0.74 ± 0.02 ; Accuracy = 90.03 ± 1.03 ; Sensitivity = 51.7 ± 4.9

Hypothesis	Variable	Coefficient
Ecosystem resistance	Intercept	-2.72**
	Precipitation of the driest month	-0.43*
	Minimum temperature of the coldest month	-0.35 ⁺
	Annual temperature range	-0.50*
	Average annual temperature of the most humid quarter	0.48**
	Soil texture (Medium)–Loamy soils	0.73*
Dispersion and Propagule pressure	Distance to the nearest river	-0.32 ⁺
	Distance to the nearest town	-0.34*
	Distance to railways	-0.41**
	Distance to the nearest road or route	-0.30 ⁺
	Area occupied by towns	0.27**
Spatial factors	Area occupied by afforestation	0.27**
	TSA (diffusion pattern from S-SW region)	0.60***
	Autocovariate	0.01***

The predictor variables are grouped by the main explanatory hypotheses analyzed

Statistical significance codes: *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$; ⁺ $p < 0.1$

Non-significant ($p > 0.1$) factors are not shown (NatForest, SoilDrain, Drain)

increasing trend from N to S), and marginal effects ($p < 0.1$) of the quadratic terms of latitude and longitude, and the latitude–longitude interaction (Additional file 1: Table S4). The trend surface analysis detected a significant diffusion pattern from the S-SW region to the rest of Uruguayan forests (Additional file 1: Fig. S1). The residuals of the occurrence model with spatial (TSA) and environmental explanatory variables were spatially autocorrelated, but the inclusion of the autocovariate solved the problem (Additional file 1: Fig. S2). Residuals also showed normal distribution and did not present any obvious evident trend (Additional file 1: Fig. S3).

The occurrence model detected the influence of several factors linked to dispersal and propagule pressures. It was detected positive effects of the surface covered by towns and afforestation, and negative effects of the distances to towns, railways, and roads (Table 2). In other words, privet occurrence probability was higher in cells with larger coverage of towns and afforestation, and in cells closer to towns, railways, and roads.

Likewise, the occurrence model detected effects of several factors possibly linked to ecosystem resistance. Privet occurrence probability was higher in loamy soil (medium soil textures) rather than in sandy or clay soils and increased with the proximity to rivers (Table 2, Additional file 1: Fig. S4). The precipitation of the driest month, the minimum temperature of the coldest month and the annual temperature range were negatively

correlated with privet occurrence probability, while the average annual temperature of the most humid quarter had a positive effect (Table 2, Additional file 1: Fig. S4).

***Ligustrum lucidum* dominance in Uruguayan forests**

The area of forests dominated by privet amounted to 9,942.3 ha (Fig. 2), which represents 1.2% of the total area of forests in Uruguay, an order of magnitude smaller than the estimated area of occupation of this species (13.4%). Privet-dominated forests were also concentrated in the S-SW region of Uruguay (Fig. 2).

The dominance model explained 35% of the spatial variability of privet coverage in forest canopy, in function of spatial and environmental factors (Table 3). The trend surface analysis also detected a diffusion pattern from the S-SW region to the rest of Uruguayan forests (Additional file 1: Fig. S1). This spatial trend was the best single predictor of privet dominance (Table 3). The spatial polynomial explained about 13% of the privet coverage variance and included the positive significant effect of longitude (i.e., increasing trend from E to W), and significant negative effects of the quadratic terms of both latitude and longitude (Additional file 1: Table S4). The inclusion of an autocovariate was needed to eliminate the spatial autocorrelation of the residuals (Additional file 1: Fig. S2) that also showed normal distribution and no significant trends (Additional file 1: Fig. S3).

Among non-spatial predictors, several minor effects of variables associated with ecosystem resistance were



Fig. 2 Map showing *Ligustrum lucidum* dominated forests in 2021, detected through remote sensing. The map also displays the native forest cover of 2016. In the inserted boxes are presented the map of the main urban areas (cities and towns) of Uruguay (upper right) and the location of Uruguay in South America (down right)

detected (Table 3). Privet dominance increased in loamy soils, in contrast to fine or coarse textured soils, and with increasing soil productivity and altitude, but decreased as native forest area increased in the cells, and with soil rockiness (Table 3, Additional file 1: Fig. S5). On the other hand, some variables associated with dispersion and propagule pressure were also included in the final model (Table 3). Privet dominance increased in cells closer to towns, roads, and railways,

and with larger afforested areas (Table 3, Additional file 1: Fig. S5).

Discussion

Low current incidence of *Ligustrum lucidum* in Uruguayan forests

We found 205 presences of *L. lucidum* in 1525 forest stands surveyed nationwide, suggesting a global incidence of 13.4%, slightly higher than previous estimates

Table 3 Summary of the best Beta regression model adjusted to evaluate the canopy coverage (dominance) of *L. lucidum* in Uruguayan forests

Model performance: $R^2 = 0.347$; AIC: - 12,139.02; Δ AIC: - 575.4

Hypothesis	Variable	Coefficient
Ecosystem resistance	Intercept	- 3.230***
	Soil productivity	0.104***
	Area occupied by native forest	- 0.108***
	Soil texture (Medium: Loamy soils)	0.093*
	Soil rockiness (High: > 25%)	- 0.203*
Dispersion and Propagule pressure	Altitude	0.048*
	Area occupied by afforestation	0.136*
	Distance to the nearest town	- 0.056***
	Distance to the nearest road or route	- 0.047***
Spatial factors	Distance to railways	- 0.044**
	TSA (increasing trend from NE to S-SW)	8.389***
	Autocovariate	< 0.001***

The predictor variables are grouped by the main explanatory hypotheses analyzed

Statistical significance codes: *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$; + $p < 0.1$

Non-significant ($p > 0.1$) factors are not shown (Population, BIO-7)

(Brazeiro et al. 2021). This result highlights the discrepancy between the prediction of a global climatic model stating almost all forests area of Uruguay is suitable for *L. lucidum* (Montti et al. 2021), and the low proportion of forest area occupied nowadays. The same discrepancy type was observed in northern Argentina by Montti et al. (2017), since they reported climate suitability to *L. lucidum* extended over almost 50% of the Yungas ecoregion (subtropical native forest), but the currently invaded percentage area on three studied “hotspots” of invasion was only of 0.22%.

Our first, non-exclusive hypothesis to explain such discrepancy, is that invasion process of Uruguayan forests by *L. lucidum* is far from the equilibrium with respect to climate limits yet, because the time since introduction, or residence time (sensu Wilson et al. 2007), has not been enough to allow the species to reach all potentially invadable sites. This hypothesis is clearly in the ground of factors associated with the introduction event, according to the MAFIA framework of Pyšek et al. (2020a). Invasion spread in trees is generally low (< 1 km per year) and usually presents a “lag phase” (Davis 2009), thus, much time would be needed for alien trees to colonize all suitable areas. *Ligustrum lucidum* has been present in Uruguay and Argentina for more than a century (Nebel and Porcile 2006; Montti et al. 2017), but its rate of expansion is less than 0.1 km per year according to the available data in Argentina: ~ 13 m/yr (Marco et al. 2011) and ~ 76 m/yr (Gavier-Pizarro et al. 2012). How much time the invasive plant has had to spread (i.e., its residence time) is a

fundamental issue to explain both the observed range size and the proportion of occupied suitable area (Wilson et al. 2007).

When the distribution of a given species is in equilibrium with the suitable habitats, the signal about the center of origin should be lost (Uden et al. 2015). Conversely, we detected spatial diffusion patterns in both privet establishment and dominance, strongly suggesting the invasion origin was in the S-SW region of Uruguay. This is another evidence supporting the hypothesis about the short residence time of *L. lucidum* in Uruguay.

The privet occurrence probability and its forest dominance were maximum at the proposed origin of invasion in the S-SW region and decreased towards the rest of the country. The S-SW region of Uruguay is where the oldest urbanizations of the country are settled, like Montevideo (1724), San José (1783) and Colonia (1680), and intensive productive activities (e.g., harbor, agriculture, livestock, transport). The occurrence of the exotic tree *Gleditsia triacanthos*, another import invasive species of Uruguayan forests, was also concentrated in the S-SW of the country (Romero et al. 2021), suggesting this region could be the invasion focus for different alien species.

The influence of settlement time on plant invasion has been previously documented. For example, McKinney (2002) found that the number of exotic plants in 77 protected areas in USA increase with the years of occupation of the area by European settlers and the human population size of adjacent counties. McKinney suggested that longer European settlement increases the establishment

of alien species, because longer habitation probably increases the probability of alien introduction, and the amount of disturbance that has occurred.

Determinants of *Ligustrum lucidum* occurrence

In addition to the effects of factors related with the introduction event, like the relative short residence time and the localization of the invasion origin at the S-SW region of Uruguay, we found evidence that local and landscape factors also contribute to restrict privet distribution to certain forests localities. These factors can be divided into anthropogenic, i.e., human actions and infrastructures altering propagule pressure or ecosystem resistance, and environmental factors, that set forest invasibility.

Among anthropogenic factors, urban areas play the major role. We found that *L. lucidum* occurrence probability was higher in cells with larger coverage of towns or closer to towns. These results support the hypothesis that urban localities, where privets are usually planted in squares and perimeter fences, function as sources of seeds that are dispersed by birds or water courses to nearby forests. In our region, high fruit consumption has been recorded by birds of the Muscicapidae (e.g., *Turdus amaurochalinus*) and Tyrannidae (e.g., *Elaenia flavogaster*) families, like in southern Brazil (Scheibler and de Melo-Junior 2003) and Buenos Aires province (Montaldo 2000). It should be noted that the high supply of privet fruits in the forests of Uruguay, according to our observations, occurs from mid-autumn to early spring, when native fruits are normally scarce, and therefore high consumption by birds is expected in these seasons.

On the other hand, urban development usually results in urban–rural gradients, with increasing disturbance on native ecosystems towards city borders (e.g., McDonnell et al. 1997; Das et al. 2024), as commonly occur in suburban areas of Uruguayan cities where forests are affected by selective logging to obtain firewood, clear felling to gain land for agricultural production, and by pollutants (solid waste, sewage). Such disturbances could reduce the ecosystem resistance of forest, favoring therefore privet establishment, as was observed with other exotic invasive plants (Davis et al. 2000; Duguay et al. 2007).

The important role of urban areas as dispersal focus of *L. lucidum* has also been documented in Argentina, for example in the mountain forests of Córdoba (Gavier-Pizarro et al. 2012) in the Espinal ecoregion, and in the Yungas forests (Grau and Aragón 2000; Montti et al. 2017). These authors agree that the historical and demographic characteristics of cities (e.g., date of founding, population) are important to predict the location and spread of the invaded forest by *L. lucidum*.

Obviously, the propagule pressure of an exotic tree species depends on its seed production and dispersal,

but also on the connectivity of the receiving ecosystem with respect to the nearest propagule source. In this context, it has been shown that roads and railways can play an important role in favoring the connectivity of invasive plants. For example, analyzing results from a large-scale invasive plant survey (254 transects with sampling points at increasing distance from roads, from 0 to 150 m) conducted in forests of western Maryland (USA), Mortensen et al. (2009) found the occurrence of the dominant invasive plant, the Japanese stiltgrass (*Microstegium vimineum*), was much higher along forest roads (83%) than deeper in the forest (15–40%). To better understand the high rate of spread of this invasive plant, and the role that site condition plays, Mortensen et al. (2009) deliberately introduced *Microstegium* patches in different habitats type (disturbed/undisturbed forest, wet meadow, and roadside), and allowed patches to naturally expand over 4 years before controlling all patches. This patch-scale experiment demonstrated that spread rates are higher in roadsides than in forested and wetland patches, even in the absence of major disturbances. More recently, Lázaro-Lobo and Ervin (2019) conducted a systematic review of how roadsides affect the distribution and dispersal of native, weedy, and exotic plant species. The review included 1098 studies, and over half of them reported the effects of roadsides on the distribution and dispersal of exotic/weed species only, of which all but one indicated a positive effect, demonstrating that roadsides serve as landscape corridors for exotic species in several regions of the world. In line with this, distribution models of the exotic tree *Gleditsia triacanthos* in Uruguay detected that the occurrence probability of this species increased with the density of roads (Romero et al. 2021). In a recent book on railway ecology, Ascensão and Capinha (2017) wrote a chapter remarking the relevance of vegetated verges bordering railways as habitat corridors for many non-native organisms. Among the cited examples, there are cases of invasive trees, as the case of the silver wattle (*Acacia dealbata*) in Portugal, one of the most widespread and damaging invasive plants in this country, that dominate the plant communities bordering railways. Interestingly, the penetration of exotic species into areas adjacent to transport corridors, such as roads or railways, appears to be greater in landscapes dominated by grasslands than in those dominated by forests, as shown the study of Hansen and Clevenger (2005) in Alberta, Canada. They discovered that the frequency of exotic species in grasslands along railways and highways was higher than at control sites up to 150 m from the corridor's edge, whereas in forested habitats the higher frequency of exotic species was only evident up to 10 m away from the corridor's edge.

Thus, the presented antecedents suggest that roads and railways can play an important role in favoring the connectivity of invasive plants, especially in grassland-dominated landscapes, like in Uruguay. Our study apported evidence in such line, since privet occurrence increases with the proximity to roads and railways, suggesting the dispersion of this alien tree increase thanks to the greater connectivity provided by these human infrastructures. Almost all railways of Uruguay have been out of use for 20 years, and thus vegetated verges had the chance to growth without control in these artificial corridors excluded of livestock, including exotic invasive trees as *L. lucidum*.

Our model also detected positive effects of afforestation area on privet occurrence probability. Afforestation (*Eucalyptus* and *Pinus*) area had been growing in Uruguay since the 1980s, reaching nowadays about 5% of the Uruguayan territory, exceeding the native forest area (Brazeiro et al. 2020). However, the positive correlation between afforestation area and privet occurrence in native forests was an unexpected result for two reasons. First, Uruguay's native forest is protected by law, it cannot be cut down and exotic tree plantations must maintain a minimum separation from the forests (20 m). Secondly, almost all forestry area in Uruguay is developed under responsible production standards (Forest Stewardship Council-FSC certification), which means, among other things, that native forest must be protected from the invasion of exotic species, and therefore, forestry companies usually carry out exotic tree control programs. According to our knowledge, a large part of the forest plantations has been carried out on old livestock ranches, where privets used to be planted in the fences and gardens. Therefore, we suggest that the mechanism behind the correlation between afforestation and privet occurrence would be the increase in propagule pressure, because old ranch hulls are sources of privet seeds.

Likewise, the occurrence model detected moderate effects of several environmental factors possibly linked to the resistance of the ecosystem, with soil texture being the most evident. A global review found that *L. lucidum* can grow successfully in different soil types (Fernandez et al. 2020). Although privet was found in different soil textures in Uruguayan forests, we found its occurrence probability was slightly higher in loamy soils (medium soil textures) rather than in sandy or clay soils. This soil preference is likely associated with the greater water-holding capacity of medium-textured soils, as *L. lucidum* requires moist conditions to establish and reproduce. The susceptibility of *L. lucidum* to water stress has been observed within its native distribution range, where adult individuals rapidly lose hydraulic conductivity after experimental drought treatments (Li et al. 2006). Within

the invaded range, it was demonstrated with field experiments that *L. lucidum* recruitment can be restricted under dry soil conditions (Aragon and Groom 2003; Aslan et al. 2012).

In dry subtropical forests of Cordoba (central Argentina), Aguirre-Acosta et al. (2014) observed that soil water content was positively correlated with seed production and seedling density of *L. lucidum*. Furthermore, these authors suggest that 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. Any climatic shifts, affecting rainfall regimes or soil nutrient cycling processes through increased atmospheric CO₂ may have stronger effects in water and nutrient demanding invasive plants like *L. lucidum*, which is very worrying in the context of current climate change (Aguirre-Acosta et al. 2014). Another evidence supporting the controlling effect of soil moisture, is that according to our modeling, privet occurrence probability increases with the proximity to rivers, as was also reported previously (Aslan et al. 2012; Montti et al. 2017).

On the other hand, our model suggested effects of some climate variables on *L. lucidum* occurrence, like a negative correlation with the annual temperature range, and positive correlation with the average annual temperature of the most humid quarter. These results suggest that lower annual variability of temperature and higher temperatures during most humid conditions, favor privet establishment. These findings are coherent with the physiology and ecology of trees' establishment, however, do not agree with the wide climatic tolerance reported in *L. lucidum* in recent global reviews (Fernandez et al. 2020; Montti et al. 2021). These authors reported that the invaded range of *L. lucidum* included areas with temperate climate like its native range, as well as warmer and wetter, semi-arid and arid areas, revealing a climatic niche shift during global scale invasion. We also observed that the precipitation of the driest month was negatively correlated with privet occurrence, which disagrees with the reported preference of privet for moisture soils (Aslan et al. 2012; Montti et al. 2017). For example, in the Yungas ecoregion, annual precipitation was positively correlated with privet occurrence, and was one of the best environmental predictors to explain the expansion of this species in forests (Montti et al. 2017). Our modeling also suggested negative effects of the minimum temperature of the coldest month on privet occurrence probability, which also disagrees with the high resistance to low temperatures (until - 15 °C) reported in this species (Fernandez et al. 2020). Indeed, when considering the broad climatic suitability of *L. lucidum* derived from regional

(Montti et al. 2017) and global (Montti et al. 2021) niche models, our results are very strange and difficult to interpret. Climate is expected to be an important determinant of alien species distribution at the continental (10,000 km) and regional (2000–200 km) spatial scales, but not necessarily at minor scales (Milbau et al. 2009), as in our study. In our study we only assessed a small subset of *L. lucidum* large climatic niche (Montti et al. 2021), and in a region where the invasive process is yet far from the climatic equilibrium. Thus, we assess the four climatic correlations observed here as spurious results, at least until new data were collected, and suggest they could be artificially produced because the distribution of privet is not in equilibrium with climatic conditions.

The determinants of the privet occurrence pattern observed here are very similar to what we observed in the case of *G. triacanthos*, another invasive tree in Uruguay (Romero et al. 2021). The occurrence probability of *G. triacanthos* was also higher in the S-W region of Uruguay, and increased with greater accessibility, for example near roads, and with greater anthropic disturbances.

Determinants of *Ligustrum lucidum* dominance

Privet-dominated forests in 2021 represent only 1.2% of the total area of Uruguayan forests, an order of magnitude smaller than the estimated area of occupancy of this alien tree (13.4%) and were also concentrated in the S-SW region of Uruguay, showing a diffusion pattern from this region to the rest of the country. These results reinforce the idea that the invasion of *L. lucidum* began in the S-SW region of the country and that the current stage within the invasion process (i.e., transport, establishment, spread/impact, sensu Lockwood et al. 2007), correspond mainly to the spread and impact stage. In addition to depending on proximity to the focus of origin in the S-SW region, the dominance of *L. lucidum* in forests also increased with proximity to urban areas, roads, and railways. The possible mechanisms of dispersal and propagule pressure underlying these relationships were already discussed previously, within the framework of establishment patterns. In short, these detected effects on privet dominance also reinforce the idea that the invasion is currently in the process of advancement and expansion from secondary foci.

Privet dominance seems to be also controlled by ecosystem resistance, since its coverage in the forest canopy increased in medium texture soils (loamy soils), with higher soil productivity and at higher altitudes, but decreased with increasing native forest area and soil rockiness.

The area of forests by cell was one of the best predictors of privet dominance, with greater dominance as forest area decreased. The area of forest in a cell may be small

due to the natural patchiness typically associated with edges of continuous forest, or to fragmentation caused by deforestation. In both cases, forest integrity will be reduced in comparison with cell with large forest areas, mainly when human-driven fragmentation occurs. The general extent of Uruguayan forests has remained relative stable since the nineteenth century, despite several local changes had been observed (Gautreau 2010). Forest loss can be mainly explained by agricultural development, storage reservoirs, and coastal urbanization (Gautreau 2010). Despite native forests are legally protected since 1987, some illegal cuts occur nowadays. For example, soybean expansion was responsible for forest loss in the western region of Uruguay, mainly affecting borders of continuous forests and small fragments (Tiscornia et al. 2014). Thus, forest area is a key indicator of forest health, which has been largely associated with invasibility.

It is well known that more dense, mature, and intact forests usually are less invaded than fragmented or disturbed forests (Richardson et al. 1994; Alpert et al. 2000; With 2002). Habitat disturbance and fragmentation often results in a reduction of native populations and higher degree of isolation, which could reduce biotic resistance and therefore, favor the growth of exotic invasive populations (With 2002; Eschtruth and Battles 2009). Reviewing studies on landscape influences on plant invasion, Vilà and Ibáñez (2011) found that fragments of small size usually have a higher density of alien species than large fragments or continuous ecosystems. Finally, we hypothesize that larger forests maintain greater ecological integrity, with communities in better conditions to control or reduce privet population growth. Some studies have pointed out the relevance of biotic interactions in controlling privet population growth. Tecco et al. (2007) experimentally demonstrated that *L. lucidum* saplings improve their survivorship in dry forests of central Argentina when they grow under the canopy of the exotic shrub *Pyracantha angustifolia*. In lowland ravine forests of Uruguay, Brazeiro et al. (2018) observed that densities of privet seedlings (height: 10–50 cm) and saplings (height: 51–200 cm), were 80% lower than those in stands dominated by the native tree *Jodina rhombifolia* and suggested the hypothesis that root parasitism exerted by *J. rhombifolia* could be the associated mechanism.

Soil fertility seems to positively affect *L. lucidum* growth and its community dominance, agreeing with previous evidence. In their revision about the role of environmental stress in the spread of exotic plants, Alpert et al. (2000) reported several studies correlating the degree of plant invasion of habitats with the availability of nutrients. In the case of *L. lucidum* invasion, Aguirre-Acosta et al. (2014) reported that fruit and seed production was lower when soil organic matter and nutrients

were reduced in fragmented forests of central Argentina, and thus they concluded that *L. lucidum* is a nutrient demanding invasive plant in their study area.

Soil texture and rockiness slightly affected privet dominance, as extreme textures (i.e., sandy or clay soils) and high rockiness (i.e., >25%) appear to somewhat reduce the ability of privet to overcome the cover of native trees in the forest canopy. Probably, these effects relate to the reduced water available in such soil types and the susceptibility of *L. lucidum* to water stress, as discussed previously.

Finally, we found that *L. lucidum* dominance increased with altitude, despite the small altitudinal gradient of Uruguay (0–400 m a.s.l.). This is an unexpected result in Uruguay, since privet is currently distributed mainly in the lowlands of the S-SW region, and less in the highlands of the E and NE. However, *L. lucidum* has invaded forests at altitudes much higher (i.e., 1000–1500 m a.s.l.) than the registered in Uruguay, like in eastern and northern Argentina (Gavier-Pizarro et al. 2012; Montti et al. 2017). Indeed, the global review of *L. lucidum* invasion showed that it can grow successfully between 0 to 2900 m a.s.l. (Fernandez et al. 2020). According to these antecedents, the relative low occurrence of privet in the highlands of the E-NE region of Uruguay can be explained by the low residence time, and the low spread from the invasion focus on the S-SW region, and not by the resistance of forest ecosystems due to greater altitudes. Indeed, once privet was established in a forest stand, according to our modeling, dominance seems to be favored as altitude increases from 0 to 400 m a.s.l. In northern Argentina, at higher altitudes (500–1500 m a.s.l.), privet forest expansion over 30 years also increased with altitude (Montti et al. 2017). Thus, the highlands of the E-NE Uruguay, currently with low occurrence due to limited dispersion, could be suitable to privet growth and dominance, so it should be monitored to early detect the presence of this invasive tree, to carry out control activities when local eradication is yet possible.

Conclusions

The invasion of Uruguayan forests by *L. lucidum* is in the spread (13.4%) and impact (1.2%) stages, currently in expansion from the invasion focus on the S-SW region of Uruguay, where the oldest urbanizations are settled, towards the rest of the country. In consequence, the geographic proximity to the invasion focus (S-SW region) is currently the main predictor of both *L. lucidum* establishment and dominance in Uruguayan forests. *Ligustrum lucidum* spread is facilitated by human infrastructures improving propagule pressure, primarily by cities, towns, and other human settlements where privet has been planted as ornamental trees, and by roads and railways

that function as corridors. Soil water content seems to be important for privet establishment because its occurrence probability increased in mid textured soils (higher water availability) and near rivers. Once established in a forest, the probability that *L. lucidum* will overgrow native trees and dominate the canopy cover, increases in small forest patches (border patches of continuous forests or fragmented forests), in rich-nutrient soils (higher fertility), and at higher altitudes, suggesting that ecosystem resistance is operating in certain local conditions.

In the field of environmental management, our results suggest that it would be appropriate to focus efforts on preventing the establishment of privet in suitable areas not yet reached, and on controlling population growth in areas of ecological relevance (e.g., protected areas) already colonized, but not currently dominated. Given that cities, towns, and other minor human settlements play a relevant role as secondary foci of privet dispersion, it is key to take measures to address such problem, controlling the current urban populations of *L. lucidum* and prohibiting its future planting.

Abbreviations

AIC	Akaike Information Criterion
AUC	Area Under the Curve
CONEAT	Comisión Nacional de Estudio Agronómico de la Tierra
DGF	Dirección General Forestal de Uruguay
FSC	Forest Stewardship Council
GEE	Google Earth Engine
GLM	Generalized Linear Models
INUMET	Instituto Nacional de Meteorología de Uruguay
IPBES	Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services
MAFIA	Macroecological Framework for Invasive Aliens
MEA	Millenium Ecosystem Assessment
NDF	Normalized Difference Fraction Index
NIS	Nonindigenous species
PAB	Propagule pressure, Abiotic characteristics and Biotic characteristics
TSA	Trend Surface Analysis
VIF	Variance Inflation Factor

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s13717-024-00512-w>.

Additional file 1: Table S1. List of all variables considered in the statistical modelling of the invasion process of *Ligustrum lucidum* in native forests of Uruguay. **Table S2.** Evaluation of the correlation between explanatory variables used in the modeling of the occurrence of *Ligustrum lucidum* in native forests of Uruguay. **Table S3.** Evaluation of the correlation between explanatory variables used in the modeling of the dominance of *Ligustrum lucidum* in native forests of Uruguay. **Table S4.** Summary of Trend Surface Analysis models. **Figure S1.** Geographic distribution of the TSA variables. **Figure S2.** Correlograms of final models. **Figure S3.** Residual analysis. **Figure S4.** Prediction of the occurrence of *Ligustrum lucidum* in native forests of Uruguay using the final GLM model.

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Author contributions

AB was responsible for the overall conceptualization of the research, analysis strategy, writing, funding development and responding to reviewers. JO performed the classification and mapping of forest invaded (dominated) by *L. lucidum*. ABen carried out the environmental data compilation and integration in the spatial grid used (GIS). IL performed the statistical modeling of occurrence and dominance in R. DR contributed with trend surface analysis. FA performed the compilation and curation of presence/absence data of *L. lucidum*. AC took drone photographs to assess *L. lucidum* dominance degree in the samples areas to measure the error of satellite mapping. All authors read and approved the final manuscript.

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Availability of data and materials

The datasets used during the current study are available from the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

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Competing interests

Not applicable.

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