Query Details

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Araújo MB, Thuiller W, Pearson RG (2006) Climate warming and the decline of amphibians and reptiles in Europe. J Biogeogr 33:1712-1728. https://doi.org/10.1111/j.1365-2699.2006.01482.x

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Factors involved in the biogeography of the honey locust tree (*Gleditsia triacanthos*) invasion at regional scale: an integrative approach

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Abstract

Native to the southeastern United States, the honey locust (*Gleditsia triacanthos*) is an invasive tree in several South American countries. Since eradication of invasive species is often costly, prevention is a better strategy. The relationship between invasive species and their habitats can be analyzed using species distribution models to produce maps of areas prone to the invasions. These maps can be used to develop efficient early detection plans of exotic species colonization. Here, we employed the Favorability Function model to assess the effects of environment and human activities on the invasive process of the honey locust in Uruguay. By integrating environmental and anthropic factors in our models, we obtained the best fitted prediction and classification indices. We showed that the southwestern region of the country concentrates the largest proportion of areas prone to the invasions. Environment was the main factor explaining the invasion of *G. triacanthos*, but the effect of human-related factors had a greatest effect in combination with environmental variables than on its own. We generated favorable risk maps and explanatory variables that can be used to more efficiently plan efforts to control the spread of this invasive.

Keywords

Disturbed territories
Environmental characteristics
Invasion risk map
Favorability Function
Anthropic influences
Spread prevention

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Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1007/s11258-021-01139-z.

Introduction

Global warming (Pearman et al. 2010; Real et al. 2013), land-use modification (Delibes-Mateos et al. 2010), and biological invasions (IUCN 2000; Beans et al. 2012; Romero et al. 2014) are among the main causes of biodiversity loss worldwide. Invasive species, animals, plants, fungi, bacteria, and virus can harm the natural resources in an ecosystem as well as threaten human use of these resources. The honey locust (*Gleditsia triacanthos*) is a highly invasive deciduous tree, native to the southeastern United States, particularly in the Mississippi River Basin (Virginia) and the southern plains, and Texas (USDA 2016), with great adaptive plasticity even in its native range (CABI 2021). It has been identified as an aggressive invader in a variety of regions and environments (USDA 2016). The species has been reported in Spain (Rivas Goday and Bellot 1948), Australia (Csurhes and Kriticos 1994) as well as in Serbia and Ukraine (Nikolić et al. 2010). In Romania, it is primarily naturalized in riverine environments and urban localities (Doroftei et al. 2009), whereas in South Africa, it occurs in savannas, shrubs, xeric shrubland, and wetland areas (Henderson 2007). The honey locust is considered a potential invader of prairie biomes (Richardson and Thuiller 2007).

In South America, *G. triacanthos* has been reported in Argentina and Uruguay (Caballero 2013; Ghersa et al. 2002; Fernández et al. 2017), and Castillo (2016) considered it could potentially invade almost all countries in the continent. In Argentina, it is found in the Dry Chaco, subtropical mountainous forests, Espinal (Fernández et al. 2017), and Pampas grasslands (Rossi et al. 2008). In Uruguay, *G. triacanthos* was introduced in the early twentieth century for ornamental purposes and to provide shade and wood. It is now one of the most important tree invaders within natural forests, and one of the main threats to forest conservation in the country (Nebel and Porcile 2006). This species colonizes recently abandoned (Mazía et al. 2001) and disturbed lands (Colombo

Speroni and de Viana 1998), germinating among shrublands (Zeballos et al. 2014) and treefall gaps and promoted by anthropic activities such as pasture clearance or road construction (Blair, 1990). Among the main environmental consequences, the honey locust can replace native vegetation (Zalba and Villamil 2002; Lewis et al. 2006; Sirombra et al. 2010; Traversa and Alejano 2013; Sosa et al. 2018), transforming entire ecosystems and modifying their ecological functioning, it has been reported in invaded riparian ecosystems (Zalba and Villamil 2002; Giorgi et al. 2014; Vilches et al. 2020).

The distribution of a species results from a combination of factors such as the dispersal characteristics of the species, its biotic and abiotic context together with historical and evolutionary factors, stochastic events, and anthropic variables (Lomolino et al. 2006). At a global scale, climate is one of the main drivers affecting biological invasions (Pearson and Dawson 2003; Vicente et al. 2010; Hardion et al. 2014; Martin et al. 2015; Cabra-Rivas et al. 2016), as Cabra-Rivas et al. (2016) reported of invasive woodies *Ailanthus altissima* and *Robinia pseudoacacia*. However, at a regional scale, factors that influence invasive processes are variable and depend on the adaptive characteristics of the invader (Hamilton et al. 2005) and the environmental characteristics of the invaded ecosystem (Catford et al. 2008). For example, Vilches et al. (2020) indicated in Pampean Streams that *G. triacanthos* grows better in disturbed sites exposed to direct sunlight, preferring a milder climate, and Walker et al. (2017) showed that at the country scale only variables related to human activity such as changes in land use, explained the distribution for *A. altissima*. Thus, important predictors have included climatic (Araújo et al. 2006) and spatial variables (Pliscoff and Fuentes-Castillo 2011), and more recently anthropic pressures or land use, to improve the explanatory capacity of predictions (Acevedo et al. 2011; Real et al. 2013; Coelho et al. 2018; Romero et al. 2019). Catford et al. (2008) also concluded that an integrative approach where different hypotheses or factors are simultaneously assessed is the most realistic way to address invasive processes in a territory. Incorporating different factors (climatic, topographic, land use, altitude, or anthropic factor, between others) in the species distribution models, their predictive capacity is improved (Márquez et al. 2011; Real et al. 2013; Coelho et al. 2018). Previously Csurhes and Kriticos (1994) applied a CLIMEX modeling package to measure the effect of climate as a driver of the *G. triacanthos* invasive process in riparian ecosystems of

Australia; however, the relative importance of different factors in this species' invasion has not yet been unraveled.

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Given that preventing invasion is the best cost effective way of dealing this threat (Wittenberg and Cock 2001), the generation of invasion risk maps is recommended as a least expensive early management procedure (Leung et al. 2002; Paneta 2007; Kaplan et al. 2014). Species distribution models (SDMs) have been widely used to predict the potential distribution of species (López-Darias et al. 2008; Real et al. 2017; Romero et al. 2019; Aximoff et al. 2020; Da Re et al. 2020), and to unravel the factors that affect these patterns (Franklin 2010; Catford et al. 2008; Romero et al. 2016; Guisan and Zimmermann, 2017; Real et al. 2017; Coelho et al. 2018). Different algorithms have been used to predict the probability (Elith et al. 2006), suitability (Franklin, 2010, 2013; Da Re et al. 2020), or environmental favorability of the distribution of a species (Real et al. 2006; Acevedo and Real 2012). According to the Favorability Function (FF), environmental favorability is obtained from the probability of a logistic regression (Real et al. 2006), identifying the areas that are favorable to the species (Real et al. 2006; Acevedo and Real 2012). Favorability values are the probability corrected by the stochastic effect of prevalence, reflecting exclusively if environmental conditions favor or not the presence of the species in each study unit. Therefore, from true presences/absences, favorability values reflect the response of the species to the predictors without prevalence bias (Acevedo and Real 2012).

By integrating different factors to generate more accurate and useful models, we use the FF as species distribution model to analyze what proportion the integrated effect of the environmental characteristics and human activities favor the invasive process of the honey locust tree in Uruguay. We analyze both a full direct model based on all factors and two partial models, environmental and anthropic, and their subsequent combination. We analyzed variables that explain the current invasive process and use these results to predict the most favorable territories likely to be invaded in the near future. Finally, we propose our integrated models as expansion risk maps for *G. triacanthos* in Uruguay that can be used as an early warning system.

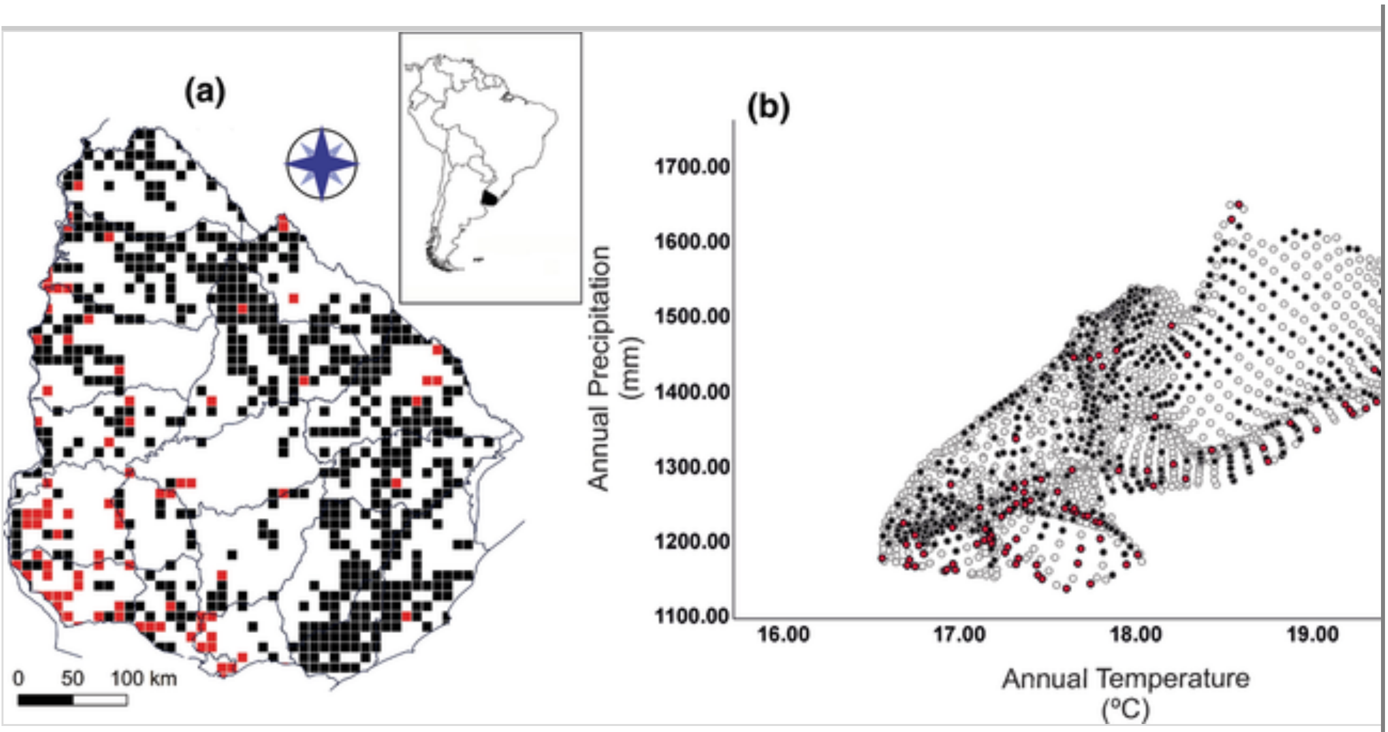
Materials and methods

Study area

The study area was the entire country of Uruguay. Uruguay is dominated by grasslands, combined with dispersed patches of native forests, and wetlands (GEO-Uruguay 2008). About 90% of the territory is used for livestock rearing for meat and milk, crop production (e.g., soybean, wheat, rice, barley, and maize), and exotic forest (*Eucalyptus sp.* and *Pinus sp.*) plantations (DIEA 2016). Uruguay has a humid subtropical climate of homogeneous conditions with moderate seasonal temperatures and rains evenly distributed throughout the year (Kottek et al. 2006; INUMET 2019). This is the same climate type of warm temperatures and high humidity typical of *G. triacanthos* native areas in the United States (see climate specifications in Kottek et al. 2006 or Beck et al. 2018). For modeling procedure, we developed a grid of country of Uruguay at a spatial resolution of 10 × 10 km cells using QGIS software 3.10 (www.qgis.org) (Fig. 1a).

Fig. 1

Study area in South America in the geographical (**a**) and environmental (**b**) context. In both, the presence of *Gleditsia triacanthos* is shown in red, the territories sampled without presence of invasion is shown in black, and the unsampled territory is shown in white



The response variable: Gleditsia triacanthos To change to italic style introduction history and distribution data

Current data of the distribution of *G. triacanthos* in Uruguay were obtained from the National Forest Inventory (Echevarria 2016; DGF 2019) and from the InBUy database (www.inbuy.fcien.edu.uy). Data from the National Forest Inventory were gathered between 2009 and 2016 following a systematic sampling design that uses the hydrographic basins of the country as strata (DGF 2019). A digital grid with cells of 1900 m sides for the national territory was intersected with the 2016 national forest map (from Landsat TM images) to define the extent of sampling. In view of the accepted error involved in the estimation of forest volume (i.e., < 10%, with a significance level of 95%), and implementation costs, a total sampling effort of 1,460 cells was possible. Sampling points (20 × 10 m quadrat) were placed in the center of each randomly selected cell where points intersected with the forest plot, otherwise another cell was chosen. Within each selected sampling point, the presence or absence of invasive woody species was recorded during field work, a total of 1460 presence/absence data points. Together with an additional 27 records from the InBUy database (http://inbuy.fcien.edu.uy), we generated the presence/absence cells of the current distribution of *G. triacanthos* in Uruguay.

We used a 10 × 10 km grid divided into cells to implement our species modeling procedure. In this way, all cells with at least one observed record of *G. triacanthos* were classified as presence, and the cells in which the species was not observed as absent. Cells without sampling information were not considered in the calibration of the distribution models. The study area covered a total of 1,887 cells in a 10 × 10 km grid, out of which we used only 654 sampling cells containing information (34.7% of Uruguay). To calibrate our distribution models, cells representing 87 presences and 567 absences homogeneously represented geographic space (Fig. 1a) and environmental space (Fig. 1b), (see details in Fig. 1b).

Environmental and anthropic factors as predictor variables

To determine the environmental characteristics that drive the invasion process of *G. triacanthos* in Uruguay, we created a set of potential predictor variables grouped as factors (spatial; topography; climatic; hydrology; land use; lithology and human activities) (see details and sources of each variable in Table 1). These were digitalized at the resolution of 10 km × 10 km of the study area in QGIS software.

Table 1

Variables and factors analyzed during the modeling process

Code	**Variables**	**Code**	**Variables**
Spatial			
YSp	Spatial logit[1] (linear polynomial combination of Latitude (ºS) and Longitude (ºW) from the spatial logistic regression)		
Topography			
A	**Average altitude (m)(2)**	S	Slope (º) (calculated from altitude)
Ori-NS	Orientation; degrees of exposure North–South (calculated from slope)	**Ori-EW**	**Orientation; degrees of exposure East–West (calculated from slope)**
Rough	**Roughness (m)**		
Climatic			

BIO$_1$	Average annual temperature (ºC)(3)	BIO$_{11}$	Mean annual temperatures of the coldest quarter (ºC)(3)
BIO$_2$	Mean diurnal range temperatures (ºC) (ºC)(3)	BIO$_{12}$	Annual precipitation (mm) (3)
BIO$_3$	Isothermality (BIO$_2$/BIO$_{17}$) (*100) (ºC)(3)	**BIO$_{13}$**	**Precipitation of the wettest month (mm)(3)**
BIO$_4$	Seasonal temperatures (ºC)(3)	BIO$_{14}$	Precipitation in the driest month (mm)(3)
BIO$_5$	Maximum temperatures in the warmest month (ºC)(3)	**BIO$_{15}$**	**Seasonal precipitation (mm)(3)**
BIO$_6$	**Minimum temperatures in the coldest month (ºC)(3)**	BIO$_{16}$	Precipitation in the wettest quarter (mm)(3)
BIO$_7$	Annual temperature range (BIO$_5$-BIO$_6$)(3)	BIO$_{17}$	Precipitation in dry quarter (3)
BIO$_8$	**Mean annual temperatures of the wettest quarter (3)**	BIO$_{18}$	Precipitation in the warmest quarter (3)
BIO$_9$	Mean annual temperatures in the dry quarter (3)	BIO$_{19}$	Precipitation in coldest quarter (3)
BIO$_{10}$	Mean annual temperatures in the warmest quarter (3)	**PMax**	**Maximum average precipitation in 24 h (mm)(3)**
ETP	Potential evapotranspiration (mm) *(3)*	**ETR**	**Monthly real evapotraspiration (mm)(3)**
WatBalAut	Water balance in Autumn (mm)(3)	WatBalSpring	Spring water balance (mm)(3)
WatBalWint	**Water balance in Winter (mm)(3)**	**WatBalSumm**	**Water balance in Summer (mm)(3)**
BhAnn	**Annual water balance (mm)(3)**	**AnnHum**	**Annual average humidity (mm)(3)**

ColdQuaHum	Coldest quarter average humidity (mm)$^{(3)}$	WarmQuaHum	Warmest quarter average humidity (mm)$^{(3)}$
AnnHum	Annual average humidity (mm)$^{(3)}$	**Frost**	**Average number of frost days** $^{(3)}$
Other			
NDVI	**Index of greenness (plant biomass productivity indicator)** $^{(4)}$	DistCost	Distance to coast continentality (km)$^{(5)}$
SunRad	Sun radiation (kwh/m2/day)$^{(6)}$		
Hydrology			
DistRiver	**Minimum distance to rivers (km)**$^{(7)}$	LengRiver	Length of rivers (km)$^{(7)}$
Land use			
Forests	**Natural forests (%)**$^{(8)}$	**Reforested**	**Reforestation (%)**$^{(8)}$
NatField	**Natural field (%)**$^{(8)}$	**Crops**	**Crops (%)**$^{(8)}$
Wetland	**Wetland (%)**$^{(8)}$		
Lithology			
SoilDepth	Soil depth $^{(9)}$	**TextSoil**	**Texture soil** $^{(9)}$
SoilRocky	**Soil rocky** $^{(9)}$	FloodSoil	Flooded soil $^{(9)}$
Human activities			
PopDen	**Population density** $^{(10)}$	**UrbGro**	**Urban ground (%)**$^{(10)}$
DistUrban	**Minimum distance to the main urban centers (km)**$^{(11)}$	**SumRoads**	**Length of roads and unpaved routes (m)**$^{(11)}$
DistRoad **Cattle**	**Minimum distance to paved roads (km)**$^{(11)}$ **Cattle density (average number of animals /km^2)**$^{(12)}$	**DistUnpavRoad**	**Distance to unpaved roads (km)**$^{(11)}$

The variables that passed the FDR and Pearson's correlation ($r > 0.8$) filters to build the distribution model of *Gleditsia triacanthos* are shown in bold

Sources: (1) Spatial variables, latitude and longitude, were generated from the QGIS (www.qgis.org) program according to the vector geometry tools: (a) with "centroids of polygons," the centroid of each cell was calculated, and (b) with "Export / Add columns of geometry," the values of length and latitude expressed in the 1984 World Geodetic System were allocated to each centroid (WGS84). (2) United States Geological Survey 1996. GTOPO30. Land Processes Distributed Active Archive Center. – EROS Data Center, https://lta.cr.usgs.gov/GTOPO30. (accessed in April 2016). (3) Ceroni (2008) from DNM-INIA. Monthly data series of thirty years for Uruguay (from 1980 to 2009). The operations to calculate the bioclimatic variables (BIO1–BIO19) were based on WorldClim. Global Climate Data available in Fick & Hijmans (2017). (4) https://www.vito-eodata.be, from SPOT-VEGETATION – S10 NDVI. (5) It was generated with the QGIS (www.qgis.org) program calculating the average distance from the centroid of the grid to the coastline layer. (6) Mapa Solar del Uruguay, versión 1.0, Memoria Técnica. G. Abal, M. D'angelo, J. Cataldo y A. Gutiérrez. Facultad de Ingeniería, Universidad de la República. June 4, 2010. https://www.fing.edu.uy/if/solar/memoria-mapa-solar-v1.pdf (accessed in October 2010). (7) It was generated with the QGIS (www.qgis.org) program, calculating the average distance from the centroid of the grid to the river line layer. (8) Oficina de Planeamiento y Presupuesto (accessed in March 2010). (9) Panario D, Gutiérrez O (2011) Mapa de ambientes: Cartografía implementada en un SIG. In: Mapa de Ambientes de Uruguay y Distribución potencial de especies, Convenio MGAP/PPR-CIEDUR, Montevideo. (10) Instituto Nacional de Estadística (accessed in June 2011). (11) It was generated from topographic charts 1.50,000 digitized by the Ministerio de Transporte y Obras Públicas. (12) Gilbert M, Nicolas G, Cinardi G, Van Boeckel TP, Vanwambeke SO, Wint GW, Robinson TP (2018) Global distribution data for cattle, buffaloes, horses, sheep, goats, pigs, chickens and ducks in 2010. Scientific data 5(1):1–11

Because spatial factor allows us to identify the existence of geographic trends that cannot be completely explained by environmental variables (Barbosa et al. 2010), such as history or spatial ecological dynamics (Legendre 1993), we considered a polynomial trend-surface analysis (Legendre and Legendre 1998) to reflect the effect of factors that may involve purely spatial trends. For it, according to Legendre (1993) in a previous step, we included latitude (La), longitude (Lo), and a quadratic and cube effect of La and Lo and interactions between them (Lo, Lo^2, Lo^3, La, La^2, La^3, LaLo, La^2Lo, $LaLo^2$) in the model procedure. Specifically, we performed a stepwise logistic regression backwards with the presence/absence of *G. triacanthos* and those nine spatial terms to eliminate non-significant spatial terms from the models (Legendre and Legendre 1998), generating a spatial linear combinations (ysp) as the only one spatial variable in the modeling procedure. Finally, we included the resulting linear combinations (ysp) with the rest of environmental variables described above.

Species distribution modeling (SDM)

To explain the *G. triacanthos* distribution, we used FF to develop SDMs from a set of variables without multicollinearity nor false discovery. From the set of variables described above prior to the modeling procedure, we applied two filters. First, we checked the pair-wise correlation of variables to avoid excessive multicollinearity (Dormann et al. 2013), eliminating the least significant variable of each Pearson correlation pair, greater than 0.8. For those variables that pass this test, we used the False Discovery Rate (FDR) to minimize Type I errors in the analysis (Benjamini and Hochberg 1995), accepting only those variables which are significant under an FDR < 0.05.

Using the set of filtered predictive variables, and presence/absence data, we calculated the FF by applying a multifactorial logistic regression according to a forward–backward stepwise procedure (Márquez et al. 2011). We calibrated favorability SDMs from the 87 cells with presences and the 567 cells with absences verified in samples (Fig. 1). We later extrapolated the SDMs to the rest of the country cells. In this way, we trained the SDMs applied in the study area only from the presences and absences observed. We obtained the FF based on the probability derived from multifactorial logistic regression according to Real et al. (2006) and Acevedo and Real (2012):

$$FF = [P/(1 - P)]/[(n1/n0) + (P/[1 - P])],$$

where F is the environmental favorability (ranging between 0 and 1), P is the probability of occurrence obtained from the multivariate logistic regression performed for each target variable, $n1$ is the number of presences and n0 in the number of absences, respectively. Favorability values factor out the weight of the initial species presence/absences ratio, inherent to any probability function (Cramer 1999; Real et al. 2006; Barbosa et al. 2013, 2016) and, thus, depend exclusively on the effect of the environmental conditions of the territory on the distribution under analysis (Acevedo and Real 2012). The FF reflects the degree (between 0 and 1) to which the probability values obtained in each model differ from that expected, according to the species' prevalence, where 0.5 indicates no difference between both probability values. We calculated Wald's test parameter with the purpose of knowing the relative weight of the variables in each model (Wald 1943). We used the fuzzySim package (Barbosa , 2016; https://modtools.wordpress.com/packages/fuzzysim/) for R (R Core Team 2020) (see script in Online Resource 1), whose stepwise procedure is based on Akaike

Information Criteria or AIC.

Using FF, we analyzed in what proportion the integrated effect of the environmental characteristics and human activities determine the invasive process of *G. triacanthos* in Uruguay. For this, we analyzed both a full direct model based on all factors as well as two partial models, environmental and anthropic, and their subsequent combination. For this, we first performed a favorability *G. triacanthos* model from the filtered variables of all factors, hereinafter F-Direct full. Following this, to determine the performance of environment and anthropic effect separately, we elaborated two partial models: an environmental model we refer to as F-Environmental (from variables that characterize the environment: spatial; topography; climatic; soil properties; and water availability); and one anthropic model, hereinafter F-Anthropic (from variables that indicate the human activities influence: land-use and anthropic variables) (see Table 1). Finally, from the combination of the variables that entered in each of the partial models, we run a new stepwise procedure to obtain a final combined model named F-Combined.

In all cases, and taking into account that a prediction is considered favorable when the probabilities of favorability are greater than 4:1 and unfavorable when they are less than 1:4 (Muñoz and Real 2006), values of $F \geq 0.8$ were classified as a high favorable risk of invasion; values between 0.2 and 0.8 as intermediate; and values of $F \leq 0.2$ as a low favorable risk.

Models assessment

We evaluated the classification and discrimination capacity of the models, both for the territory used to train the model (654 cells with presences/absences) and for the whole country (1887). According to Zurell et al (2020), we evaluated the classification capacity of models using four threshold-dependent indices: (1) sensitivity, (2) specificity, (3) Correct Classification Rate (CCR), and (4) True Skill Statistic (TSS) (Liu et al. 2009). These classification indices employ a range from 0 to 1 and the value of $F = 0.5$ as the classification threshold. The TSS index is a general measure of classification obtained from the subtraction of true positive from false positive rates, independent of prevalence. These TSS range from -1 to $+1$, where TSS = 1 indicates perfect agreement, and values of TSS ≤ 0 indicate a performance worse than random (Allouche et al. 2006). The discrimination capacity was evaluated using the area under the curve (AUC) of the receiving operating characteristic (ROC), which is independent of any favorability threshold (Hanley and McNeil 1982; Dodd and Pepe 2003; Guisan et al. 2017).

We checked also the spatial autocorrelation using the Moran's I spatial autocorrelation statistic from the residuals of the models (Cliff and Ord 1981) and the excessive multicollinearity using the variance inflation factor or VIF (Montgomery and Peck 1992), testing that any variables with VIF > 10 were included in the model. Finally, we used histogram graphs to evaluate the number of occupied invaded cells versus the number of predicted favorable cells for each model.

Relative importance of the different explanatory factors

In the SDM models, part of the influence of the environment could be attributed to each of the single factors, and another part could be simultaneously attributed to a shared effect of other factors, resulting from correlations between variables (Márquez et al. 2011; Real et al. 2013). To determine the contribution (as a proportion) the different relevant factors make to the *G. triacanthos* invasive spread, we applied a variation partitioning procedure (Borcard et al. 1992; Real et al. 2013). Specifically, this calculated the proportion of the variation in the favorability model that is explained by the effect of the different factors separately (environment and human influence), and the proportion explained by the shared effect of the combination of factors. Statistical analysis were performed using the modEvA package (Barbosa et al. 2013, 2016, https://modtools.wordpress.com/packages/modeva/). The R script used is presented as an Appendix in supplementary material.

Results

Favorable territories and explanatory factors

All models (direct, partial, and combined models) highlight a main high favorability zone in the southwest of the country (maps in Figs. 2, 3 and 4). Some scattered cells of the highest favorability were detected in the F-Anthropic partial model (in Fig. 2c), or in the east in the F-Environmental, F-Combined, and F-Direct full models (in maps in Fig. 2).

Fig. 2

a F-Direct full model, **c** F-Environmental and F-Anthropic partial models, and **e** F-Combined model. We show histograms that represent, on the first "y-axis" the total number of cells by value of favorability range: low ($F \leq 0.2$), intermediate ($0.2 > F < 0.8$) or high ($F \geq 0.8$), and, on the second “y-axis,” highlighted with the red line, the number of cells occupied by *G. triacanthos* in each favorability model (b, d and f respectively)

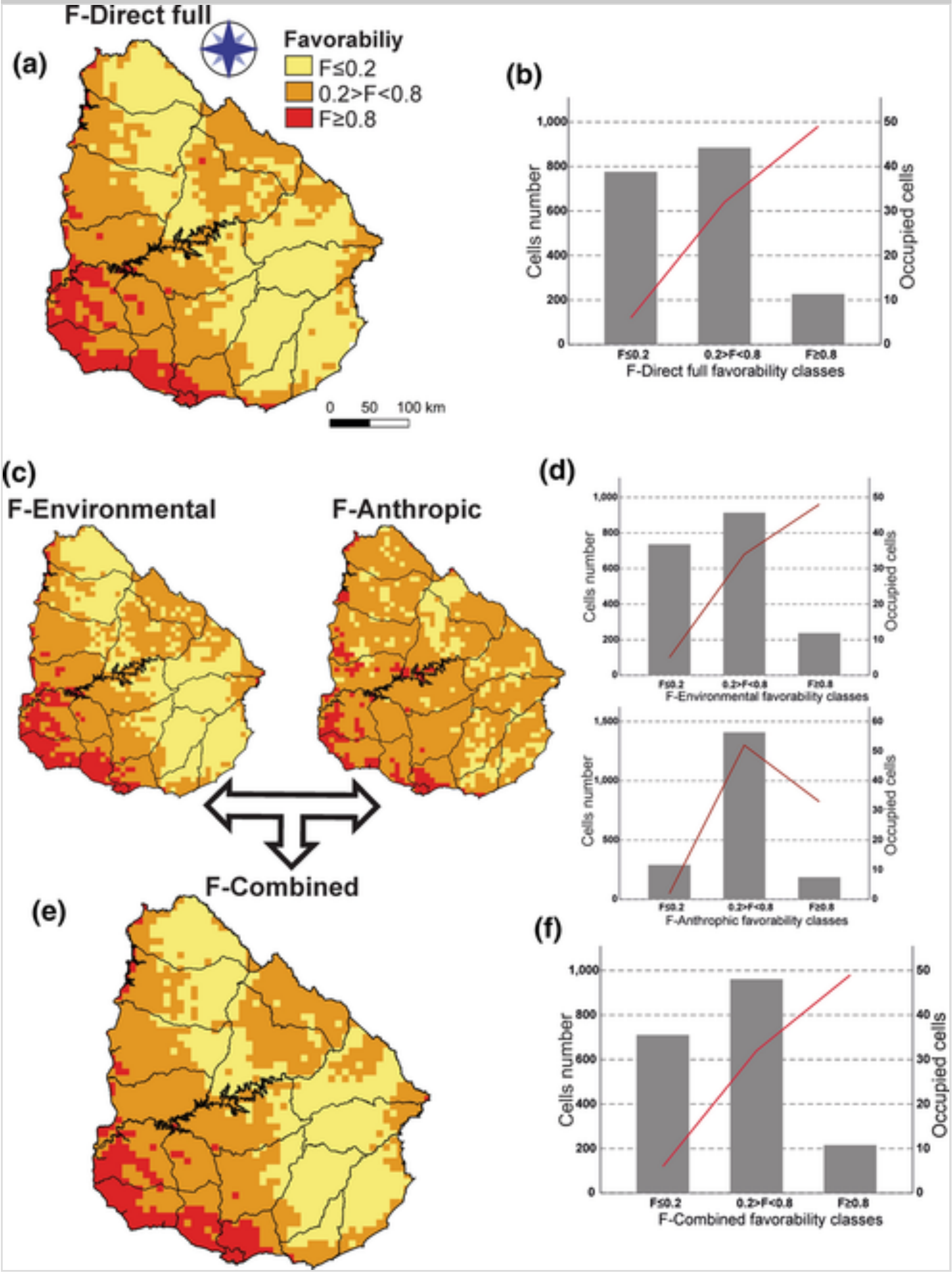


Fig. 3

F-Direct full and F-Combined favorability models. Indicated with (**a** and **d**) the geographical space of the favorability model, with (**b** and **e**) the environmental space of the most relevant three variables according to the Wald test and with (**c** and **f**) those three variables separately correlated with the favorability values

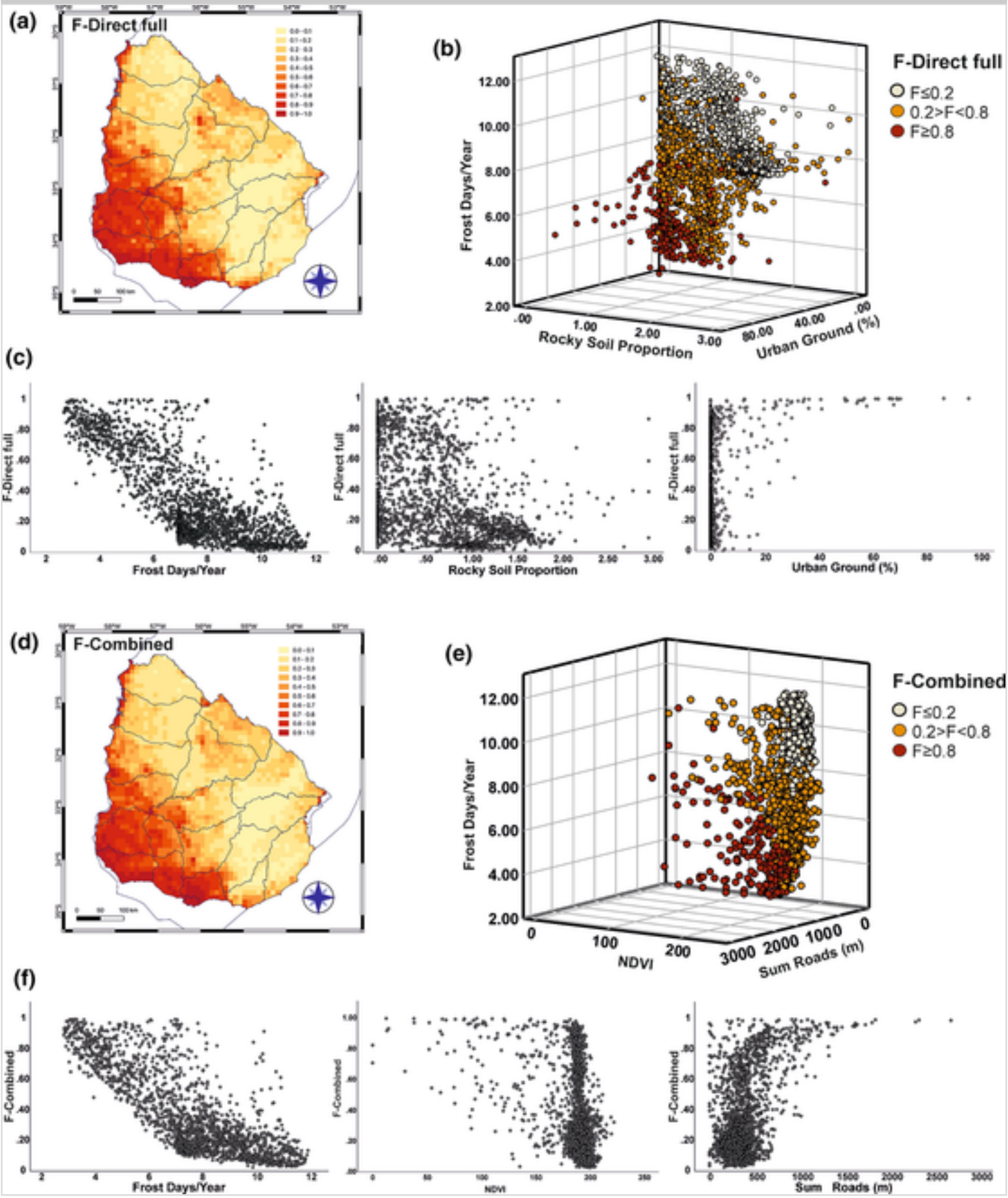
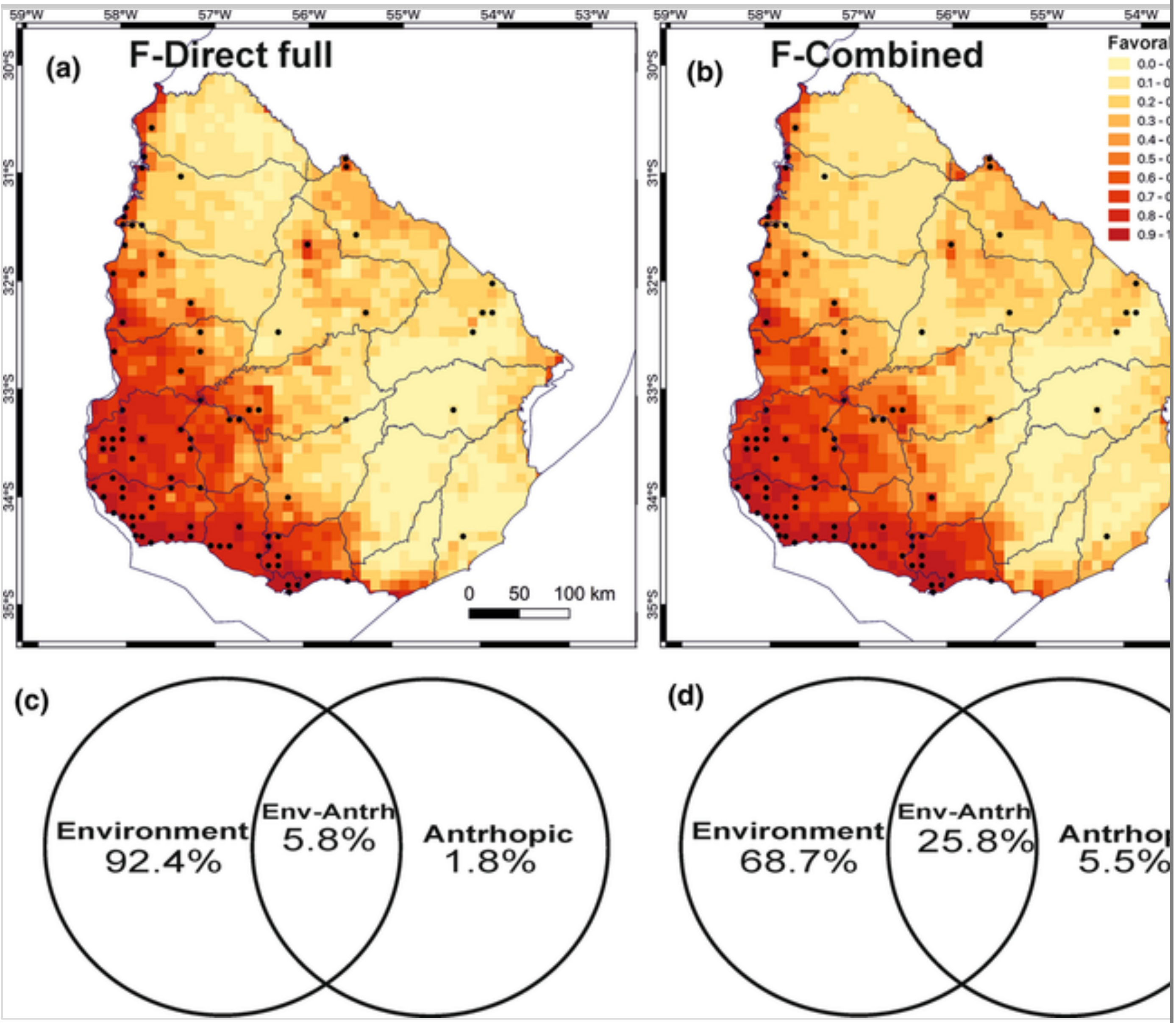


Fig. 4

F-Direct full and F-Combined models. We showed (**a** and **b**) the geographical favorability models with points of *G. triacanthos* presences in black, and (**c** and **d**) the variation partitioning of each one showed the proportion of invasion explained by each of both factors—environmental characteristic and anthropic effect—separately, and by their shared effects (interactions between both factors)



There was no explicit spatial structure in the trend surface nor in the explanatory factors. According to the Wald test values, occurrence of frost days, proportion of rocky soil, and proportion of urban surface were the most relevant variables explaining the *G. triacanthos* distribution by the F-Direct full model (see Table 2 and Fig. 3b, c). In terms of partial factors, the occurrence of frost days, NDVI (an indicator of plant biomass productivity) and proportion of rocky soil explained the F-Environmental model; and proportion of natural fields, forest, and length of roads (in meters) were the ones that explained the F-Anthropic model (Table 2). A combination of variables for both partial models explained the species invasion according to the F-Combined model (see Table 2 and Fig. 3e, f). Therefore, in the whole model that included climatic variables, the occurrence of frost days was the most important explanatory variable.

Table 2

Predictor variables included in the direct full (F-Direct full), environmental (F-Environmental), anthropic (F-Anthropic), and combined (F-Combined) models of *Gleditsia triacanthos*

Variables	**Favorability models**			
	F-Direct full	**F-Environmental**	**F-Anthropic**	**F-Combined**
Ori-EW		4.288 (+)		
Frost	54.056 (−)	54.296 (−)		37.823 (−)
NDVI	7.238 (−)	18.871 (−)		18.470 (−)
DistRiver	4.463 (−)	3.912 (−)		
NaturalField			46.275 (−)	
Forests			21.556 (−)	
Reforested			12.247 (−)	
Wetland			7.243 (−)	
RockySoil	14.582 (−)	17.878 (−)		10.177 (−)
SumRoads			18.168 (+)	11.798 (+)
UrbGro	9.393 (+)			

Wald parameter indicates the relative importance of every variable on each model. Signs in brackets show the positive or negative relationship between favorability and the variables in the models. Variable abbreviations are included in Table 1

According to the variation partitioning, for the F-Direct full model, environmental variables explained 92% of invasion patterns observed, anthropic activity variables 2%, and the shared effect of both factors 6% (partitioning variation in Fig. 4c). For the F-Combined model, environmental variables explained 69%, anthropic activity 5.5%, and shared effect 26% (Fig. 4d).

Model assessment

All models had a high discrimination capacity (AUC > 0.75) having (AUC > 0.75) according to Hosmer and Lemeshow (2000) having a high classification capacity in terms of presences and absences (sensitivity, specificity, and CCR values were higher than 0.7, and TSS was higher than 0.4; see Table 3). Comparing the F-Direct full model with the partial ones to determine the relevance of different factors (environmental characteristics and anthropic activities), the F-Direct full model always showed higher values of discrimination and classification than the partial models, with the exception of the F-Anthropic partial model, which provided a slightly better classification of absences (Specificity = 0.815). For the partial models, all indices, with the exception of specificity, the F-Environmental partial model showed higher values for the discrimination and classification indices than the F-Anthropic one. The F-Combined model had a slightly lower value of discrimination index but had higher specificity and general classification indices, CCR and TSS. Slightly lower values for all classification and discrimination indices were obtained for the whole territory (named "Total" in Table 3), despite without diminishing the predictive capacity of the models.

Table 3

Comparative assessment of models for *G. triacanthos* according to their discrimination

Evaluation indices		**Favorability models**					
		F-Direct full		**F-Environmental**		**F-Anthropi**	
		Sampled (654)	**Total (1887)**	**Sampled (654)**	**Total (1887)**	**Sampled (654)**	**(**
Discrimination	AUC	0.881	0.835	0.874	0.827	0.857	(
Classification	Sensitivity	0.828	0.827	0.816	0.816	0.747	(
	Specificity	0.811	0.731	0.809	0.718	0.815	(
	CCR	0.813	0.735	0.810	0.722	0.806	(

	TSS	0.634	0.559	0.626	0.534	0.562	(

Finally, “Sampled” indicates the evaluation indices for the trained model, and “Tota to the total territory. The number of grids involved in each case is shown in bracket

AUC area under the ROC (receiving operating characteristic) curve; *CCR* correct cl skill statistic

Finally, we did not find residuals spatial autocorrelation invalidating our results (all Moran’s I-values n.s.).

G. triacanthos To change to italy style favorable invasion pattern

The current *G. triacanthos* distribution covered 5% (87 cells) of Uruguay (Fig. 1a). Using the intermediate favorability values ($0.2 > F < 0.8$) to denote areas that had favorable conditions for *G. triacanthos* invasion, results indicated that the F-Direct full, F-Combined, and F-Environmental models detected between 47% (884 cells) and 49% of the territory (about 900 cells) (maps and histograms in Fig. 2). Considering the highest favorability threshold ($F \geq 0.8$), these models showed that 12% (about 230 cells) of the territory had the highest invasion risk. Anyway, these territories were distributed in a large proportion in the western half of the country (maps in Figs. 2, 3, and 4). On the other hand, the F-Anthropic model classified 75% of Uruguayan territory as favorable for *G. triacanthos,* according to the intermediate favorability values threshold (1400 cells), while classifying 10% of the territory, according to $F \geq 0.8$ threshold (187 cells) (Fig. 2c). Finally, the model detected with high favorability the presences for the species in independent databases (GBIF and iNaturalist, accessed February 2021).

Discussion

In this study, we analyzed the factors involved in the invasion distribution of the honey locust tree in Uruguay to determine to what extent environmental or anthropic factors can explain the distribution of areas favorable for the expansion of this species. We use FF models and show that the most satisfactory models were those that combined environmental and human-related variables. These provided the most complete explanation of the invasion by *G. triacanthos,* even at a regional scale. From the well-known invaded territory in

Uruguay, we showed that the environmental conditions (climate and soil properties), rather than human influence, could be the main factors explaining the *G. triacanthos* invasion process. We also show that anthropic activities (as a measure of the degree of human disturbance of the territory), were most notable in their shared effect with environmental characteristics of the invaded territory. Thus, the most favorable areas for the expansion of *G. triacanthos* were those closer to already occupied territories, with available land (not occupied by natural or artificial forests), free of rocky soil, a few days of frost but accessible to human activity. The process of invasion by *G. triacanthos* is one which the species first reaches territories disturbed by anthropic activities, and then, environmental conditions enable its spread and establishment. The results also indicated that when the territory is a well-conserved natural ecosystem, the favorability for this invasive tree decreases.

Factors involved in the Gleditsia triacanthos To change to italic style invasion distribution

Our trend-surface analysis did not find a spatial structure for the current invasion pattern of *G. triacanthos* in Uruguay. This suggests that the species does not have a geographical historical origin in the country (Legendre and Legendre 1998; Nebel and Porcile 2006) and that the invasion process occurs in the expansion phase and, therefore, the species is not at environmental equilibrium (Robertson et al. 2004; Barbet-Massin et al. 2018). Different authors have pointed out the possible role of cattle in the dispersal of *G. triacanthos* seeds (Sosa et al. 2018), recommending excluding cattle farming in riparian zones in Pampean Streams in Argentina (Vilches et al. 2020). However, because there are less livestock numbers in the invaded territory in southwestern Uruguay (Achkar et al. 2016), this factor may not be a significant explanation of the current *G. triacanthos* invasion pattern in the country.

Most authors agree that climate is one of the main drivers involved in invasive species spread (Pearson and Dawson 2003; Vicente et al. 2010; Hardion et al. 2014; Cabra-Rivas 2016), but factors involved vary according to the species and the region under study (Hamilton et al. 2005). We show this for *G. triacanthos*. Nonetheless, some authors have shown that anthropic disturbance is also a key driver in the invasive process for the honey locust (Gavier-Pizzarro et al. 2010; Mazía et al. 2001; 2010); abundance of the invasive increases in territories affected by human activities (Blair 1990). In our study, our anthropic partial model clearly indicated that territories accessible to human activities (and not occupied by well-preserved natural forests or reforested areas) were the most favorable for invasion. However, in those models that integrated environmental and anthropic factors, even though some anthropic variables were always relevant, anthropic influence explained less than the environmental characteristics of the territory. This could be because the entire country is under agricultural use, especially from extensive livestock rearing practices (Dominguez et al. 2018).

Our results suggest that the invasion spread of *G. triacanthos* is mainly driven by environmental factors: frost days, the proportion of rock in the soil and the NDVI indices (Table 2; Fig. 3) in line with the biological characteristics described for the species. Different authors indicated a certain tolerance of *G. triacanthos* to frost under agricultural growing conditions (Roberts and Schnipke 1994; Calkins and Swanson 1998, in CABI), although they also detected severe winter injury in some specimens (Roberts and Schnipke 1994). Vilches et al. (2020) indicated that *G. triacanthos* grows better in disturbed sites exposed to sunlight and of milder climate. Seed emergence rate is optimal at 30 °C, but less at lower temperatures, frost days limiting seed emergence and therefore invasion in Uruguay (Burton and Bazzaz 1991). Blair (1990) has also identified rocky soils limit the development of this tree species in its native area; Marco and Páez (2000) showed that *G. triacanthos* does not colonize rocky environments, high altitude, or steep slopes. In Uruguay, Gazzano et al. (2019) has indicated that the NDVI index, which reflects plant biomass productivity, represents variability in intensification of agricultural use, the highest values being linked to areas less suitable for agriculture and, therefore, with higher natural plant biomass values. The negative relationship of the NDVI as an explanatory variable in our models could be indicating that cells inhabited by natural or artificial forests prevent, due to competition for available resources, limit establishment of *G. triacanthos* (Tognetti et al. 2019). Some authors have verified that *G. triacanthos* cannot regenerate under closed canopy (Grime and Jeffrey 1965; Tognetti et al. 2019), in shady environments of the understory nor in mature forest (Mazía et al. 2001). Given these findings, frost days and NDVI could affect survival of *G. triacanthos* in its early stages, thus, affecting the invasion in Uruguay, as Sosa et al. (2018) found locally.

Finally, the anthropic variables in the combined models indicated that territories with the environment disturbed favor to the establishment and development of this invasive plant (Blair 1990; Mazía et al. 2010; Chaneton et al. 2012; Liu et al. 2017; Fernández et al. 2017). Although urban activities explain part of the invasion pattern of the species in Uruguay, both the Wald index and the partition of variation highlighted the greater effect of environmental characteristics in the invasion of *G. triacanthos* in the country.

Gleditsia triacanthos To change to italic style favorability models and prevention measures

Local adaptation to subtropical climates and the seedling plasticity of this species (Csurhes and Kriticos 1994; Tognetti et al. 2019), will favor its expansion into those cells detected as highly favorable near already occupied territories. Currently, occupied and favorable territories of the species are concentrated in the western half of the country. So far, only 5% of the Uruguayan territory is occupied by the honey locust (Echeverría 2016, MGAP), but all our models predict that at least 12% of the country offers favorable conditions for the species. Assuming that the species could expand into those cells identified as favorable by the models, we predict that the territory occupied by the species could increase two to six times more in the near future to its current extension, according to the minimum or maximum risk of a favorable invasion that is considered. On the other hand, climate change models have projected a decrease or disappearance in the number of frost days in Uruguay (Burton and Bazzaz 1991; Picasso et al. 2013), suggesting that favorable areas for *G. triacanthos* could increase in the near future. In addition, since dispersal by hydrochory and livestock is highly favorable in Uruguay (Henderson 2007), a high rate of spread of this species is likely, especially in the most favorable areas. The predictors that explain the current invasion pattern of honey locust in Uruguay show that, as detected for other invasive trees (Thuiller et al. 2012), in Uruguay, the invasion of *G. triacanthos* could spread to territories that are already degraded and affected by human activities (Mazía et al. 2001; Marco and Páez 2000; Chaneton et al. 2012). Monitoring of areas of the country that have favorable environmental and anthropic conditions can help in understanding the expansion of the invasive into unoccupied areas (Chaneton et al. 2012). Although seed dispersal by cattle seem does not explain the current distribution of *G. triacanthos* in Uruguay, more local studies should be carried out to detect and prevent its possible effect on invasion long-term spread.

It is widely recognized that prevention of the establishment of biological invasives is the best cost-efficient strategy (Wittenberg and Cock 2001; Pimentel 2011; Jackson 2015; Diagne et al. 2020). In this regard, favorability distribution models can be used as risk prediction maps that can help monitoring and control efforts. Favorability models should be used to locate those cells where different measures should be applied, i.e., prevention, control, or eradication (Paneta 2007), as well as avoid and control negative effects on community structure where the species is already established (Sosa et al. 2018; Vilches et al. 2020). We, therefore, recommend prevention measures to be implemented in highly favorable cells. These areas are unoccupied or lower numbers of the species, particularly in cells close to invaded territories, in disturbed landscapes (of low NDVI) accessible to anthropic activities along roads. More drastic control measures, such as felling of trees and/or the application of herbicides (Di Marzio et al. 2009; Sosa et al. 2015), in inhabited cells and in cells around already established favorable nuclei in the south and north of the western half of the country.

Conclusion

Our research has shown that the integration of hypotheses can generate best-fitting models to better explain the invasion of *G. triacanthos* at the regional scale. We found that the environmental conditions (climate and soil properties) as well as anthropic activities (a measure of human disturbance) in a territory were the key factors explaining the current invasion situation of *G. triacanthos* in Uruguay. The results of our models suggest that when the territory contains well-conserved natural ecosystems, the favorability for this invasive tree is lowest. Finally, predictions of our favorability models can be used as a preventive tool for the early detection of new cases, or new foci of invasion. More specifically, we suggest focusing prevention efforts in territories that are favorable and unoccupied at the same time increasing control measures in the neighboring cells of occupied areas without rocky soils and disturbed. Our results can provide a biogeographical zonation of an invaded territory so as to increase the efficiency for the control of *G. triacanthos.*

Finally, irrespective of the specific origin of the populations of *G. triacanthos* that started the invasive process in Uruguay and taking into account the plasticity described of the species, the conditions detected for Uruguay could be in part local adaptations of the invasive process of this species to the territory invaded in Uruguay. So comparative analysis of native area and invaded area on a large scale as well as genetics analysis of these populations would be a priority in order to understand the biogeography history of this invasive process.

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Publisher's Note

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Declarations

Conflict of interest The authors declare that they have no competing interests.

Supplementary Information

Below is the link to the electronic supplementary material.

Supplementary file1 (PDF 503 kb)

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