Austral ECOLOGY A Journal of ecology in the Southern Hemisphere

Austral Ecology (2022) **0**, 1–10

Invasion determinants of honey locust in agroecosystems of the Rolling Pampa, Argentina

JUAN S. GUIDOBONO,[1] LAURA M. CALFAYAN,[1] ANA FAGGI[1,2] AND MARÍA BUSCH[1]

[1]*Instituto de Ecología, Genética y Evolución de Buenos Aires (IEGEBA), CONICET – Universidad de Buenos Aires, Intendente Güiraldes 2160, Pabellón II, 4° piso, Ciudad Universitaria, Cuidad Autónoma de Buenos Aires, C1428EGA, Argentina (Email: jsguidobono@ege.fcen.uba.ar); and* [2]*Facultad de Ingeniería, Universidad de Flores, Buenos Aires, Argentina*

Abstract The honey locust (*Gleditsia triacanthos*) is one of the most aggressive tree invaders of savannas and grasslands worldwide. The objective of the study was to determine whether landscape elements could act as potential determinants on honey locust invasion of woodlots of an agricultural matrix of the Pampean ecoregion. Specifically, we assessed the effect of distance to the previously established woodlots, to corridors such as riparian habitats, railway terraces and roads, and the presence of livestock and land use through generalized linear models. The study was carried out in a rural area of the Exaltación de la Cruz Department of the Buenos Aires Province (34°19' S and 59°14' W), located in the Pampean ecoregion, in the Rolling Pampa complex, Argentina. In each woodlot, the presence or absence of honey locust and the number of individuals intercepted along line transects were recorded. Furthermore, the presence of cattle and the land use around the woodlot were registered. All woodlots were geo-positioned to calculate distances to landscape elements of interest. According to our results, the colonization capacity and the abundance of honey locust increases as distance to the nearest woodlot with the presence of the species decreases, suggesting that propagule pressure is a key factor for honey locust invasion. Also, cattle promote the increase in the abundance of the species in woodlots of the agricultural system studied. The probability of presence was also increased with the proximity to main roads and decreased with the proximity to the nearest human settlement. Our results highlight the importance of reducing the abundance of the species in invaded woodlots and cattle pathways and in case of moving animals from an invaded to a non-invaded area. It is also recommended to maintain animals in quarantine before transporting them in order to allow animals to eliminate honey locust seeds.

Key words: agroecosystems, bovine cattle, *Gleditsia triacanthos*, invasive woody plants, landscape elements.

INTRODUCTION

Biological invasions are viewed as a significant component of global change (Vitousek *et al.* 1996), and their impact on communities and ecosystems has been widely recognized for decades (Sakai *et al.* 2001; Vitousek *et al.* 1996). Nowadays, according to IUCN (2000) biological invasions are one of the main causes of global biodiversity loss. Among the negative consequences of biological invasions, displacement of native species, changes in processes such as water and nutrient cycles, changes in the frequency, intensity and type of disturbance, as well as impacts on human health and economic costs have been highlighted (Mack and D'Antonio 1998; Sakai *et al.* 2001; Vilà *et al.* 2011; Vitousek *et al.* 1997). Biological invasions could not be approached exclusively as ecological processes, because they often result from the interplay of biological and anthropogenic mechanisms. Human interference may not be ignored since human activity is a relevant driver for invasion processes, especially through the initial introductions of many alien species that act as an obligatory switchpoint for the invasions that follow (Kowarik 2003). In plant communities, invasions from alien plant species are often triggered by changes in land use patterns (Vitousek *et al.* 1997).

Changes in disturbance regimes and resource abundance have been considered central for the establishment and spread of woody species within grassland matrices, and changes in climate, CO_2 concentration, livestock grazing and fire frequency have been the particular proposed drivers (Briggs *et al.* 2002). In the Pampean grasslands, many human activities, such as zero tillage agriculture, livestock husbandry and forestry, have produced several changes that favoured the establishment and invasion

*Corresponding author.

Accepted for publication January 2022.

doi:10.1111/aec.13150

of exotic woody species, whose success was associated with the release of resources generated by the disturbance regime, which relax the competition with grasses (Ghersa *et al.* 2002; Mazía *et al.* 2010; Zalba and Villamil 2002). Invasive woody plants have increased significantly in abundance in the last 100 years in savannas and grasslands worldwide (Briggs *et al.* 2002), and nowadays the landscape of the Pampean grassland includes woodlots of exotic and native species (Matteucci 2012), with many tree species encroaching corridors of natural remnant grassland, as borders of roads, streams and railways, as well as abandoned houses, silos and stockyards (Ghersa *et al.* 2002; Ghersa and León 1999). In these marginal areas, the absence of agricultural activities and the dispersal of seeds by cattle, birds and foxes facilitate the establishment of exotic and native tree species (Ghersa *et al.* 2002; Ghersa and León 1999; Muschetto *et al.* 2015).

Among plant families, the Fabaceae have a high number of invasive woody species and honey locust (*Gleditsia triacanthos*) is considered a common invader in abandoned fields (Burton and Bazzaz 1991; Fernandez *et al.* 2017; Schnabel and Hamrick 1995) and areas with anthropogenic land use changes, such as pasture clearance and road construction (Blair 1990; Fernandez *et al.* 2017). This species is native from East and Central United States (Marco and Páez 2000) and currently is an invasive species in Argentina, Uruguay, Spain, Australia, South Africa and in several countries of Central and Eastern Europe (Fernandez *et al.* 2017). The invasion of honey locust has been probably supported by its adaptation to temperate and subtropical climates and its tolerance of high temperatures and drought (Fernandez *et al.* 2017). The invasiveness of the species was associated with the absence of natural enemies, propagule pressure, disturbance and abandonment of fields as well as road, railway and riparian corridors, and the spread by waterbodies and by cattle pods ingestion (Fernandez *et al.* 2017; Ghersa *et al.* 2002; Leggieri 2010). Additionally, its expansion is also improved by the increment of germinability produced by factors such as mechanical scarification of seeds by soil particles, water and wind erosion, temperature changes and the chemical scarification produced by the passage of seeds through the digestive tract of native and domestic fauna (Blair 1990; Ferreras and Galetto 2010), as well as being stimulated by fire (Moreschi *et al.* 2019). While it was suggested that honey locust does not have a negative impact on biodiversity in Central and Eastern Europe, in Australia and Uruguay this species competes with pastures, replaces native vegetation, obstructs water access and hurts livestock as a result of its spines (Fernández *et al.*, 2017). In the Pampean region, woody invasion is transforming grasslands at a level in which they cannot be restored without human intervention (Ghersa *et al.* 2002), with the loss of many native grasses. In north-western Buenos Aires, honey locust is invading woodlots of *Celtis tala*, a native tree that forms xeric forests named 'talares' (Delucchi and Torres Robles 2006), as well as other woodlots of native and naturalized species, as 'ombú', and Humboldt's willow (*Salix humboldtiana)*.

Previous research has focussed on the relation between landscape elements and honey locust invasion (*e.g.* Ghersa *et al.* 2002; Leggieri 2010). However, to the best of our knowledge, these studies were mainly focussed on areas invaded by honey locust such as roads or riparian habitats. This approach does not allow to detect the differential effect of landscape elements on honey locust invasion. Consequently, our objective was to determine whether landscape elements could act as potential determinants (being pathways in the case of geographic elements, or drivers in case of cattle or land use effects) on honey locust invasion in a rural matrix. Specifically, we want to assess whether the distances to some landscape elements were associated with the colonization capacity and with the changes in abundance of honey locust.

The hypotheses being tested were:

1. The colonization of new areas and the abundance of honey locust are enhanced by the proximity to previously encroached woodlots and the proximity to corridors as riparian habitats, railway terraces and roads.
2. The colonization capacity and the abundance of honey locust are enhanced by cattle pods ingestion.
3. The colonization of new areas and the abundance of honey locust are enhanced by the proximity to human settlements.

MATERIALS AND METHODS

Study site

The study was carried out in an area of 213.2 km^2 with its centre located in the town of Diego Gaynor, Exaltación de la Cruz Department (34°19' S and 59°14' W), Buenos Aires Province, Argentina. This area was selected due to the presence of honey locust and different landscape elements that may be related to its presence, as well as to the accessibility to woodlots that were placed in private lands. The area is located in the Pampean ecoregion, in the Rolling Pampa complex, which includes part of Buenos Aires, Córdoba and Santa Fe provinces, within banks of La Plata and Paraná rivers at north-east, Salado river and Matanza river at south-east (Matteucci 2012). This region presents a highly undulating topography in comparison with other neighbour areas, forming an exoreic drain system (Bilenca and Miñarro 2004). Climate is temperate oceanic, with monthly average temperatures between 20°C in summer and 12°C in winter (Matteucci 2012). Mean annual precipitation is about 1000–1200 mm in the north-east and of 800–900 mm in the south-west, with high inter-annual variability and is slightly higher in summer and autumn than in winter (Matteucci 2012). Nevertheless, water deficit may occur during summer, due to a high evaporation rate (Bilenca and Miñarro 2004).

Vegetation structure corresponds to a prairie during wet years, while in dry years it corresponds to a pseudo-steppe (Bilenca and Miñarro 2004). Currently, 90% of the land is devoted to crops, such as soybean, wheat, corn and sunflower (Guidobono *et al.* 2016; Paruelo *et al.* 2005; Viglizzo *et al.* 2001). As a result, the landscape is a matrix of crops and livestock fields, with patches of woodlots, poultry farms, small towns and grassland corridors along crop edges.

Woodlots are of about 0.5 to 2.5-ha and present exotic species such as honey locust, chinaberry tree (*Melia azedarach*), mulberry (*Morus alba*), privet (*Ligustrum* spp.), eucalyptus (*Eucalyptus* spp.), cottonwood (*Populus* spp.) and willow (*Salix* spp.), among others, but there also some native tree species such as 'tala' (*Celtis tala*), Jerusalem thorn (*Parkinsonia aculeata*) and 'ñapindá' (*Acacia bonariensis*) (Ghersa *et al.* 2002; Guidobono *et al.* 2016; Matteucci 2012).

Sampling design

We first identified woodlots in Google Earth (Google 2015) images of the area, and then we confirmed the presence of honey locust in field. Fieldworks were performed from September 2015 to March 2016, and a total of 94 woodlots were sampled and geo-referenced using a portable Garmin Etrex 30 GPS device. In each woodlot, we recorded the presence (as a proxy of their colonization) and the number of individuals intercepted along line transect. The number of transects varied in number and length according to the size and shape of each woodlot. Line transects were spaced at 10-metre intervals. The type of land use (cropfield, livestock and human settlements – small towns) in the surroundings of each woodlot and bovine cattle presence (independently of the land use – as cattle is sometimes made to pasture after crops have been harvested) were also recorded.

The following landscape variables were also taken into account: the distance to the nearest woodlot with and without the presence of honey locust, the distance to the nearest main road, the distance to the nearest secondary road, the distance to the nearest railway, the distance to the nearest human settlement (small towns), the distance to the nearest permanent watercourse (which were streams), the distance to the nearest non-permanent watercourse (courses of running water, dry except during periods of heavy rain) and the distance to the nearest flood area (Fig. 1). Shapefiles of roads, railways and human settlements were drawn using base maps from Google Earth images (Google 2019) on QGIS desktop program (3.4.3 version, QGIS Development Team 2019). Layers of the flood areas and watercourses were obtained from the National Geographic Institute of Argentina (Instituto Geográfico Nacional 2019). The distances between woodlots and landscape elements were calculated using Nearest-Neighbor Join plugging on QGIS desktop program (3.4.3 version, QGIS Development Team 2019).

Statistical analysis

We studied the association between the landscape elements with honey locust colonization and abundance per woodlot. For both analyses, an information-theoretic approach was applied for the selection of models and parameter estimators (Burnham and Anderson 2002). This approach proposes to fit all the possible candidate models based on the combination of explanatory variables, including interactions (for this purpose we used the *MuMIn* package; Bartoń 2019). The number of parameters included in each candidate model was limited by the number of cases used for each model (Burnham and Anderson 2002). The Akaike's information criterion with correction for small sample size (AICc) was used to rank the candidate models. The best model had the smallest value of AICc, but we considered that all models with AICc values smaller than that of the null model (Symonds and Moussalli 2011) and with a ΔAICc lower than 2 in relation to the best model (Richards 2005) were also supported by data. Akaike weights (*wi*) were also computed as the weights of evidence in favour of model *i* being the best model in the candidate set (Burnham and Anderson 2002). Selected models were averaged to obtain a final model using the model averaging function (*MuMIn* package; Bartoń 2019). The magnitude of the effect of explanatory variables on each response variables was assessed through their relative importance value (the sum of weights of the models where the variable was included) and through the limits of the confidence intervals of the estimators. A variable was considered to have a significant effect if the 95% confidence interval (CI_{95}) of the estimate did not include the zero. Statistical analyses were carried out using the R statistical program (R Development Core Team 2021).

In order to explain honey locust colonization, generalized linear models (GLM, using the base package *stats*; R Development Core Team 2021) with binomial error structure, a logit-link function and the Laplace approximation method (Bolker *et al.* 2009; Crawley 2012; Zuur *et al.* 2009) were used to fit all candidate models. The response variable was the presence or absence of honey locust per woodlot, and the explanatory variables were the surrounding land use, the presence of cattle (independently of the land use) and the distance to other landscape elements surveyed. As the coefficient of determination (R^2) is not suitable to judge the effectiveness of models with binary response variables (Cox and Wermuth 1992), the simplest way to express agreement between data and the model predictions is through the proportion of concordant observations, also called the index of observed agreement or simple agreement. The problem is that part of this agreement is due to chance. Therefore, it is interesting to quantify the degree of agreement beyond chance (Latour *et al.* 1997). In this sense, the most used index is the 'kappa index (k)' (e.g. Casey *et al.* 2009; Latour *et al.* 1997) proposed by Cohen (1960)

doi:10.1111/aec.13150

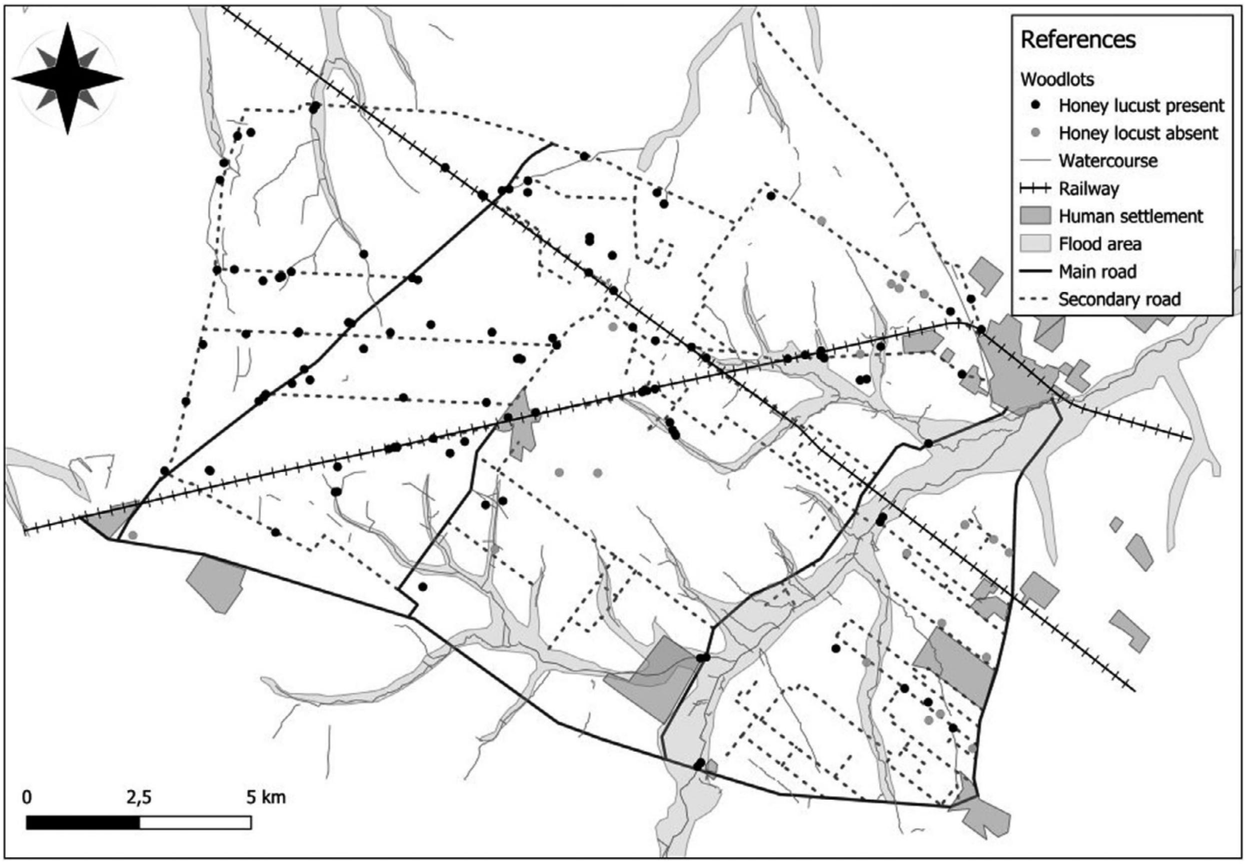

Fig. 1. Map of the sampled area showing the disposition in the terrain of the woodlots with and without honey locust presence and the different landscape variables surveyed.

considering the labels of the relative strength of agreement with data ($k < 0.00$ poor, $0.00 < k < 0.20$ slight, $0.21 < k < 0.40$ fair, $0.41 < k < 0.60$ moderate, $0.61 < k < 0.80$ substantial and $0.81 < k < 1.00$ almost perfect) designed by Landis and Koch (1977). The kappa index, the sensitivity and the specificity (two estimators associated with the kappa index) were calculated for the candidate and averaged models (using the package *presence-absence*, Freeman 2008).

In order to assess the effect of landscape variables on honey locust abundance per woodlot, we used GLM (using the package *glmmTMB*, Brooks *et al.* 2017), with a negative binomial error structure and a logarithmic-link function (Bolker *et al.* 2009; Zuur *et al.* 2009) to fit all candidate models. The models were fitted using as response variable the number of individuals per woodlot and the total length line transects per woodlot was used as offset variable. The explanatory variables were the same as in the case of honey locust presence. The explained variances of the candidate and average models were estimated by the squared correlation between the number of individuals observed per woodlot and predicted values estimated by the model (Faraway 2016).

To avoid redundancies, in both analyses the collinearity between explanatory variables was estimated by the variance inflation factor (VIF) of a saturated and additive model (Zuur *et al.* 2007). According to Fox and Weisberg (2019) and Zuur (2010), VIF < 3 indicates the absence of collinearity. For variables that showed VIF values >3, we conducted pairwise correlations using the package *psych* (Revelle 2021). If two or more variables were correlated, we removed from the analysis the variable with less biological importance.

RESULTS

Honey locust was present in 73 out of 94 woodlots (77.63%, Fig. 1). The total sampling effort was of 38633.42 linear metres of transects, with the sampling effort per woodlot varying according to its size between 8.21 and 1573.55 linear metres of transect.

The presence of honey locust was explained by 4 candidate models with AICc values lower than the null model (AICc $_{\text{null model}}$ = 110.14) and with a ΔAICc <2 with respect to the best model (AICc of the best model was 67.8, Table 1). According to the average model, variables with the highest relative importance value (RVI = 1.00) were the distance to the nearest woodlot with honey locust, the distance to the nearest main road and the distance to the nearest human settlement (Table 2). The increase in

doi:10.1111/aec.13150

distance of the nearest woodlot with the presence of the species and the increase in distance to the nearest main road had a negative effect on the probability of presence of honey locust, while the increase in distance to nearest human settlement had a positive effect. The cattle presence, the distance to main roads, the distance to woodlots without the presence of the species and the interaction between them scored to high–medium RVI values, but had no significant effect on honey locust presence given that their confidence intervals included the zero value. The distance to permanent watercourses had a low RVI and a confidence interval that includes the zero value (Table 2). Analysing the performance of the average model, the strength of agreement with data was moderate to substantial (kappa = 0.68 ± 0.09), the sensitivity was 0.93 ± 0.03 and the specificity was 0.76 ± 0.10 (Table 2). Collinearity between variables was not detected (VIF < 3 for all explanatory variables).

For the abundance of honey locust per woodlot, we decided to remove the distance to nearest human settlement (VIF = 6.91) and the distance to the nearest flood area (VIF =3.07). The correlation matrix showed that both variables were correlated with 5 of the other explanatory variables (for details see Appendix S1). To explain the changes in abundance, 14 candidate models with ΔAICc <2 with respect to

Table 1. Candidate models for honey locust presence in woodlots. Explanatory variables were: distance to the nearest woodlot with honey locust (DwHl), distance to the nearest woodlot without honey locust (Dw), cattle presence independently of the land use (Cp), distance to the nearest permanent watercourse (DPwc), distance to the nearest main road (DMrd) and distance to the nearest human settlement (Dhs). Table entries state the corresponding statistics: Kappa concordance index (value ± standard deviation), sensitivity index (value ± standard deviation), specificity index (value ± standard deviation), Akaike's information criterion corrected for small sample size (AICc), difference between AICc of the best model and the AICc of model *i* (ΔAICc) and Akaike's weights (Wi)

Model terms	Kappa	Sensitivity	Specificity	AICc	ΔAICc	Wi
DwHl+Dw + Cp + DMrd+Dhs + Cp:DMrd+Cp:Dw	0.67 ± 0.10	0.98 ± 0.02	0.62 ± 0.11	67.8	0.00	0.45
DwHl+Dw + Cp + DMrd+Dhs + Cp:Dw	0.62 ± 0.10	0.96 ± 0.02	0.62 ± 0.11	69.5	1.64	0.20
DwHl+Dw + Cp + DPwc+DMrd+Dhs + Cp:DMrd+Cp:Dw	0.65 ± 0.09	0.93 ± 0.03	0.71 ± 0.10	69.6	1.82	0.18
DwHl+DMrd+Dhs	0.62 ± 0.10	0.96 ± 0.02	0.62 ± 0.11	69.7	1.86	0.17

Null model AICc = 110.14.
Number of estimable parameters in the global model: 22.

Table 2. Average model for honey locust presence in woodlots. Explanatory variables were: distance to the nearest woodlot with honey locust (DwHl), distance to the nearest woodlot without honey locust (Dw), cattle presence independently of the land use (Cp), distance to the nearest permanent watercourse (DPwc), distance to the nearest main road (DMrd) and distance to the nearest human settlement (Dhs). Table entries state the corresponding statistics: estimators of the association with the response variable, standard error of the estimator (SE), relative variable importance (RVI), Kappa concordance index (value ± standard deviation), sensitivity index (value ± standard deviation) and specificity index (value ± standard deviation). Estimator values in bold implies an important explanatory variable (the CI95 of the estimator excluded zero)

Model Terms	Estimator	SE	RVI	CI95 – Low.-Lim	CI95 – Upp.Lim
(Intercept)	2.09	0.67		0.77	3.44
DwHl	**−2.06**	0.40	1.00	**−2.86**	**−1.28**
Dw	0.01	0.15	0.82	−0.29	0.30
Cp	−11.60	3207.00	0.82	−6828.26	6806.89
DPwc	0.14	0.13	0.18	−0.13	0.40
DMrd	**−0.88**	0.26	1.00	**−1.40**	**−0.37**
Dhs	**1.53**	0.36	1.00	**0.80**	**2.22**
Cp × DMrd	−52.20	6872.00	0.82	−13674.97	13570.67
Cp × Dw	110.20	10780.00	0.63	−22786.58	22981.03

Kappa index = 0.68 ± 0.09.
Sensitivity = 0.93 ± 0.03.
Specificity = 0.76 ± 0.10.

doi:10.1111/aec.13150

Table 3. Candidate models for honey locust abundance in woodlots. Explanatory variables were: distance to the nearest woodlot with honey locust (DwHl), distance to the nearest woodlot without honey locust (Dw), cattle presence independently of the land use (Cp), distance to the nearest permanent watercourse (DPwc), distance to the nearest non-permanent watercourse (DNwc), distance to the nearest main road (DMrd). Table entries state the corresponding statistics: squared correlation between the observed data and the predicted values (SqCor – a proxy of the explained variance), Akaike's information criterion corrected for small sample size (AICc), difference between AICc of the best model and the AICc of model *i* (ΔAICc) and Akaike's weights (Wi)

Model terms	SqCor	AICc	ΔAICc	Wi
DwHl+Cp + DNwc	0.31	613.00	0.00	0.12
DwHl+Cp + DMrd	0.23	613.26	0.26	0.10
DwHl+Cp + DNwc+DMrd	0.30	613.28	0.28	0.10
DwHl+Cp	0.23	613.56	0.56	0.09
DwHl+Cp + DNwc+Cp:DwHl	0.32	613.92	0.92	0.07
DwHl+Cp + DNwc+Cp:DNwc	0.31	613.98	0.98	0.07
DwHl+Cp + DNwc+DMrd+Cp:DwHl	0.31	614.48	1.48	0.06
DwHl+Cp + DMrd+Cp:DwHl	0.23	614.53	1.53	0.06
DwHl+Cp + DwHl:Cp	0.24	614.58	1.58	0.05
DwHl+Cp + DPwc+DMrd	0.20	614.71	1.71	0.05
DwHl+Cp + DNwc+DMrd+Cp:DNwc	0.29	614.79	1.79	0.05
DwHl+Cp + DNwc+DMrd+Cp:DwHl+Cp: DNwc	0.31	614.88	1.88	0.05
DwHl+Cp + DPwc+DNwc+DMrd	0.28	614.93	1.93	0.05
DwHl+Dw + Cp + DNwc	0.29	614.95	1.95	0.04
DwHl+Cp + DPwc+DNwc	0.30	614.98	1.98	0.04

Null model AICc = 635.53.
Number of estimable parameters in the global model: 16.

the best model were included. The AICc of the best model was 613, while the AICc of the null model was 635.53. The total variability explained account for 20% to 31% (Table 3). The average model showed the importance of the distance to the nearest woodlot with the presence of the species and the presence of cattle (RVI = 1.00 for both variables, Table 4). According to these results, the abundance of honey locust increases as distance to the nearest woodlot with the presence of the species decreases (Table 4). Secondly, the abundance of species also increases with the presence of cattle (Fig. 2). Although the RVI suggests that the distance to non-permanent watercourses had a medium importance contribution, there was not a significant effect because the confidence interval includes the zero value. The other variables showed relative importance values <0.46, and their confidence intervals included zero (Table 4).

DISCUSSION

The Pampean agroecosystems suffered great transformations that have led to the reduction in original grasslands to relict areas such as roadsides, cropfield and stream edges and woodlots, among others (Ghersa *et al.* 2002; Ghersa and León 1999). In the last years, practices as zero tillage and livestock husbandry have also facilitated the advance of invasive species such as honey locust (Ghersa *et al.* 2002; Mazia *et al.* 2001; Mazía *et al.* 2010). Consequently, our objective was to study the environmental determinants that facilitate the invasion of the species in Pampean agroecosystems. Our findings suggest that the proximity to woodlots previously colonized by honey locust facilitates not only its colonization of new areas, but also an increase in abundance after colonization. This result highlights the importance of propagule pressure as an expansion mechanism for this species (Fernandez *et al.* 2017; Mazia *et al.* 2001). Propagule pressure was recognized as a main determinant of the expansion of several woody alien species in other systems. For example, Rouget and Richardson (2003) predicted that more than 70% of the variations in the canopy cover of the woody invaders *Acacia cyclops*, *Acacia saligna* and *Pinus pinaster* in the Agulhas Plain of South Africa was associated with factors related to the propagule pressure and some other environmental determinants. Even in other regions of Argentina, as Sierra Grande Mountains of Cordoba, Giorgis *et al.* (2011) concluded that propagule pressure seems to be the main factor that favours the expansion of *Betula*

Table 4. Average model for honey locust abundance in woodlots. Explanatory variables were: distance to the nearest woodlot with honey locust (DwHl), distance to the nearest woodlot without honey locust (Dw), cattle presence independently of the land use (Cp), distance to the nearest permanent watercourse (DPwc), distance to the nearest non-permanent watercourse (DNwc), distance to the nearest main road (DMrd). Table entries state the corresponding statistics: estimators of the association with the response variable, standard error of the estimator (SE), relative variable importance (RVI), squared correlation between the observed data and the predicted values (SqCor – a proxy of the explaned variance) and the lower (CI95 – Low.-Lim) and upper (CI95 – Upp.lim) limits of the 95% confidence intervals. Estimator values in bold implies an important explanatory variable (the CI95 of the estimator excluded zero)

Model Terms	Estimator	SE	RVI	CI95 – Low.-Lim	CI95 – Upp.Lim
(Intercept)	1.87	0.29		1.26	2.47
DwHl	**−0.80**	0.19	1.00	**−1.17**	**−0.41**
Dw	0.03	0.05	0.04	−0.07	0.13
Cp	**0.79**	0.36	1.00	**0.05**	**1.57**
DPwc	0.03	0.04	0.14	−0.05	0.11
DNwc	0.36	0.23	0.65	−0.10	0.84
DMrd	−0.12	0.08	0.46	−0.28	0.04
Cp × DwHl	−0.68	0.62	0.28	−1.91	0.56
Cp × DNwc	−0.42	0.40	0.17	−1.21	0.37

SqCor = 0.30.

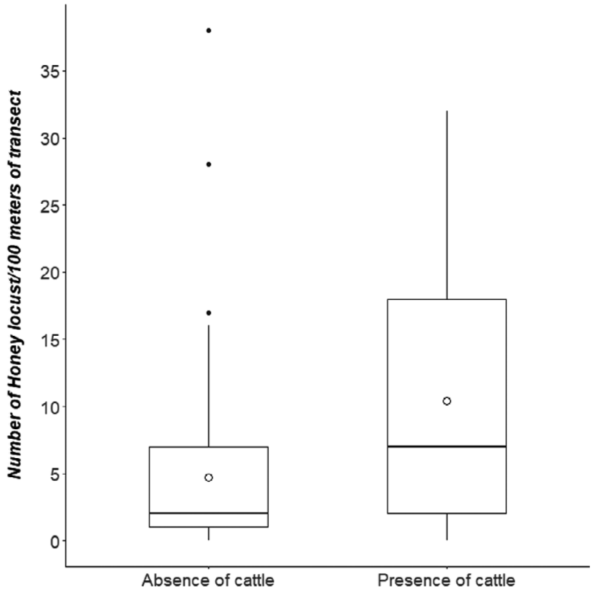

Fig. 2. Number of honey locust individuals per 100 metre of linear transect in woodlots with or without the presence of cattle independently of the land use. Inside boxplots, the white points correspond to the mean values and black lines to the median value. Black point outside boxplots represents outliers.

pendula, *Morus alba*, *Rosa* spp., as well as other woody alien species.

We expected that livestock enhances colonization and increases the abundance of honey locust, mainly by the dispersion of seeds and the facilitation of germination (Blair 1990; Ferreras and Galetto 2010). In both models, the cattle presence had a high RVI, but we only detected a significant effect on abundance. The inclusion of the zero in the confidence intervals in the colonization model may have been the result of the high standard errors of the estimates for the main effect and their interactions (see Table 2). In this context, our findings confirm the role of cattle promoting honey locust invasion.

Another factor that contributed to explain the colonization capacity of honey locust was the proximity to main roads, which may be associated with households of farmers, which usually are placed near main roads but far from human settlements. According to the bibliography, the honey locust was introduced in the Pampean ecoregion mainly as living hedge and as a source of timber, shade or shelter beds (Hudson *et al.* 1918; Ghersa *et al.* 2002; Tecco *et al.* 2016; Zalba and Villamil 2002). Furthermore, the ornamental use of honey locust was also recognized as the first step of its introduction in Europe (Doroftei *et al.* 2009; Dana *et al.* 2001; Glišić *et al.* 2014), Australia (Csurhes and Kriticos 1994) and Uruguay (Nebel and Porcile 2006), among others. Although in such cases humans may have promoted the establishment of honey locust, near urban areas it was not abundant, mainly because other species, such as eucalyptus (*Eucalyptus* spp.), silk-floss tree (*Ceiba speciosa*), 'ceibo' (*Erythrina crista-galli*) and 'ombú' (*Phytolacca dioica*), are preferred for ornamental purposes and as sources of shade (personal observation).

The results of this study showed that in our system the expansion of honey locust occurs from previously established foci, with cattle enhancing the process of invasion. Considering that around 77% of the surveyed woodlots is already invaded, it is clear that

doi:10.1111/aec.13150

honey locust is an aggressive invader and a considerable threat to grasslands and native species and the Rolling Pampas physiognomy (Fernandez *et al*. 2017; Ghersa *et al*. 2002) which requires urgent efforts. These conclusions could be important to other regions in which honey locust is used as fodder and as an ornamental tree, and where the species became invasive, as Europe, Australia and other South American countries as Uruguay (Csurhes 2004; Nebel and Porcile 2006; Krumm and Vítková 2016). In order to restrict honey locust expansion, it is recommended to reduce the abundance of the species (adults, saplings and seeds) in invaded woodlots and cattle pathways and, in case of moving animals from an invaded to a non-invaded area, we recommend to maintain animals in quarantine before transporting them in order to allow animals to eliminate honey locust seeds.

ACKNOWLEDGEMENT

We appreciate the collaboration of BSc. Esteban Nicolás Rodofili in the field work and his suggestions for data analysis and writing of this manuscript. This work was supported by Universidad de Buenos Aires (UBACYT X027) and Consejo Nacional de Investigaciones Científicas y Tecnológicas (PIP 1410) grants.

AUTHOR CONTRIBUTIONS

Juan Santiago Guidobono: Conceptualization (equal); data curation (equal); formal analysis (equal); investigation (equal); methodology (equal); project administration (equal). **Laura M. Calfayan:** Data curation (equal); formal analysis (equal). **Ana Faggi:** Conceptualization (equal); methodology (equal). **María Busch:** Conceptualization (equal); funding acquisition (lead); investigation (equal); methodology (equal); project administration (equal).

FUNDING

This study was funded by Universidad de Buenos Aires (UBACYT X027) and Consejo Nacional de Investigaciones Científicas y Tecnológicas (PIP 1410) grants.

CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

REFERENCES

Bartoń K. (2019) MuMIn: Multi-Model Inference. R package version 1.43.17. CRAN mirror. Retrieved from https://CRAN.R-project.org/package=MuMIn. Accessed 29 January 2019.

Bilenca D. N. & Miñarro F. (2004) *Identificación de áreas valiosas de pastizal (AVP) en las Pampas y campos de Argentina, Uruguay y sur de Brasil*. Fundación Vida Silvestre, Buenos Aires, Argentina.

Blair R. M. (1990) *Gleditsia triacanthos* L. (Honey locust). In: *Hardwoods Agriculture Handbook* (eds R. M. Burns & B. H. Honkala) pp. 358–64. Tech. Coords. Silvics. of North America. USDA Forest Service, Washington, DC.

Bolker B. M., Brooks M. E., Clark C. J. *et al.* (2009) Generalized linear mixed models: a practical guide for ecology and evolution. *Trends Ecol. Evol.* **24,** 127–35.

Briggs J. M., Knapp A. K. & Brock B. L. (2002) Expansion of woody plants in tallgrass prairie: a fifteen-year study of fire and fire-grazing interactions. *Am. Midl. Nat.* **147,** 287–94.

Brooks M. E., Kristensen K., van Benthem K. J. *et al.* (2017) glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. *R J.* **9,** 378–400.

Burnham K. P. & Anderson D. R. (2002) *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*, 2da edn. Springer, New York.

Burton P. J. & Bazzaz F. A. (1991) Tree seedling emergence on interactive temperature and moisture gradients and in patches of old-field vegetation. *Am. J. Bot.* **78,** 131–49.

Casey P., Altobelli G. & PignatelliLLI P. (2009) Application of the hypothesis analysis method using Cohen's kappa index to measure the agreement between leather sorters. *J. Soc. Leather Technol. Chem.* **94,** 144–8.

Cohen J. (1960) A coefficient of agreement for nominal scales. *Educ. Psychosoc. Meas.* **20,** 37–46.

Cox D. R. & Wermuth N. (1992) A comment on the coefficient of determination for binary responses. *Am. Stat.* **46,** 1–4.

Crawley M. J. (2012) Generalized linear models. In: *The R Book*, pp. 511–26. Wiley, Chichester, UK.

Csurhes S. M. (2004) Successful control of honey locust trees (*Gleditsia triacanthos* L.) in Queensland. *Weed Manag. Balanc. people, planet, profit. 14th Aust. Weeds Conf. Wagga Wagga, New South Wales, Aust. 6-9 Sept. 2004 Pap. Proc.*, 673–675.

Csurhes S. M. & Kriticos D. (1994) *Gleditsia triacanthos* L. (Caesalpiniaceae), another thorny, exotic fodder tree gone wild [honey locust; Queensland; New South Wales]. *Plant Prot. Q.* **9,** 101–5.

Dana E., Cerrillo M. I., Sanz E. M., Sobrino E. & Mota J. F. (2001) Contribución al conocimiento de las xenófitas en España: Catálogo provisional de la flora alóctona de Almería. *Acta Bot. Malacit.* **26,** 264–76.

Delucchi G. & Torres Robles S. S. (2006) Las especies vegetales invasoras en los talares bonaerenses. In: *Talares Bonaerenses y su Conservación* (eds E. Márida & J. Athor) pp. 146–65. Fundación de HIstaria Naturañ "Feliz de Azara" – Vázquez Mazzini Editores, Buenos Aires, Argentina.

Doroftei M., Mierlă M. & Marinov M. (2009) Ecology of some alien plant species in Danube Delta. *"Ovidius" Univ. Ann. Nat. Sci. Biol. – Ecol. Ser.* **9,** 1–4.

doi:10.1111/aec.13150

Faraway J. (2016) *Extending the Linear Model with R*. Chapman and Hall/CRC, New York.

Fernandez R. D., Ceballos S. J., Malizia A. & Aragón R. (2017) Gleditsia triacanthos (Fabaceae) in Argentina: a review of its invasion. *Aust. J. Bot.* **65,** 203–13.

Ferreras A. E. & Galetto L. (2010) From seed production to seedling establishment: Important steps in an invasive process. *Acta Oecologica* **36,** 211–8.

Fox J. & Weisberg S. (2019) *An R Companion to Applied Regression*, 3rd edn. Sage, Thousand Oask, CA.

Freeman E. (2008) PresenceAbsence package: An R package for presence-absence model analysis. *J. Stat. Softw.* **23,** 1–31.

Ghersa C. M., de la Fuente E., Suarez S. & Leon R. J. C. (2002) Woody species invasion in the Rolling Pampa grasslands, Argentina. *Agric. Ecosyst. Environ.* **88,** 271–8.

Ghersa C. M. & León R. J. C. (1999) Landscape changes induced by human activities in the rolling pampas grassland. In: *Proceedings of the VI International Rangeland Congress, Vol 2* pp. 624–628. Queensland, Australia.

Giorgis M. A., Tecco P. A., Cingolani A. M., Renison D., Marcora P. & Paiaro V. (2011) Factors associated with woody alien species distribution in a newly invaded mountain system of central Argentina. *Biol. Invasions* **13,** 1423–34.

Glišić M., Lakušić D., Šinžar-Sekulić J. & Jovanović S. (2014) GIS analysis of spatial distribution of invasive tree species in the protected natural area of Mt. Avala (Serbia). *Bot. Serbica* **38,** 131–8.

Google (2015) Google Earth Pro. Retrieved from https://www.google.com/intl/es/earth/desktop/. Accessed 1 April 2015.

Guidobono J. S., Muñoz J., Muschetto E., Teta P. & Busch M. (2016) Food habits of Geoffroy's cat (Leopardus geoffroyi) in agroecosystem habitats of Buenos Aires, Argentina. *Ecol. Austral* **26,** 40–50.

Hudson W. H., Graham R. B. C., Pozzo F., de Pozzo C. R. & Mosca F. (1918) Allá lejos y hace tiempo. 185.

Instituto Geográfico Nacional (2019) Capas SIG. Retrieved from http://www.ign.gob.ar/NuestrasActividades/InformacionGeoespacial/CapasSIG. Accessed 29 January 2019.

IUCN (2000) *Biodiversity, IUCN Guidelines for the Prevention of Species, Loss Caused by Alien Invasive*. IUCN, Gland Switzerland.

Kowarik I. (2003) Human agency in biological invasions: secondary releases foster naturalisation and population expansion of alien plant species. *Biol. Invasions* **5,** 293–312.

Krumm F. & Vítková L., eds (2016) *Introduced Tree Species in European Forests: Opportunities and Challenges*. European Forest Institute, Freiburg, Germany.

Landis J. R. & Koch G. G. (1977) The measurement of observer agreement for categorical data. *Biometrics* **33,** 159–74.

Latour J., Abraira V., Cabello J. B. & López S. J. (1997) Las mediciones clínicas en cardiología: validez y errores de medición. *Rev. Española Cardiol.* **50,** 117–28.

Leggieri L. R. (2010) Invasión de *Gleditsia triacanthos* en los corredores de los sistemas fluviales de la Pampa Ondulada y su efecto sobre la distribución de Myocastor coypus. *Ecol. Austral.* **20,** 185–99.

Mack M. C. & D'Antonio C. M. (1998) Impacts of biological invasions on disturbance regimes. *Trends Ecol. Evol.* **13,** 195–8.

Marco D. E. & Páez S. A. (2000) Invasion of *Gleditsia triacanthos* in Lithraea ternifolia montane forests of central Argentina. *Environ. Manag.* **26,** 409–19.

Matteucci S. D. (2012) Ecorregión pampa. In: *Ecorregiones y Complejos Ecosistémicos Argentinos* (eds J. Morello, S. D. Matteucci, A. F. Rodríguez & M. Silva) pp. 391–445. Ortientación gráfica S.R.L, Buenos Aires.

Mazía C. N., Chaneton E. J., Machera M., Uchitel A., Feler M. V. & Ghersa C. M. (2010) Antagonistic effects of large- and small-scale disturbances on exotic tree invasion in a native tussock grassland relict. *Biol. Invasions* **12,** 3109–22.

Mazia N. C., Chaneton E. J., Ghersa C. M. & León R. J. (2001) Limits to tree species invasion in pampean grassland and forest plant communities. *Oecologia* **128,** 594–602.

Moreschi E. G., Funes G., Zeballos S. R. & Tecco P. A. (2019) Post-burning germination responses of woody invaders in a fire-prone ecosystem. *Austral Ecol.* **44,** 1163–73.

Muschetto E., Mazia N., Cueto G. R. & Busch M. (2015) Are rodents a source of biotic resistance to tree invasion in Pampean grasslands? Tree seed consumption under different conditions. *Austral Ecol.* **40,** 255–66.

Nebel J. & Porcile J. (2006) *La Contaminación del Bosque Nativo por Especies Arbóreas y Arbustivas Exóticas*. Departamento de bosque nativo, manejo y protección forestal, Uruguay. Available from: http://www.guayubira.org.uy/monte/Contaminacion_monte_nativo_exoticas.pdf. Accessed 15 April 2019.

Paruelo J. M., Guerschman J. P. & Verón S. R. (2005) Expansión agrícola y cambios en el uso del suelo. *Cienc. Hoy.* **15,** 14–23.

QGIS Development Team (2019) QGIS geographic information system. Available from: https://qgis.org.

R Development Core Team (2021) *R: A Language and Environment for Statistical Computing*. CRAN mirror. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/. Accessed 6 September 2021.

Revelle W. (2021) psych: Procedures for Personality and Psychological Research. R package version 2.1.9. CRAN mirror. Northwestern University, Evanston, IL. Retrieved from https://CRAN.R-project.org/package=psych. Accessed 6 September 2021.

Richards S. A. (2005) Testing ecological theory using the information-theoretic approach: Examples and Cautionary results. *Ecology* **86,** 2805–14.

Rouget M. & Richardson D. M. (2003) Inferring process from pattern in plant invasions: A semimechanistic model incorporating propagule pressure and environmental factors. *Am. Nat.* **162,** 713–24.

Sakai A. K., Allendorf F. W., Holt J. S. *et al.* (2001) The population biology of invasive species. *Annu. Rev. Ecol. Syst.* **32,** 305–32.

Schnabel A. & Hamrick J. L. (1995) Understanding the population genetic structure of *Gleditsia triacanthos* L.: the scale and pattern of pollen gene flow. *Evolution (N.Y.)* **49,** 921–31.

Symonds M. R. E. & Moussalli A. (2011) A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. *Behav. Ecol. Sociobiol.* **65,** 13–21.

Tecco P. A., Pais-Bosch A. I., Funes G. *et al.* (2016) Mountain invasions on the way: are there climatic constraints for the expansion of alien woody species along

doi:10.1111/aec.13150

an elevation gradient in Argentina? *J. Plant Ecol.* **9,** 380–92.

Viglizzo E. F., Lértora F., Pordomingo A. J., Bernardos J. N., Roberto Z. E. & Del Valle H. (2001) Ecological lessons and applications from one century of low external-input farming in the pampas of Argentina. *Agric. Ecosyst. Environ.* **83,** 65–81.

Vilà M., Espinar J. L., Hejda M. *et al.* (2011) Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. *Ecol. Lett.* **14,** 702–8.

Vitousek P. M., D'Antonio C. M., Loope L. L., Rejmánek M. & Westbrooks R. (1997) Introduced species: A significant component of human-caused global change. *N. Z. J. Ecol.* **21,** 1–16.

Vitousek P. M., D'Antonio C. M., Loope L. L. & Westbrooks R. (1996) Biological invasions as global environmental change. *Am. Sci.* **84,** 468–79.

Zalba S. M. & Villamil C. B. (2002) Woody plant invasion in relictual grasslands. *Biol. Invasions* **4,** 55–72.

Zuur A. F., Ieno E. N. & Elphick C. S. (2010) A protocol for data exploration to avoid common statistical problems. *Methods Ecol. Evol.* **1,** 3–14.

Zuur A. F., Ieno E. N. & Smith G. M. (2007) *Analysing Ecological Data*. Springer Science+business Media, LLC, New York, NY.

Zuur A. F., Ieno E. N., Walker N. J., Saveliev A. A. & Smith G. M. (2009) *Mixed Effects Models and Extension in Ecology with R*. Springer Science+business Media, LLc, New York, NY.

SUPPORTING INFORMATION

Additional supporting information may/can be found online in the supporting information tab for this article.

Appendix S1. Correlation matrix of continuous environmental variables: Distance to the nearest woodlot with Honey locust (DwHl), Distance to the nearest woodlot without Honey locust (Dw), the distance to the nearest railway (Drw), distance to the nearest flood area (Dfa), distance to nearest human settlement (Dhs), Distance to the nearest main road (DMrd), the distance to the nearest secondary road (DSrd), Distance to nearest permanent watercourse (DPwc), Distance to nearest not permanent watercourse (DNwc).

doi:10.1111/aec.13150