

## *Gleditsia triacanthos* (Fabaceae) in Argentina: a review of its invasion

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**Abstract.** *Gleditsia triacanthos* L. is a woody species native to North America that has invaded Uruguay, Spain, Australia, South Africa and several countries of Central and Eastern Europe. In Argentina, it has become one of the most important invasive woody species and has a high potential to continue spreading. In this study, we review different aspects of *G. triacanthos* invasion in Argentina that include descriptions of invaded ecoregions and environments, intrinsic characteristics of the species, invasion dynamics and impacts. In addition, we discuss mechanisms that potentially explain its success, control strategies and natural barriers to its invasion. We reviewed a total of 91 articles and book chapters, of which 62 were developed in Argentina. Studies reported that the invasion of *G. triacanthos* in different ecoregions was favoured by intrinsic characteristics of the species, together with the interaction with cattle and disturbances, which cause negative impacts on flora, fauna and ecosystem processes. Disturbances were proposed as the main mechanism to explain this species' invasion, but other hypotheses such as the release of natural enemies and/or propagule pressure might also be important. Further studies are required, mainly on the impacts on ecosystem processes and on the control, production of organic compounds and mutualistic interactions (with nitrogen-fixing bacteria and mycorrhizal fungi).

**Additional keywords:** dry chaco, espinal, exotic plants, invasiveness, pampean grasslands, subtropical mountain forests.

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### Introduction

Exotic plant species are those whose presence in a given area is due to intentional or accidental introduction because of human activity (Richardson *et al.* 2000). These species become invaders when they produce reproductive offspring, often in very large numbers and with the potential to spread over an extensive area (Richardson *et al.* 2000). Invasive exotic plants can modify water and nutrient cycles, the frequency, intensity and type of disturbances, and can displace native species (Vitousek *et al.* 1997; Mack and D'Antonio 1998; Rejmánek 1999; Ehrenfeld 2003; Vilà *et al.* 2011). Nowadays, biological invasions are considered the second most important cause of global biodiversity loss, with consequences for both ecosystem services provision, and human well being (IUCN 2000).

The Fabaceae family is considered one of the families with the highest number of invasive woody species (Binggeli 1996; Rodríguez-Echeverría 2009; Richardson and Rejmánek 2011). Many species of this family were introduced because they are fast growing species, are adapted to degraded sites, and in many cases can fix nitrogen and improve soil conditions (Hughes

and Styles 1987; Rodríguez-Echeverría 2009). For example, several *Acacia* species were introduced for sand and slope stabilisation, wind protection, fodder, shade, forestry and ornamental purposes (Paynter *et al.* 2003; Crisóstomo *et al.* 2013). However, such introductions have not always been beneficial (Hughes and Styles 1987), and in many cases led to invasion of ecosystems.

*Gleditsia triacanthos* L. (honey locust, Fabaceae) is a deciduous tree species, native of the United States and Canada (USDA 2016) and is considered a common invader in abandoned fields (Burton and Bazzaz 1991; Schnabel and Hamrick 1995). It has a wide natural range and its abundance frequently increases with anthropogenic land use change, such as pasture clearance and road construction (Blair 1990). In addition, this species grows in steep, rocky slopes, grasslands and humid forests (Schnabel *et al.* 1998), which illustrates the wide range of suitable environments for its spreading.

*Gleditsia triacanthos* is currently an invasive species in Argentina, Uruguay, Spain, Australia, South Africa and in several countries of Central and Eastern Europe (Henderson 1991; Csurhes and Kriticos 1994; Dana *et al.* 2001; Nebel and

Porcile 2006; Sudnik-Wójcikowska *et al.* 2006; Doroftei *et al.* 2009; Piaggio and Delfino 2009; Nikolić *et al.* 2010; Blanco *et al.* 2012; Ferus *et al.* 2013; Glišić *et al.* 2014). The invasion of this species in abandoned fields, flooded plains, forest edges, and road margins (Csurhes and Kriticos 1994; Paynter *et al.* 2003; Glišić *et al.* 2014) was probably favoured by its adaptation to temperate and subtropical climates (Csurhes and Kriticos 1994) and its tolerance of high temperatures and drought (Burton and Bazzaz 1991; Graves *et al.* 1991; Graves and Wilkins 1991; Godoy *et al.* 2011). Most of the studies about its impacts and control strategies are from Australia and Argentina (Zalba and Villamil 2002; Csurhes 2004). Stimm and Heinrichs (2015) suggest that *G. triacanthos* causes no negative impact on biodiversity in Central and Eastern Europe, whereas studies in Australia and Uruguay mention that this species can compete with pastures, replace native vegetation, obstruct water access and hurt the livestock with its spines (Csurhes and Kriticos 1994; Caballero 2013; Stimm and Heinrichs 2015). A successful program to eradicate *G. triacanthos* using chemical and mechanical techniques has been implemented in Queensland (Australia) (Csurhes 2004). More recently, in Uruguay, a chemical control of *G. triacanthos* was evaluated and considered effective, although long-term monitoring to evaluate the toxicity of the herbicide on the recovering native vegetation was recommended (Sosa *et al.* 2015).

In Argentina, *G. triacanthos* was introduced at the end of the 18th century, probably for ornamental purposes, shade and fencing (Prieto *et al.* 2004). It became one of the most important invasive species, with great potential to continue expanding its range (Grau and Aragón 2000; Ghersa *et al.* 2002; Giorgis *et al.* 2011; Giorgis and Tecco 2014). At present, it is distributed in several ecoregions with different climates (De Viana and Colombo Speroni 2000; Zalba and Villamil 2002; Chaneton *et al.* 2004) in the north, east and centre of the country (Zuloaga *et al.* 2008).

Studies on biological invasions have traditionally focussed on the intrinsic characteristics of the invasive species (Rejmánek and Richardson 1996), the invaded environments (Williamson 1996) and the impacts over biodiversity (Macdonald *et al.* 1989). Also, studies have generally assessed the potential mechanisms which might favour their spreading and the control strategies (Mack *et al.* 2000; Keane and Crawley 2002; Colautti *et al.* 2004; Hierro *et al.* 2005; Lockwood *et al.* 2005; Simberloff 2009). Here, we follow this traditional approach to perform an exhaustive review of the invasion of *G. triacanthos* in Argentina. We report invaded environments and ecoregions, describe intrinsic characteristics of the species that favour its invasion and dynamics, and then discuss its impacts over fauna, flora and ecosystem processes. Additionally, we summarise the mechanisms that explain its success, and the control strategies and natural barriers to its invasion.

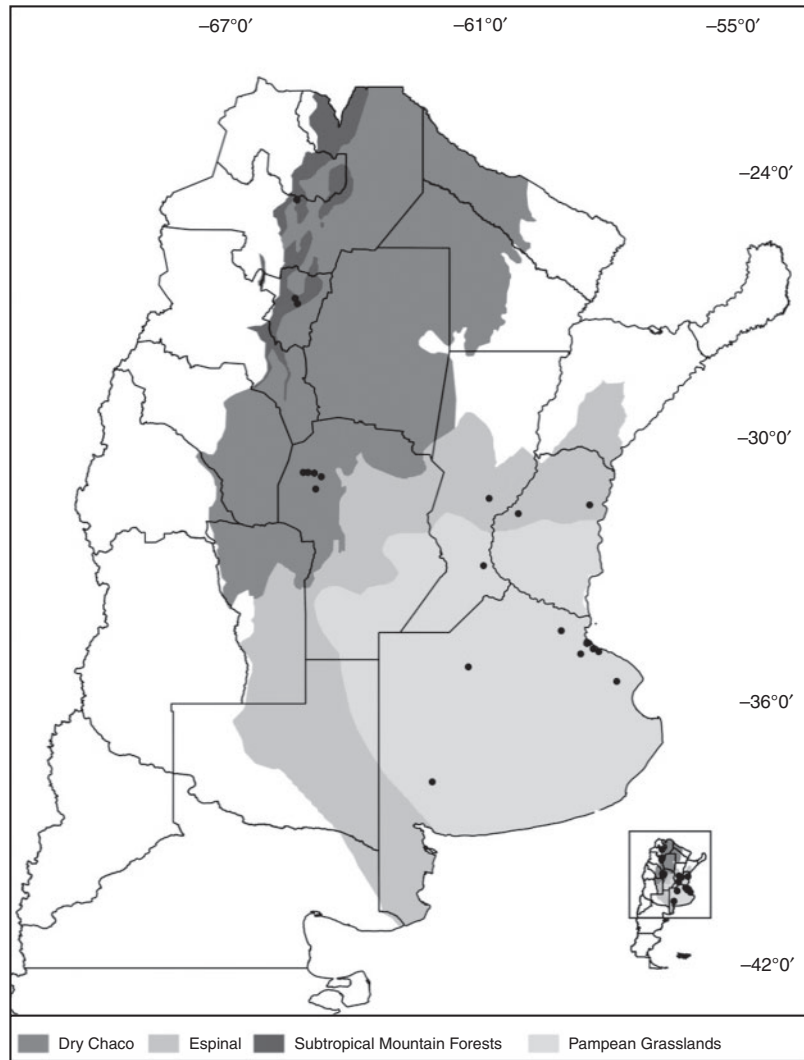
In order to achieve this, we searched for articles and book chapters on the web, using databases and search engines such as Global Compendium of Weeds (Randall 2012), Catálogo de Plantas Vasculares del Cono Sur (Zuloaga *et al.* 2008), Google Scholar, Scielo and ResearchGate. The search was performed using different combinations of the following keywords: '*Gleditsia triacanthos*', 'honey locust', '*Acacia negra*', 'Argentina', 'inva\*' (i.e. invasive, invasion, invaded; both in

English and Spanish). We reviewed a total of 91 articles and book chapters, of which 62 were from Argentina. Thirty-eight studies of those 62 articles specifically investigated aspects of its invasion, whereas the rest mentioned the presence of this species without it being the focus of the study. Most of the studies carried out in the country were performed in the last decade (69%), showing that *G. triacanthos* is currently on the spotlight for many researchers in Argentina.

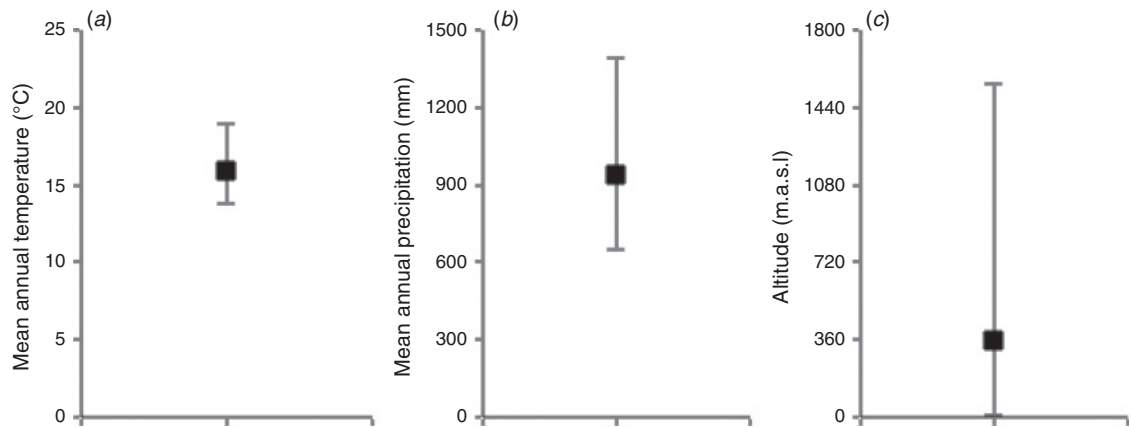
This review summarises the main research topics about the invasion of *G. triacanthos* in Argentina to date. The information provided here can help predict areas at risk from invasion by the species and to formulate sustainable management strategies both in Argentina and in other countries where it has already been introduced. Also, the references of this review can be used for comparative purposes, especially in countries of the southern hemisphere with similar climate than Argentina and Australia.

### Invaded ecoregions and environments

*Gleditsia triacanthos* has invaded four different ecoregions in Argentina: The Dry Chaco (Marco and Páez 2000; Marco *et al.* 2002; Hoyos *et al.* 2010; Giorgis *et al.* 2011; Ferreras *et al.* 2014), the Subtropical Mountain Forests (also known as Yungas; De Viana and Colombo Speroni 2000; Grau and Aragón 2000; Fernández *et al.* 2016), the Pampean Grasslands (Ghersa *et al.* 2002; Zalba and Villamil 2002) and the Espinal (Ruiz Selmo *et al.* 2007; Bortoluzzi *et al.* 2008). Based on the information provided by the reviewed bibliography, we developed a map of the invaded localities in QGIS software (Quantum GIS geographic information system 2011) (Fig. 1; see Table S1 available as Supplementary Material to this paper). The species is distributed throughout several environments across the centre, east and north of the country, from lowlands to mountain areas, and has invaded dry and humid forests, palm forests, temperate-humid savannas, shrublands, grasslands, coastal dunes, riparian environments, disturbed and cleared areas, routes and roads edges, peri-urban areas and agricultural fields (Ansin and Marlats 1997; Boffi Lissin *et al.* 1999; De Viana and Colombo Speroni 2000; Grau and Aragón 2000; Haene 2000; Marco and Páez 2000; Mazía *et al.* 2001; Ghersa *et al.* 2002; Zalba and Villamil 2002; Chaneton *et al.* 2004; Faggi *et al.* 2006; Lewis *et al.* 2006; Cappello and de la Peña 2007; Ruiz Selmo *et al.* 2007; Aceñolaza *et al.* 2008; Bortoluzzi *et al.* 2008; Rossi *et al.* 2008; Mazía *et al.* 2010; Sirombra and Mesa 2010; Giorgis *et al.* 2011; Paiaro *et al.* 2011; Quiroga and Juliá 2011; Argüello 2012; Buguña and Peralta 2012; Chaneton *et al.* 2012; Tecco *et al.* 2012; Franceschi and Boccanelli 2013; Giorgi *et al.* 2014). *G. triacanthos* is distributed along a wide range of temperature (13.8–19°C mean annual temperature), precipitation (650–1390 mm mean annual precipitation) and altitude gradients (10–1550 m above sea level) (Fig. 2). Rossi *et al.* (2008) point out that its excellent adaptation to temperate weather has favoured its naturalisation in diverse regions of Argentina, particularly in the east and centre, where it has invaded grasslands. Although the species is present in a wide range of ecosystems, some environments have not been colonised, such as rocky areas at high altitudes and steep slopes (Marco and Páez 2000), first order creeks and basin upper areas (Ghersa *et al.* 2002).



**Fig. 1.** Distribution of the localities invaded by *Gleditsia triacanthos* in Argentina, as reported in literature. Shades of grey represent the different ecoregions. Dots represent localities, which were obtained from the articles listed in Table S1, available as Supplementary Material to this paper.



**Fig. 2.** Temperature (a), precipitation (b) and altitude (c) of the areas invaded by *Gleditsia triacanthos* in Argentina. ‘Boxes’ represent mean values and ‘whiskers’ represent minimum and maximum values.

### Intrinsic characteristics of the species

Invasiveness refers to the features of exotic organisms that define their capacity to invade, such as their life-history traits and modes of reproduction (Richardson *et al.* 2011). In this section, we list the intrinsic characteristics of *G. triacanthos* that enhance its invasion success in Argentina as follows.

- (i) Sexual reproduction and the ability to resprout, which is often stimulated by intense pruning and cattle consumption (Blair 1990; Rossi *et al.* 2008).
- (ii) Fast growth rate (10 mm year<sup>-1</sup> increment in diameter at breast height) (Marco and Páez 2000), which is faster than that of many native woody species in Dry Chaco communities (Tecco *et al.* 2010; Tecco *et al.* 2013). For example, its growth rate is 60% higher than that of one of the dominant species in Dry Chaco ecoregion, the 'molle de beber' (*Lithraea ternifolia* (Hook.) F.A. Barkley, Anacardiaceae) (Marco and Páez 2000).
- (iii) Short juvenile period, reaching the reproductive stage in 7 years (Marco and Páez 2000).
- (iv) Abundant seed production (mean number of seeds plant<sup>-1</sup>: 14 450); i.e. 140% larger than that of *L. ternifolia* (Marco and Páez 2000) In addition, *G. triacanthos* seeds are larger (11 mm) and exhibit higher germination percentages (15%) than *L. ternifolia* seeds (0.3%) (Marco and Páez 2000). Importantly, the coating of *G. triacanthos* seeds is impermeable and the seeds are viable for at least 3.5 years (Ferrerías *et al.* 2015).
- (v) The density of seed and seedlings surrounding adult individuals is higher than that of the native species 'tusca' (*Acacia aroma* Gillies ex Hook. and Arn., Fabaceae) (Ferrerías *et al.* 2014). This could explain the formation of monospecific woodlands of *G. triacanthos* observed in many areas (Marco and Páez 2000; Mazía *et al.* 2001; Ghersa *et al.* 2002; Ferrerías and Galetto 2010).
- (vi) Seed dispersal by cattle that eat the pods and favours their subsequent germination (Blair 1990; Cozzo 1994; Grau and Aragón 2000; Ferrerías and Galetto 2010; Ferrerías *et al.* 2015). Pods and leaves of *G. triacanthos* are valuable feed for ruminants due to their high content of protein and fibre (Rossi *et al.* 2008; Quiroga and Juliá 2011). These characteristics might explain why cattle prefer this species over several native species (Rossi *et al.* 2008). For example, in Dry Chaco, cattle faeces contained numerous seeds of *G. triacanthos* (an average of 409 ± 354 seeds per fecal unit) in comparison to the low number of seeds of the native species *A. aroma* (a maximum of four seeds per fecal unit) (Ferrerías *et al.* 2015).

Other intrinsic characteristics of *G. triacanthos* that have been studied in its native range but not in Argentina are as follows.

- (i) *Gleditsia triacanthos* is a non-nodulating species with a symbiotic nitrogen-fixation in the roots, resembling rhizobial bacteroids (Friesner 1926; Bryan *et al.* 1996). This symbiosis confers legumes a competitive advantage over other species in nitrogen-limited terrestrial ecosystems (Rodríguez-Echeverría *et al.* 2012; Crisóstomo *et al.* 2013).
- (ii) Roots of *G. triacanthos* might exhibit biochemical inhibition (allelopathy), suggested by the fact that the

species reduced the growth and vigour of grasses in its surroundings (Whitcomb 1972; Whitcomb and Roberts 1973).

- (iii) The species is adapted to most soil types, and is tolerant of drought, salinity (Blair 1990) and high soil temperature (Graves *et al.* 1991).
- (iv) Branches with leaves and flowers of *G. triacanthos* produce monoterpene as biogenic volatile organic compounds for pollinator attraction (Baghi *et al.* 2012).

### Dynamics of the invasion of *G. triacanthos*

*Gleditsia triacanthos* exhibits the typical behaviour of a pioneer species (Grau and Aragón 2000; Grau *et al.* 2010), colonising recent abandoned lands (Mazía *et al.* 2001; Grau *et al.* 2010): *G. triacanthos* establishes in open and disturbed areas (Colombo Speroni and de Viana 1998; Ruiz Selmo *et al.* 2007; Quiroga and Juliá 2011) or under shrubs (Giantomasi *et al.* 2008; Zeballos *et al.* 2014), but it is a poor competitor in the shady environment of the understory and hence cannot regenerate inside mature forests (Mazía *et al.* 2001; Trossero *et al.* 2005; Grau *et al.* 2010; Quiroga and Juliá 2011). However, although the species does not regenerate under closed canopies in native forests, it may regenerate in tree fall gaps (Colombo Speroni and de Viana 1998; Mazía *et al.* 2001).

In an initial stage, *G. triacanthos* generates large banks of seeds and seedlings (Marco and Páez 2000; Ferrerías and Galetto 2010), which are the main determinant of the success of its populations (Cannas *et al.* 2003). Once established, saplings usually grow fast and form dense, low, monospecific thickets (Faggi *et al.* 2006; Quiroga and Juliá 2011). For example, in the Pampean Grasslands, *G. triacanthos* forms thorny thickets with up to ~1600 adult trees per hectare, which reduces the productivity of herbaceous species and impedes livestock movement (Mazía *et al.* 2010). The rapid formation of dense shrublands might be due to the attributes of the species (see 'Intrinsic characteristics of the species' above), that confer advantages over other leguminous native tree species (Ferrerías and Galetto 2010; Tecco *et al.* 2012). The invasion of *G. triacanthos* might also be favoured by a lower predation of their seeds compared with those of native tree species in the Pampean Grasslands. For example, Busch *et al.* (2012) observed that rodents mainly predated small seeds of native species such as the 'caldén' (*Prosopis caldenia* Burkart, Fabaceae) while their effect on the seeds of *G. triacanthos* was low.

### Impacts over flora and fauna

Several studies show that the invasion of *G. triacanthos* generally impacts on the composition and structure of flora and fauna (Colombo Speroni and de Viana 1998; Marco and Páez 2000; Ghersa and León 2001; Zalba and Villamil 2002; Lewis *et al.* 2006; Leggieri 2010; Sirombra and Mesa 2010; Quiroga and Juliá 2011; Busch *et al.* 2012; Moreno Ruiz Holgado 2012; Giorgi *et al.* 2014). In Subtropical Mountain Forests, *G. triacanthos* displaced native species and produced remarkable physiognomic and structural changes in plant communities (Sirombra and Mesa 2010). These changes were more evident in the riparian forests, which acquired xerophytic characteristics that widely differ from previously existent communities

(Sirombra and Mesa 2010). *G. triacanthos* also displaced native vegetation in other ecoregions, such as the Dry Chaco and Espinal (Marco and Páez 2000; Lewis *et al.* 2006).

The effect of *G. triacanthos* on the structure and composition of plant communities was evident in the Pampean grasslands. Zalba and Villamil (2002) observed that this species invaded grasslands patches, replacing native species (e.g. ‘crown grass’ *Paspalum quadrifarium* Lam., Poaceae), giving rise to woody formations or shrublands. These communities modified the physiognomy of several areas of the Pampas, where grasslands with isolated ‘ombú’ trees (*Phytolacca dioica* L., Phytolaccaceae) used to predominate in the interior, and ‘humboldt’s willow’ (*Salix humboldtiana* Willd., Salicaceae) dominated in riparian areas (Zalba and Villamil 2002). Riparian forests dominated by *G. triacanthos* affect the structure of aquatic communities by modifying temperature and light that reaches the streams (Giorgi *et al.* 2014). For example, Giorgi *et al.* (2014) observed that invertebrate species richness and macrophytes cover were higher in a non-invaded section (a conserved riparian area with grasslands) compared with an invaded section (with high density of *G. triacanthos* trees) in the margins of a Pampean stream. The invasion caused changes in the composition of aquatic species, such as reductions of thread algae and the development of epipelagic algae (mainly Diatomeae and Cyanophyceae) in the invaded section, probably due to the reduction of light conditions (i.e. 95% less in the invaded section) (Giorgi *et al.* 2014).

In the Dry Chaco, Moreno Ruiz Holgado (2012) found that patches dominated by *G. triacanthos* alter the native bird community. Patches dominated by *G. triacanthos* exhibited lower bird species diversity and evenness (e.g. one or two dominant species in *Gleditsia* forests vs six dominant species in native forests) and differences in species composition in comparison to native forests. Certain bird species, such as the ‘saffron-billed sparrow’ (*Arremon flavirostris* Swainson, 1838, Emberizidae), the ‘house wren’ (*Troglodytes aedon* Vieillot, 1809, Troglodytidae) and the ‘rufous-bellied thrush’ (*Turdus rufiventris* Vieillot, 1818, Turdidae) were usually present in the low and medium vegetation strata within native forest (Moreno Ruiz Holgado 2012). The reduced diversity of birds in *G. triacanthos* forests might be due to the simplification of vegetation structure (Moreno Ruiz Holgado 2012).

*Gleditsia triacanthos* also causes fragmentation of riparian ecosystems, with direct consequences over native fauna using forest patches as shelters, feeding and movement areas (Ghersa and León 2001). These habitats are very important for supporting native vertebrate populations, such as the ‘coyapu’ (*Myocastor coypus bonariensis* Hollister, 1914, Myocastoridae), the ‘pampas fox’ (*Lycalopex gymnocercus* Fischer, 1814, Canidae), the ‘thick-tailed opossum’ (*Lutreolina crassicaudata* Desmarest, 1804, Didelphidae), the ‘wild guinea-pig’ (*Cavia aperea* Erxleben, 1777, Caviidae), the white-banded tree frog (*Hypsiboas pulchellus* Duméril and Bibron, 1841, Hylidae), the ‘gold tegu’ (*Tupinambis teguixin* Linnaeus, 1758, Teiidae), the ‘brown pintail’ (*Anas georgica* Gmelin, 1789, Anatidae) and the ‘black-crowned night-heron’ (*Ncticorax ncticorax* Linnaeus, 1758, Ardeidae) (Ghersa and León 2001). Leggieri (2010) suggested that the invasion of *G. triacanthos* in riparian ecosystems of the Pampean Grasslands might generate losses of

native biota (e.g. the presence of *G. triacanthos* was negatively associated with the presence of *M. coypus bonariensis*) probably due to a decrease in habitat quality.

It is worth mentioning that several studies reported a negative impact of *G. triacanthos* over native biodiversity, but a positive response of an exotic seed beetle species: *Bruchidius endotubercularis* Arora, 1980, Bruchinae (Di-Iorio 2005). This seed beetle has been accidentally introduced in Argentina in the 90s probably facilitated by *G. triacanthos*, due to the high number of seeds consumed by these larvae. This caused an increase in the populations of *B. endotubercularis*, which can develop more than a generation per year over the same group of pods (Di-Iorio 2005). The high number of seeds that remain on the plant for a long time (i.e. at least six months) without suffering any significant deterioration may be another characteristic that facilitates the invasion of the exotic seed beetle.

### Impacts over ecosystems processes

Few of the papers assessed the impact of the invasion of *G. triacanthos* on ecosystem processes. For example, its impact on nutrient cycling is expected to be high due to its deciduous phenology, its capacity to form monospecific patches and its ability to fix atmospheric nitrogen, which can accelerate the rates of some biogeochemical processes in the soil, and modify nutrient concentrations (Furey *et al.* 2014; Vilches *et al.* 2014). Vilches *et al.* (2014) compared invaded and non-invaded areas in Pampean streams and reported that *G. triacanthos* modified water nutrient concentrations (e.g. leading to less concentration of soluble reactive phosphorus and ammonium and higher concentration of nitrates in invaded areas), mainly at high and intermediate densities; although higher nitrate concentrations at lower invasion densities have also been found. Leggieri (2010) documented that its deciduous phenology results in more litter reaching aquatic ecosystems, which enhances the respiration of decomposers and thus reduces the net productivity of these ecosystems. In the Dry Chaco, leaf litter decomposability of *G. triacanthos* tended to be lower than that of most native species. Although these differences were small, the effect of this exotic species on decomposition processes may be high due to its high abundance (Furey *et al.* 2014). In addition, in Pampean Grasslands, Gantes *et al.* (2011) found that the replacement of herbaceous riparian vegetation by *G. triacanthos* forests modified decomposition rates. Furthermore, the litter of this species decomposes more rapidly in invaded than in non-invaded sites, which might be due to the differential activity of invertebrates in each site. In the same study area, Giorgi *et al.* (2014) found that in the river sections invaded by *G. triacanthos*, temperature range, light reaching the stream, ecosystem respiration and net primary productivity decreased both in spring and winter. These environmental modifications might be the actual cause of the decrease in invertebrate richness in invaded sites (Giorgi *et al.* 2014).

### Proposed mechanisms to explain invasion

Numerous mechanisms have been postulated to explain the success of exotic species, but few have been rigorously tested (see Hierro *et al.* 2005). In the case of *G. triacanthos*, only the

disturbance hypothesis (Mack *et al.* 2000) has been strictly tested (Mazia *et al.* 2001; Chaneton *et al.* 2004; Mazia *et al.* 2010). Disturbances favour the germination, survival and biomass accumulation of *G. triacanthos* (Chaneton *et al.* 2004; Mazia *et al.* 2001, 2010). In Pampean Grasslands, Mazia *et al.* (2001) found that the experimental removal of grasslands at a small scale (quadrants of <math>1\text{ m}^2</math>) increased the establishment of *G. triacanthos* almost 50 times in comparison with its establishment in non-disturbed grasslands. Subsequently, in the same region the removal of aboveground biomass enhanced total biomass production and growth of *G. triacanthos* seedlings (Mazia *et al.* 2013).

Forest clearing has also been cited as a disturbance contributing to the invasion of *G. triacanthos* (Ruiz Selmo *et al.* 2007; Leggieri 2010; Buguña and Peralta 2012). In Dry Chaco, Salazar *et al.* (2013) found that *G. triacanthos* is mainly distributed near urban centres, creek margins and deforested areas. In the same ecoregion, agriculture activities and tourism caused the reduction of forested areas (Zak *et al.* 2004; Verzino *et al.* 2005), leading to changes in native vegetation and consequently to the enhancement of exotic species invasion, including *G. triacanthos* (Marco and Páez 2000). In Subtropical Mountain Forests, several agriculture lands that have lost their soil productivity, are now secondary forests dominated by species such as *G. triacanthos* (Grau and Aragón 2000; Grau *et al.* 2008; Grau *et al.* 2010).

Fire also favours the invasion of *G. triacanthos* in different ecoregions of the country. In the Pampean Grasslands, Chaneton *et al.* (2004) found that areas invaded by *G. triacanthos* had been previously burned. Also, in a peri-urban area, fire had been used for grasslands clearing, which allowed the expansion of this species (Faggi *et al.* 2006). In open areas of 'El Palmar' National Park (i.e. palm forests), fire has been suggested as a potential cause of the spread of *G. triacanthos* (Ruiz Selmo *et al.* 2007). Even though fire reduces the germination of *G. triacanthos* seeds, this species has the ability to resprout from below-ground tissues, such as roots, after a fire event (Ferrerías *et al.* 2015; Herrero *et al.* 2016). It has also been suggested that fire could relieve this species from competitors and change nutrient availability, promoting its establishment and invasion (Ferrerías *et al.* 2015). However, the effect of fire on *G. triacanthos* invasion may be overridden by other disturbances. Mazia *et al.* (2010) performed an experiment to evaluate the effect of anthropic disturbance (fire), natural disturbance (the formation of cavities by armadillos) and the interaction of both types of disturbances, on the invasion of *G. triacanthos*. Fire increased community invasibility, but only in the absence of frequent disturbance by simulated armadillo diggings, since artificial diggings virtually precluded tree recruitment (Mazia *et al.* 2010).

The release or absence of natural enemies might also favour the invasion of *G. triacanthos*. In the Dry Chaco, Angulo and Raimúndez (2000) observed that fruits and seeds of this species are consumed less than those of *A. aroma* and the 'espinillo' (*Acacia caven* (Molina) Molina, Fabaceae), both common native species of this ecoregion. It is likely that *G. triacanthos* has specific toxic secondary compounds which protect it against insect attacks (Angulo and Raimúndez 2000). However, the natural enemies' hypothesis requires an explicit

comparison of the species in its native and introduced ranges (Hierro *et al.* 2005), which has not been performed yet for *G. triacanthos*. In addition, to test this hypothesis about the invasion of *G. triacanthos*, further studies assessing the role of generalist enemies (Keane and Crawley 2002) and the acquisition of new local enemies at invaded sites are needed (Di-Iorio 2005).

Finally, the hypothesis of propagule pressure may also explain the invasion of *G. triacanthos*. Propagule pressure is the primary determinant of the establishment success of an invasive species (see Lockwood *et al.* 2005). Higher propagule pressure (given by the number of introduction events and/or the number of individuals per introduction event) reduces stochastic effects and increases the likelihood of establishment of an invasive species (Simberloff 2009). The focal points of *G. triacanthos* invasion are close to urban and rural areas (De Viana and Colombo Speroni 2000; Faggi *et al.* 2006), which may act as propagule sources. However, this mechanism should be experimentally tested due to the lack of historical records about the number of introduced individuals and the number of release events.

### Control and barriers to invasion

Different techniques have been used to control the invasion of woody species, and the integration of several techniques could be the best option to accomplish cost-effective management. DiTomaso *et al.* (2006) concluded that the use of prescribed fire in the United States is an effective management tool only for a few woody species, but it becomes more effective when integrated with other management techniques such as mechanical removal or herbicide application. For populations of 'mimosa' (*Mimosa pigra* L.), an invasive Fabaceae in Australia, it has been demonstrated that integrating herbicide mechanical removal with fire and biological control is a successful strategy to avoid its spreading (Buckley *et al.* 2004; Paynter and Flanagan 2004).

In Argentina, different selective and non-selective mechanisms have been applied to control the invasion of *G. triacanthos*. Selective control includes the use of agrochemicals (e.g. BT Togar, picloran, 2,4D) on individuals previously cut with chainsaw and ring-barking (Maranta 2001). However, these methods require human effort, are expensive and inefficient (Leggieri 2010). In particular, the BT Togar herbicide poses a risk to aquatic environments, potentially causing groundwater contamination and toxicity to soil organisms, hence, its application is not recommended (Di Marzio *et al.* 2009). Large-scale controls include the use of bulldozer machines, fire and aerial applications of agrochemicals, which result in a huge environmental impact on the entire community (Maranta 2001; Chaneton *et al.* 2004; Cappello and de la Peña 2007).

Due to the lack of effective control systems for *G. triacanthos* to date, the design of successful controls requires more attention, particularly in the case of recently established populations. As done with invasive pines in the Pampean Grasslands, it is necessary to compare the cost and effectiveness of different control techniques in order to select the most appropriate (Cuevas and Zalba 2009), and to evaluate which options are better to control seedlings and adults of this species. For

example, pruning is often effective to control adults of other woody species (Natale *et al.* 2014), but this is likely not suitable for the control of *G. triacanthos* since it stimulates its ability to re-sprout. However, mechanical control might be effective for seedlings, which can be hand pulled, and reach a certain level of control if repeated. Finally, and given its wide distribution in Argentina, economical resources should be allocated to the control of the species in invaded protected areas (Cordo 2004; Ruiz Selmo *et al.* 2007).

Biological control may be an alternative option for reducing growth of the populations of *G. triacanthos*. Di-Iorio (2005) documented a case of unplanned biological control of *G. triacanthos*, whose seeds are consumed by the exotic seed beetle species *B. endotubercularis*. Each larva affects one seed by consuming its cotyledons and embryo, causing the death of the embryo and thus becoming a spontaneous biological control of the species (Di-Iorio 2005). However, this control has not proven to be effective at large scales to date. Also, the introduction of *B. endotubercularis* may have unpredictable consequences for the native flora and fauna, and its spread is facilitated by *G. triacanthos* (Di-Iorio 2005). Therefore, further studies are needed before using biological control, especially if the control agent is also an exotic species.

Importantly, disturbances caused by small mammals may act as a barrier to the invasion of *G. triacanthos* (Mazía *et al.* 2010, 2013; Muschetto *et al.* 2015). One experimental study consisting of field simulations carried out in the Pampean Grasslands showed that soil removal by armadillos (cavities and mounds) negatively affected the germination and survival of the seeds of *G. triacanthos* (Mazía *et al.* 2010). In addition, the presence of armadillos favours natural grasslands, removing soil and litter and increasing luminosity and nitrogen availability. Although the operating mechanism remains unknown, the results of the study suggest that cavities built by armadillos increase resistance of the community towards tree invasion in native grasslands relicts (Mazía *et al.* 2010). Apparently, rodents may play a similar role, since they consume the seeds of *G. triacanthos*, thus acting as a first filter for its establishment (Mazía *et al.* 2013; Muschetto *et al.* 2015).

Pasture cover is an effective biotic barrier that affects the survival and growth of *G. triacanthos* seedlings in grassland communities (Aranda *et al.* 2015). Pastures present advantages in capturing aerial and below-ground resources due to their greater total biomass compared with that of tree seedlings. Therefore, the maintenance of a competitive pasture cover together with grazing management might help minimising the invasion of *G. triacanthos* in grassland communities (Aranda *et al.* 2015).

In Pampean Grasslands, Mazía *et al.* (2013) observed that different plant communities vary in their resistance to the invasion of *G. triacanthos*. These authors compared the establishment and growth of seedlings of *G. triacanthos* in four monospecific patches and found that species identity played an important role in the resistance to the establishment of this exotic woody species. For example, the diameter, height and biomass of *G. triacanthos* seedlings were lower in patches dominated by the perennial 'bermuda grass' (*Cynodon dactylon* (L.) Pers., Poaceae) compared with patches dominated by other herbaceous plants and grasses (Mazía *et al.* 2013). Finally, it is

likely that weather conditions act as a barrier to the invasion of *G. triacanthos*. Since seeds of *G. triacanthos* need water to germinate, rainfall may be a limiting factor for the germination and subsequent development of the species (Chaneton *et al.* 2004; Mazía *et al.* 2010; Muschetto 2012) and probably preclude its invasion in Argentinian ecoregions with a long dry season. Mazía *et al.* (2010) reported a reduced and delayed emergence of the seeds of *G. triacanthos* in a below-average rainfall year, and an enhanced emergence in high-rainfall years.

## Conclusions

*Gleditsia triacanthos* is an invasive exotic species in several countries, and it has been widely studied in Argentina. In this country, *G. triacanthos* is considered one of the most invasive woody species, with a great potential to continue expanding its range. Its importance as an invasive species is illustrated in the numerous descriptive and experimental studies that explore several aspects of the invasion and which have been summarised in this review. Most of the studies were conducted in the last decade, demonstrating that this species is in the spotlight for many researchers in Argentina.

*Gleditsia triacanthos* has successfully colonised, established and spread in the centre, east and north of the country. The invasion of this species affected the structure, composition and ecosystem processes, as well as their functioning. Disturbances (e.g. livestock grazing, deforestation, and fire) have been mentioned as the main cause of the success of *G. triacanthos*, favouring germination, establishment, survival, growth, and biomass accumulation of this species (Mazía *et al.* 2001; Chaneton *et al.* 2004; Mazía *et al.* 2010; Quiroga *et al.* 2011). In addition, we believe that other mechanisms such as the release or absence of natural enemies or propagule pressure might be important for explaining the invasion of *G. triacanthos*, and are probably operating jointly.

Despite all the studies that have been completed on *G. triacanthos* invasion, some topics such as ecophysiological features, impact on ecosystem processes and mechanisms of control, have been little explored. Other aspects such as mutualistic interactions (i.e. mycorrhizal fungi and nitrogen-fixing bacteria) and production of organic compounds remain hardly unknown, even though these factors improve the host's nutrient status and are important in the invasion process of other woody legume species (Rodríguez-Echeverría *et al.* 2012; Crisóstomo *et al.* 2013; Birnbaum *et al.* 2014). Finally, given the poor effectiveness and high costs of control measures, we consider that reducing the frequency and intensity of disturbances may be an option for controlling *G. triacanthos* invasion. In addition, monitoring programs that allow an early detection and control of recently established populations (i.e. both new arrivals and the enlargement of already occupied sites) are highly recommended, especially within protected areas. By characterising the vegetation and habitat features of sites invaded by *G. triacanthos*, this review might be useful for predicting new areas with potentially high invasion risk.

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