Management of Biological Invasions (2012) Volume 3, Issue 1: 37–44
doi: http://dx.doi.org/10.3391/mbi.2012.3.1.04

Open Access

Research Article

Assessing invasion process through pathway and vector analysis: case of saltcedar (*Tamarix* spp.)

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Received: 24 May 2012 / Accepted: 5 November 2012 / Published online: 15 December 2012

Handling editor: Elias Dana, University of Almeria, Spain

Abstract

Biological invasions are one of the most pervasive environmental threats to native ecosystems worldwide. The spontaneous spread of saltcedar is a particular threat to biodiversity conservation in arid and semiarid environments. In Argentina, three species belonging to this genus have been recognized as invaders. The aim of the present study was to identify main dispersal vectors and pathways to refine risk analysis and increase our ability to predict new areas at risk of *Tamarix* establishment. We surveyed and categorized 223 populations, 39% as *invasive*, 26% as *established*, 21% as *contained* and 14% as *detected in nature*. Dispersion of saltcedar was found to be associated with watercourses and human-driven disturbances; in addition roads were found to be relevant for the introduction of propagules in new environments. Considering the potential impact of saltcedar invasion and that it is an easily wind-dispersed invasive, it is necessary to implement strategies to monitor dispersal pathways and take actions to eliminate invasion foci, particularly in vulnerable and high-conservation value areas.

Key words: dispersal routes; invasive alien species; prevention; South America; risk assessment

Introduction

Biological invasions are one of the most pervasive environmental threats to native ecosystems worldwide. Detailed knowledge about the ecology of invading species and invaded systems is needed to effectively face this challenge (Richardson et al. 2003). Invasion depends not only on the ecological matching between the species and the new environment, but also on the ability of the invader to reach the site in sufficient number to establish a founding population. Dispersal ability is affected by the abundance and physical attributes of diaspores and their relationship with natural and man-made vectors (physical agents introducing and/or dispersing an invader) and pathways (economic and cultural forces that initiate and sustain the movement of organisms) (Mack 2003; Williamson 1996). Therefore, combining information on environmental spreding constraints with models of potential range can help identify the most probable sites of future invasion, therefore increasing our ability to predict the real chances of establishment of the invader in a new location (Barney 2006).

Biological Invasions occur along pathways which can be divided into three phases: initial colonization, establishment and spread (Ward et al. 2006). Research efforts have often been directed to the latter phases of this process by attempting to identify factors that influence the ability of a species to establish in a new location (its ‘invasiveness’), or the vulnerability of native ecosystems to new arrivals (their 'invasibility') (Floerl and Inglis 2005; Mack 2003). Much less is known about the mechanisms by which species initially arrive at a site and how they subsequently expand from there (Barney 2006; Johnson et al. 2006). Although Prevention has been stressed as the strategy of choice for managing biological invasions, the lack of knowledge about the introduction and expansion stages has become a serious obstacle to the effective management of the problem in a long term (Richardson et al. 2003).

According to Richardson et al. (2003), the formulation of systematic plans for dealing with alien species at national and regional scales requires attention to be paid to the identification and assessment of the relative importance of present and future pathways of introduction and rapid spread of this species.

Tamarix spp. are among the most successful invasive plants in desert riparian ecosystems in the United States, Australia and Mexico, where they are assumed to alter species composition and ecosystem processes (Australia Weeds Committee 2004; De Loach et al. 2000; Hart et al. 2005; Shafroth and Briggs 2008). Saltcedar was introduced for its use as windbreak, shade cover, ornamental plant and erosion control agent along roads and waterways. *Tamarix* produces massive quantities of minute seeds that are readily dispersed by wind and water; in addition the species have the ability to propagate from buried or submerged stems (De Loach et al. 2000; Glenn and Nagler 2005). Local elevation, soil and topography greatly influence saltcedar distribution, growth and invasive behaviour, with a remarkable association with watercourses, lakes and reservoirs. Taylor and McDaniel (2004) reported that low temperature limits saltcedar invasions at elevations exceeding 2,100 m asl. According to these authors, the density of saltcedar increases downhill, from narrow belts along river edges at medium altitudes to dense stands in basal floodplains.

The presence of four species of *Tamarix*, *T. gallica* L., *T. ramosissima* Ledeb., *T. chinensis* Lour. and *T. parviflora* DC., has been confirmed in Argentina, having, the first three, the ability to grow spontaneously and to invade natural and semi-natural environments in the country (Natale et al. 2008). *T. ramosissima* and *T. chinensis* have been reported to hybridize in their invaded ranges in USA (Gaskin and Kazmer 2009); in Argentina, this phenomenon has, so far, not been reported.

In Argentina, saltcedar occurs from 49°14′ 11.42″ to 23°26′17.93″S and from 70°35′45.33″ to 56°59′46.46″W with a potential distribution area of 1,654,127 km^2, calculated on the basis of climate and habitat matching analysis (Natale et al. 2011). The region exposed to invasion includes several sites of high biodiversity value that might be seriously affected by satlcedar advance (11% of the Important Bird Areas, 14.3% of Valuable Grasslands Areas and 17% of Natural Reserves that are part of the Federal System of Protected Areas). Furthermore, *Tamarix* species also affect social and economical values by invading both, lands of high productive value and subsistence agriculture areas (Natale et al. 2010b).

In the present study, we analyzed the main vectors and pathways of saltcedar dispersal in potentially invasible areas in Argentina. For this, we correlated data of species distribution and population characteristics of saltcedar nuclei in the country with potential dispersion routes (managed and unmanaged watercourses, roads and railways). In orden to evaluate the relative importance of active dispersal for the propagation of the species local populations use and perception of saltcedar were also assessed.

We expected to find the oldest populations growing in close association with human activity areas, such as farmhouses and corrals, representing the originally planted stands. In contrast, we expected younger *Tamarix* populations (with high percentages of small plants) to be related to roadsides, railways, flooding areas, rivers and channels. Finally, and unlike the situation described for the USA, where the spontaneous advance of *Tamarix* is widely recognized as a problem (De Loach et al. 2000), we expected humans to play an important role in the spread of these species.

Materials and methods

We updated the available information on saltcedar distribution and population invasion status (Natale et al. 2008) by reviewing the herbarium collections of the National Universities Sur (HBBB), Córdoba (HMBC), and Río Cuarto (RCV Natural Sciences Department and FAV) and of the "Darwinion Institute" (SI) in Buenos Aires city, Argentina. We also emailed a questionnaire (Kadoya et al. 2009) to scientists, technicians and park-guards and made field surveys. The questionnaire elicited information

Table 1. Population characteristics of the invasion categories used.

Population status	Description	Population structure of the patch	Reproductive Success
Contained (Co)	Composed exclusively or mainly of the originally planted individuals	Mostly (80-100%) adult trees	Unsuccessful
Detected in nature (DN)	Small patches of individuals growing in natural and semi-natural environments	Composed mainly (80-100%) of young individuals (up to 1,5m in height)	Do not get to successfully reproduce or do not represent an invasion at the moment of the observation
Established (Es)	Patches of variable size found in natural or semi-natural habitats	50-80 % adults, 20-50 % young individuals or seedlings (up to 0.5m height, with scarce or no branches)	Reproduce in their immediate environment, without a wide dissemination
Invasive (In)	Extensive colonization of natural or semi-natural habitats	Heterogeneous structure with seedling dominance in most cases (20-50% adults, 30-80% youngs and ≥40% seedlings)	Extensive dissemination far away from the original introduction point

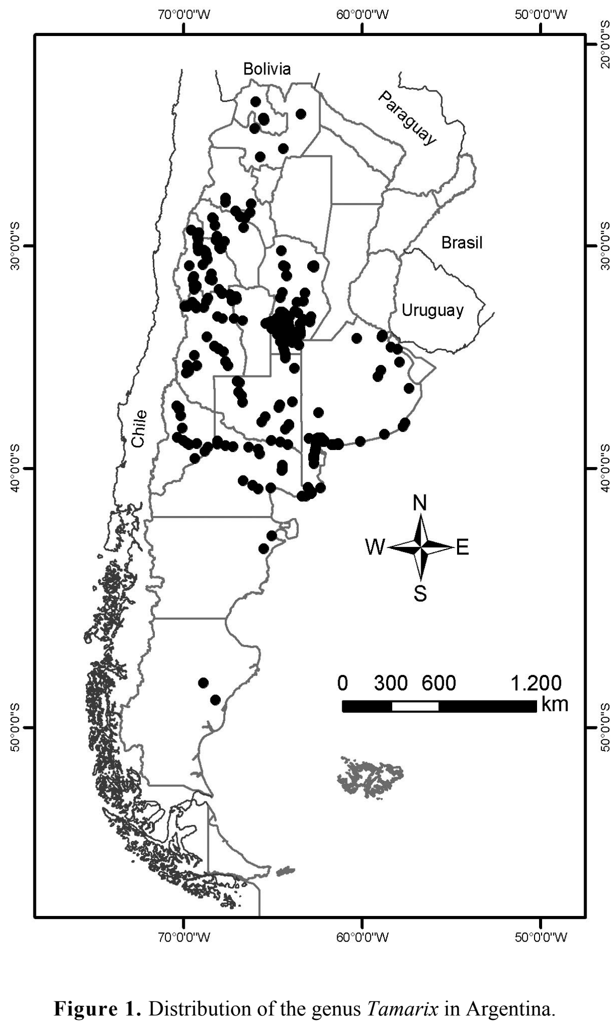

Figure 1. Distribution of the genus *Tamarix* in Argentina.

on: 1) population location and size; 2) presence of originally planted individuals; 3) spontaneous recruitment; 4) presence of seedlings more than 20 m apart from the main population nucleus; 5) seed production, and 6) population structure. It also included questions about soil type, environmental features and specific uses of *Tamarix*. We georeferrenced all population and herbarium records to build up a distribution layer for saltcedar in Argentina.

Based on the responses to email inquiries and data from field surveys we classified the populations using the categories of population status proposed by the Inter-American Invasive Species Information Network (I3N, IABIN) (INBIAR 2006), which are intended to reflect the state of the invasion process (Table 1).

Information about watercourses, roads and railways that may act as dispersion pathways was obtained from the GIS database produced by the Instituto Geográfico Militar of Argentina (2004) at a 1:250,000 scale. Soil flooding data were obtained from the Soil Atlas of Argentina at a scale of 1:500,000 (INTA 1995) (Table 2). The software ArcGIS 9.3 (ESRI, Redlands, CA, USA) was used to build a database and generate maps containing all this information.

All statistical analyses were performed using SPSS 17.0 software and a 10% significance level was selected. To study the associations between environmental variables (water courses, drainage, land use type, saltcedar use, flooding, roads, railways and cover type) and invasion categories, chi-square independence tests were carried out. Based on these results, a multiple

Table 2. Categories of environmental variable considered.

Variable	Categories	Description
Water course	Natural (WN)	River or stream without human intervention
	Modified (WM)	Water courses with some degree of human regulation (irrigation channels, ditches, etc.)
	Without water course (WW)	When the population nuclei is located more than 500 meters of watercourse
Roads	Presence (PR)	When the population nuclei is situated less than 500 meters from the road
	Absence (AR)	When the population nuclei is situated more than 500 meters from the road
Flooding	Flood (F)	Temporary inundation by flowing water
	Unflood (UF)	No inundation by flowing water.
Natural Drainage Classes (Soil Survey Division Staff 1993)	Somewhat poorly drained (SPD)	Water is removed slowly so that the soil is wet at a shallow depth for significant periods during the growing season. The occurrence of internal free water commonly is shallow to moderately deep and transitory to permanent. The soils commonly have one or more of the following characteristics: low or very low saturated hydraulic conductivity, a high water table, additional water from seepage, or nearly continuous rainfall
	Very poorly (VPD)	Water is removed from the soil so slowly that free water remains at or very near the ground surface during much of the growing season. The occurrence of internal free water is very shallow and persistent or permanent. The soils are commonly level or depressed and frequently ponded.
	Poorly (PD)	Water is removed so slowly that the soil is wet at shallow depths periodically during the growing season or remains wet for long periods. The occurrence of internal free water is shallow or very shallow and common or persistent. The soil, however, is not continuously wet directly below plow-depth. Free water at shallow depth is usually present. This water table is commonly the result of low or very low saturated hydraulic conductivity of nearly continuous rainfall, or of a combination of these.
	Moderately well (MWD)	Water is removed from the soil somewhat slowly during some periods of the year. Internal free water occurrence commonly is moderately deep and transitory through permanent. They commonly have a moderately low or lower saturated hydraulic conductivity in a layer within the upper 1 m, periodically receive high rainfall, or both.
	Well(WD)	Water is removed from the soil readily but not rapidly. Internal free water occurrence commonly is deep or very deep; annual duration is not specified. The soils are mainly free of the deep to redoximorphic features that are related to wetness.
	Samewhat excessively (SED)	Water is removed from the soil rapidly. Internal free water occurrence commonly is very rare or very deep. The soils are commonly coarse-textured and have high saturated hydraulic conductivity or are very shallow.
	Excesively (ED)	Water is removed very rapidly. The occurrence of internal free water commonly is very rare or very deep. The soils are commonly coarse-textured and have very high hydraulic conductivity or are very shallow
Land use type	Unused (UUL)	Without specific use, abandoned fields
	Protected area y/o Turism (PTL)	usos para recreación, investigación, conservación, etc.
	Farming (FL)	Agricultural and/or livestook production
	Urban (UL)	Post or cite presence

correspondence analysis was performed with all variables that were significantly associated, except the variable use of Tamarix due to its high relationship with land use. In addition, in order to find whether there is a clear distribution pattern that could be related to dispersion pathways, a visual analysis of spatial overlapping among known populations of *Tamarix* and landscape elements (roads, railways and watercourses) was carried out by using the software ArcGIS 9.3.

Results

We recorded 297 *Tamarix* populations, 165 from field surveys, 55 from the questionnaires and 77 from herbaria (Figure 1). With the information available, we categorized 223 populations as *invasive* (39 %), *established* (26%), *contained* (21%) and *detected in nature* (14%) (Table 1).

Chi-square independence tests showed that there is statically significant evidence that the

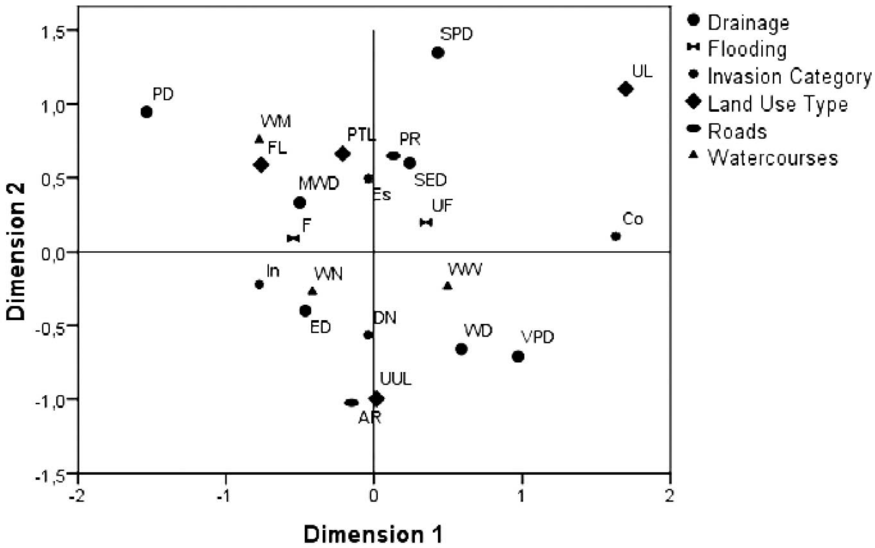

Figure 2. Correspondence analysis between invasion categories of *Tamarix* populations and watercourses; drainage, flooding, roads and land use.

invasion category is associate at 1% with watercourses (p=0.001), drainage (p< 0.001), land use type (p=0.001) and saltcedar use (p< 0.001); at 10% with flooding (p=0.072) and presence of roads (p=0.10); however, it did not show any significant association with railways (p=0.546) and cover type (p=0.298).

The (Figure 2) shows the correspondence analysis between invasion categories of *Tamarix* populations and watercourses; drainage, flooding, roads and land use. *Invasive* populations were consistently associated with natural watercourses, excessively drained sites and flooded site.

Established populations were found to be related to watercourses showing some degree of human regulation (irrigation channels, ditches, etc.), sites which are moderately well to poorly drained as well as flooded site. In addition, they were also related to sites of high human activity such as touristic, agricultural and livestock production areas. Populations *detected in nature* were found to be associated with well or very poorly drained sites. In addition we observed an apparent preference for sites away from roads and without any type of land use. Finally, *contained* population*s* were mainly related to non-flooded sites, presence of roads, somewhat poorly drained site and urban use.

The associations that were found in the correspondence analysis was consistent with those observed in the maps obtained from the overlapping among landscape elements and invasion categories (Figure 3).

Discussion and conclusions

Through the present study we were able to consistently associate a set of land uses and dispersion pathways with *Tamarix* invasion processes in arid and semi-arid regions of Argentina. The invasion stages considering in our study were significantly correlated with human activities and landscape elements. Many of these found associations are consistent with invasion patterns of *Tamarix* in other regions of the world (Hart et al. 2005; Glenn and Nagler 2005; Taylor and McDaniel 2004). This knowledge could be key to predict the species dispersion direction and therefore to design prevention, containment and control strategies. Furthermore, newly found invasion foci, which are small nuclei not subject to significant human use, would be easier and less expensive to aboard by designing control or eradication strategies (Inglis et al. 2006).

Because questionnaires, herbaria collections, and even field surveys can be associated with roads, some argument could be raised against the method employed for data collection, Nevertheless, our analysis failed to detect any consistent associations between the populations and the roads variable.

The association of *invasive* and *established* populations with disturbed riparian habitats is in agreement with the results reported by Levine and Stromberg (2001) for southeastern United States and by Nagler et al (2011) for western United States. According to these authors,

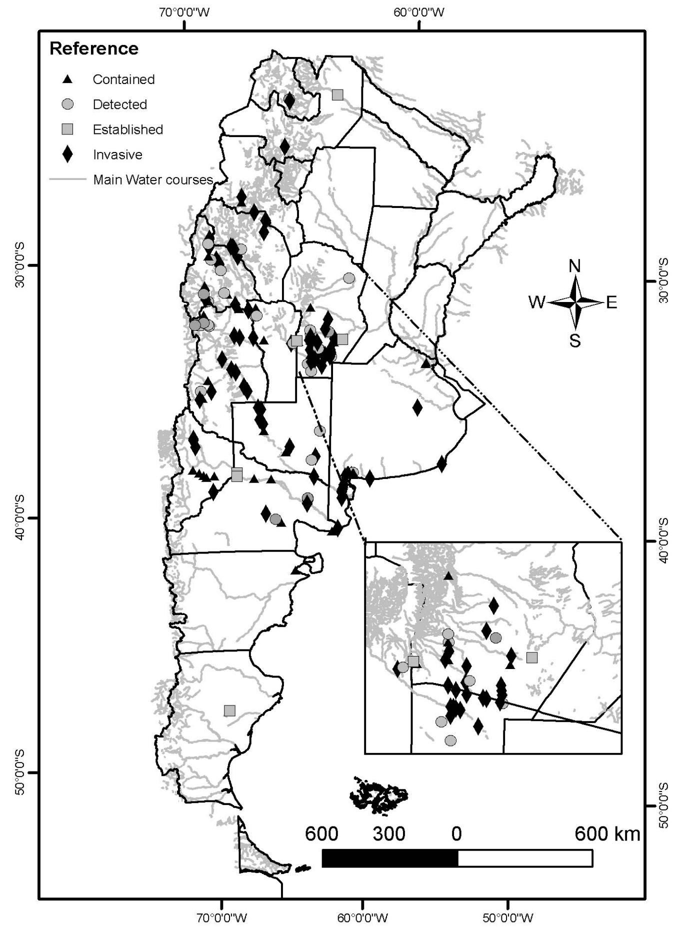

Figure 3. Distribution of the genus *Tamarix* in relation to the main watercourses.

changes in the water regime could inhibit recruitment of native plants, and therefore create ‘functional gaps’ in riparian communities. These unoccupied niches become prime colonization sites for more opportunistic, stress-tolerant, or xerophytic plants, and can trigger large-scale replacement of riparian vegetation by homogeneous stands of native plants or exotic species. Accordingly, *Tamarix* species have many traits that may contribute to successful colonization, including a high degree of stress tolerance and reproductive plasticity (Glenn and Nagler 2005; De Loach et al 2000). On the other hand, the *invasive* populations studied were also found to be associated with natural watercourses, coinciding with Nagler et al. (2011) and reinforcing the ideas proposed by Whiteman (2006) that human intervention is not a requirement for *Tamarix* expansion along rivers and streams. Patches classified as *detected in nature* were also associated with pristine watercourses, suggesting that these environments might act as natural dispersion pathways to vulnerable habitats.

The relationship between *invasive* populations and flooding areas could reflect the importance of water availability due to flood events or phreatic level rises for the establishment and subsequent dispersion of *Tamarix* populations. Accordingly, the relationship between *Tamarix* populations, watercourses and soil drainage is noteworthy; populations classified as *invasive* or *detected in nature* are either near a river or a stream or, when far from a watercourse, growing on a poorly drained soil; giving them eventual access to a watersource. This assumption is consistent with results reported by Natale et al. (2010a), who experimentally determined that *T. ramosissima* was very sensitive to water deficit, with an absence of recruitment with soil osmotic potential below -0.4 MPa. This value is common in soils that are considered to have good water availability level, such as those in the sub-humid region of Argentina. The dominance of *contained* populations in areas away from watercourses could reflect the difficulties of *Tamarix* to spread in absence of aquatic pathways.

Contrary to other invasive species growing along roadsides that are unable to colonize less disturbed natural environments (Pauchard and Alaback 2004) and in agreement with the results reported by Gelbard and Belnap (2003) for southern Utah, our results suggest that roads may serve as introduction points or as propagule reservoirs more than a necessary pathway along which *Tamarix* would disperse. The presence of *invasive* populations near roads would probably be a consecuence of planting *Tamarix* on roadsides to stabilize road margins in flooding areas. Thus, a propagule source would have been put in contact with a potentially receptive environment (wetlands).

Likewise, *contained* populations are consistently associated with cities and villages, where they are typically established near watercourses. Therefore, human settlements may be complementary propagule sources. Spread from these nuclei may occur through wind or watercourses.

Land use does not only affect the invasion process by creating new sources of propagules but also by modifying disturbance regimes and environmental conditions. Areas with high human intervention, such as agricultural or urban landscapes, usually serve as sources for invasion into more pristine environments (Pauchard and Alaback 2004). This may explain the close relationship found between *Tamarix established* populations and farming soils, likely because of *Tamarix* ability to tolerate environmental stress conditions. Nevertheless, the presence of *invasive* and *detected in nature* populations of *Tamarix* in slightly disturbed environments supports the idea that *Tamarix* species are not limited to highly disturbed sites.

Hulme et al (2008), postulate that alien species may arrive and enter a new region through three broad mechanisms: importation of a commodity, arrival of a transport vector, and/or natural spread from a neighbouring region where the species is itself alien, we conclude that. These three mechanisms result in six main pathways, depending on the dregree of human intervention: voluntary release, escape, contaminant, stowaway, corridor and unaided. In this sense *Tamarix* introduction in Argentina responds to direct human intervention through the importation of the genus for shade cover, windbreak or fencing, and for the stabilization of railway banks. Thus, populations may have dispersed through different pathways, from escape, through natural or modified watercourses, to corridors, through roads, in a lower proportion.

Saltcedar were introduced into the United States in 1830 (De Loach et al 2000; Di Tomaso 1998), in 1900 in México (Chambers and Hawkins 2004; Hart et al. 2005) and in 1930 in Australia (Australia Weeds Committee 2004); In Argentina the earliest record found is from 1720 but it became oftenly registered in the 1900s. Although this early introduction of the specie in Argentina, the invasion process here does not seem to be as serious as the cases reported in the USA, Mexico and Australia (Glenn and Nagler 2005). This could be due to a lower initial propagules pressure or the fact that the environment where saltcedar was introduced was not suitable to facilitate the dispersion and invasion processes.

Finally, considering the special challenges associated with the control of invasive plants in riparian environments and flooding areas, where the use of chemicals and heavy machinery is particularly complex, we recommend implementing prevention actions. In this sense the elimination of propagule sources would be a better option to treat invaded areas by considering direction of water flow and prevailing winds.

Acknowledgements

Evangelina Natale and Sergio Zalba received financial support from CONICET (Consejo Nacional de Investigaciones Científicas y Técnicas, Argentina). This work was funded by Secyt-UNRC (H. Reinoso). The experiments described in this article meet the current laws of Argentina. The authors wish to thank Verónica Andreo, Jorgelina Brasca and Ana Laura Monqaut for reviewing the language of the manuscript.

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