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REVIEW

Feasibility assessment for the classical biological control of *Tamarix* in Argentina

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Abstract Saltcedars are woody plants in the genus *Tamarix* L. (Caryophyllales: Tamaricaceae) and are native to Eurasia and Africa. Several species have become invasive in the Americas, Australia and South Africa. In Argentina there are four species of *Tamarix* distributed in arid, semi-arid and coastal areas of most provinces. The taxonomic isolation of *Tamarix* spp. in Argentina, their widespread distribution, negative impact to natural areas and lack of impact from existing natural enemies all indicate that *Tamarix* is an ideal candidate for classical biological control in Argentina. Biological control of *Tamarix* spp. has been rapid and highly successful in the USA after the introduction of four *Diorhabda* spp. (Coleoptera: Chrysomelidae). Biological control of *Tamarix* spp. in Argentina could be implemented easily, rapidly, and at a low cost by utilizing the information developed in the USA.

Keywords Tamaricaceae · Chrysomelidae · Invasive species · Test plant list · Niche modeling · Potential distribution

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Introduction

Invasive exotic plants constitute threats to economic activity and human welfare (Mack et al. 2000), and are also one of the greatest threats to rare, endangered, and threatened species (Simberloff et al. 2013). Exotic trees are among the most widespread and damaging invasive species (Richardson and Rejmánek 2011). In the past few decades invasive trees have escalated in importance worldwide due to the rapid increase in the human-mediated transport and dissemination of thousands of species for a wide range of purposes namely, forestry, agroforestry, ornamental horticulture and food production (Richardson et al. 2014). According to the National System on Information on Exotic Invasive Species of Argentina (INBIAR-UNS 2016), there are 90 invasive alien shrubs and trees in Argentina, many of which cause major ecological and economic problems. Among these, saltcedars, *Tamarix* spp. (Caryophyllales: Tamaricaceae), are widely colonizing riparian and wetlands systems in arid and semi-arid inland and coastal areas of Argentina (Natale et al. 2008, 2013; APN-SIB 2016). Native to Eurasia and Africa, several *Tamarix* spp. have also become invasive weeds in USA, Mexico, Australia and South Africa after their introduction for ornamental, windbreak, shade tree, sand dune stabilization, and erosion control (Pasiecznik 2016). Environmental changes associated with *Tamarix* proliferation in invaded areas include water course modifications, recruitment within riverbeds that can block the flow of rivers and cause flooding events, displacement of native vegetation, soil salinization and increased fire frequency (DeLoach et al. 2000).

In Argentina, although *Tamarix* seem to be at early stages of their invasion process, there remains the potential to invade more than three quarters of the arid and semi-arid areas of the country, constituting one of the main threats to biodiversity (Natale et al. 2013). *Tamarix* is reported as an invasive weed in several protected natural areas of Argentina (APN-SIB 2016), including the Llancanelo and Guanacache lakes, two RAMSAR sites in the Cuyo region of central-western Argentina (FAO GEF 2017; INBIAR-UNS 2016). Due to the socio-economic impact and effect on biodiversity, the *Tamarix* species complex has been prioritized as one of the six pilot programs of the National Strategy on Invasive Alien Species (NSIAS) (FAO GEF 2017).

Damage from invasive species cannot easily be reversed, and once established, invaders often persist indefinitely and spread to their ecological limits (van Driesche et al. 2010). Current methods to limit the continued spread of *Tamarix* in Argentina rely on mechanical removal and chemical treatments (Sosa et al. 2006; Natale et al. 2014). However, to achieve *Tamarix* suppression or prevent expansion at the landscape level, classical biological control (CBC) should be considered and integrated with other control approaches. Weed CBC constitutes an ecologically sound, cost effective, and sustainable control option as a component of an integrated pest management program (van Driesche et al. 2010).

Biological control of *Tamarix* spp. has been rapid and highly successful in the USA after the introduction of four *Diorhabda* spp. (Coleoptera: Chrysomelidae) (Pattison et al. 2011; Hultine et al. 2015; DeLoach et al. 2014). When a CBC project has been successful in one country, the costs associated with the exploratory surveys, risk assessments and rearing procedures of suitable biological control agents are considerably reduced in other countries. Transferring this technology from one country to another has been defined as the "fast track" or "short route" (Harley and Forno 1992). As a consequence, biological control of *Tamarix* spp. in Argentina could be expedited and developed at a lower cost by utilizing the information developed in the USA.

The *Diorhabda* spp. introduced into the USA may share similarly narrow host ranges but they respond differently to environmental conditions (Milbrath and DeLoach 2006; Dalin et al. 2010), latitude (Bean et al. 2007) and invertebrate predation (Knutson et al. 2014) that will likely influence the establishment, spread, and success of *Diorhabda* spp. in suppressing *Tamarix* in Argentina. To investigate environmental factors, Maximum Entropy Species Distribution Model (MaxEnt) was developed to assess the suitability of Argentina's climate for colonization by *Diorhabda* spp., their potential distribution and resulting overlap of the herbivores and their host *T. ramosissima* Ledeb. (Phillips et al. 2006).

The objective of this work is to examine the suitability of *Tamarix* spp. as a target for CBC in Argentina. Here we present and discuss factors relating to CBC feasibility, including: (1) taxonomy and geographic distribution, (2) environmental and economic damage (3) available control methods, (4) uses of *Tamarix* in Argentina and potential conflicts of interest (5) potential for classical biological control of *Tamarix* spp. in Argentina and (6) suitability of Argentina's climate for colonization by *Diorhabda* species.

Taxonomy and geographic distribution

The Tamaricaceae are found in temperate and subtropical regions of Africa and Eurasia (Stevens 2001). This family comprises about 100 species in five genera: *Hololachna* Ehrenb., *Myricaria* Desv., *Reaumuria* L., *Myrtama* Ovcz. & Kinzik., and *Tamarix* L., which is the largest genus containing 54 species (Crins 1989). Originating from western China, *Tamarix* has radiated to Mongolia, Korea, India, and across the Middle East to the eastern Mediterranean area, southern Europe, and northeastern and southern Africa (Crins 1989; Pasiecznik 2016). Although no *Tamarix* species occur naturally in the western hemisphere or in Australia, a few species have become naturalized and invasive in deserts and semi-arid areas of North America, Australia, South Africa and South America (Pasiecznik 2016).

In Argentina, *Tamarix* occurs along a wide range from 49°14′11″ to 23°26′17″S, and from 70°35′45″ to 56°59′46″W (Fig. 1). To date, four species of *Tamarix* are found in Argentina, namely: *T. gallica* L., *T. ramosissima* Ledeb., *T. chinensis* Lour. and *T. parviflora* DC. (Natale et al. 2008). Hybridization between *T. ramosissima* and *T. chinensis* has been reported in their invaded ranges in USA (Gaskin and Kazmer 2009). However, in Argentina, this phenomenon has, so far, not been reported (Natale et al. 2012). The first three species colonize natural and semi-natural habitats, although *T. ramosissima* has the highest number of invading populations and is considered to be the most aggressive species (Natale et al. 2008).

The Tamaricaceae have been historically considered the sister family of the Frankeniaceae for sharing morphological characters and secondary chemistry (Gaskin et al. 2004). Both families are placed in the order Caryophyllales (Stevens 2001) (Fig. 2). The Frankeniaceae is a small family of four genera and ca. 80 species of small halophytic shrubs or herbs of mostly temperate distribution, where *Frankenia* is the largest genus and the only genus of the family that is native to the western hemisphere (Whalen 1987). Ten species of *Frankenia* occur in southern South America, seven of which occur in Argentina (Zuloaga and Morrone 2009).

Environmental and economic damage

The effects of *Tamarix* invasions, specifically of *T. ramosissima,* have been well-documented in riparian areas (Shafroth et al. 2005). In western USA, *Tamarix* is considered one of the most dominant complexes of woody species, occupying 470,000–650,000 ha across 23 western states (Zavaleta 2000). *Tamarix* roots bind together gravel and cobble riverbeds, resulting in enlarged bars and narrowed channels that increase the likelihood of floods (Cooper et al. 2003). *Tamarix* negatively affects the structure and function of riparian ecosystems by affecting habitat quality for wildlife, reducing biodiversity and altering food webs (Zavaleta 2000; Shafroth et al. 2005). *Tamarix* spp. have displaced native plant communities and may be a major contributor to the decline of many native plants and animals, including endangered species (Dudley and DeLoach 2004). Other effects of *Tamarix* invasions include limiting recruitment of native riparian trees (e.g. *Populus* and *Salix* species) through increased salinity (Dudley and DeLoach 2004) and suppression of arbuscular mycorrhizal fungal communities (Beauchamp et al. 2005). The leaf litter and foliage produced by *T. ramosissima* is flammable and encourages the spread of wildfires (DeLoach et al. 2000). Native vegetation and wildlife is destroyed in these fires, while *T. ramosissima* seedlings are able to increase their spread due their ability to re-sprout more successfully than native plants following fire (Drus et al. 2012).

Tamarix thickets can cause increased water loss in riverine systems via transpiration (Shafroth et al. 2005). In arid areas of the western USA, losses of stream-flow and ground water caused by *Tamarix* are estimated at US$133 to $285 million annually (Zavaleta 2000). Other economic losses include reduced utilization of parks and natural areas by hunters, fishermen, campers, bird watchers, wildlife photographers and others (Pasiecznik 2016). Losses due to non-consumptive, recreational uses in Arizona and New Mexico were estimated at US$29.5 and US$15.8 million per annum, respectively (Pasiecznik 2016).

There is no estimation of the economic impact caused by invasive alien species in Argentina (FAO GEF 2017). However, developing countries in general, like Argentina, are particularly vulnerable to the threats posed by invasive species. Invasive species can have a disproportionate impact on the biodiversity and economies of developing countries because these countries typically rely more heavily on agriculture, forestry and fishing than more developed countries, and have fewer resources to combat them (GISP 2007). In Argentina, *Tamarix* spp. affect the social and economic value of both highly productive land and subsistence agriculture areas (Natale et al. 2010). Also, the *Tamarix* spp. threaten biodiversity and

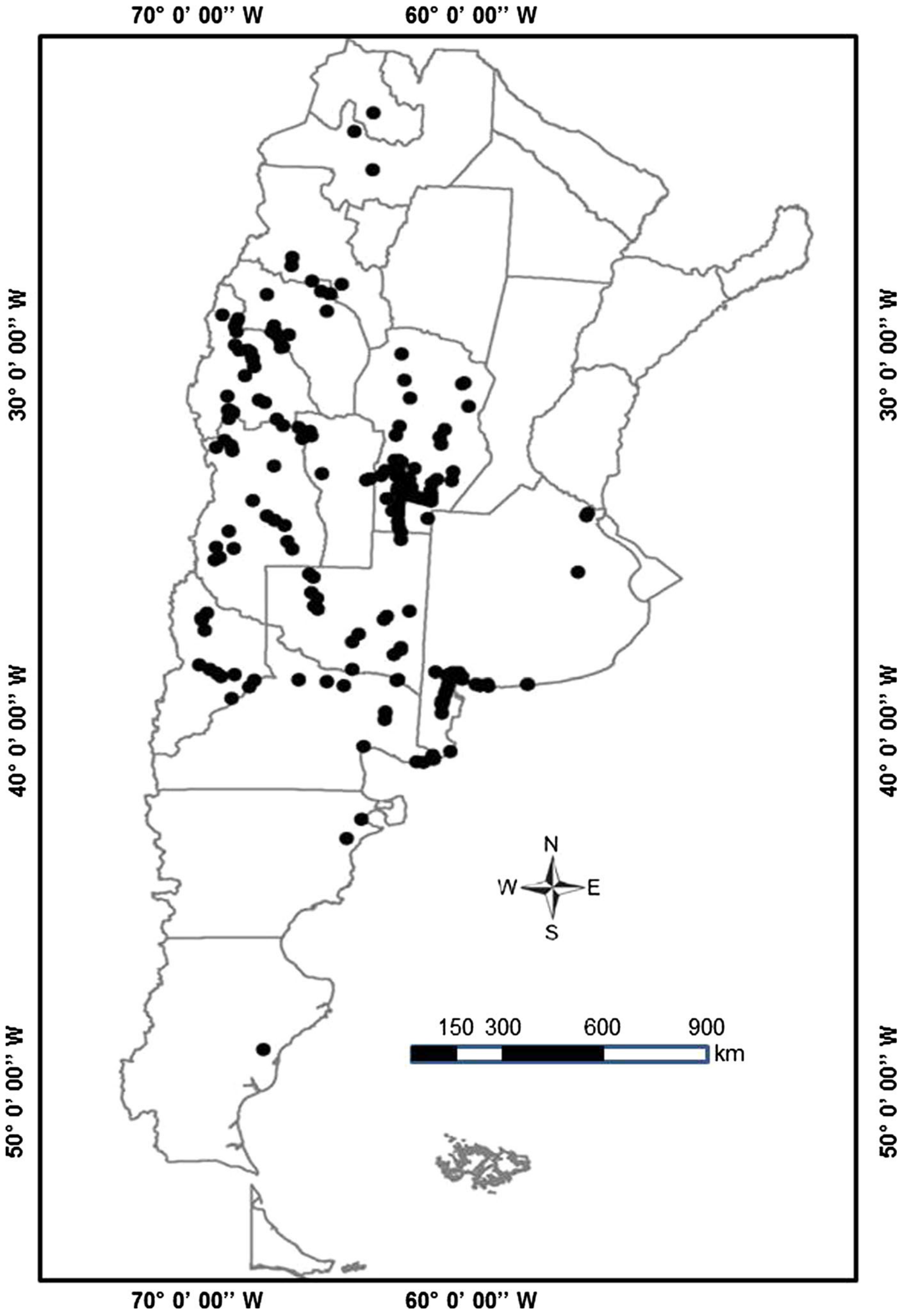

Fig. 1 Distribution of *Tamarix* spp. in Argentina (from Natale et al. 2008)

conservation in dry ecosystems, including national parks and several protected areas, because of these species' superior capacity to access and take up groundwater (FAO GEF 2017; APN-SIB 2016). At the RAMSAR site of Llancanelo Lake Reserve in the Cuyo region, *Tamarix* affects soil salinization, hydrological changes, loss of wild habitat and nesting sites for aquatic birds (Sosa et al. 2006).

Uses of *Tamarix* in Argentina and potential conflicts of interest

Species of *Tamarix* are mainly used as ornamentals, windbreaks, shade trees and for dune fixation along the coasts (Hurrell et al. 2004; Karlin et al. 2010). *Tamarix* spp. flowers constitute a nectar source for honeybees and are used as an astringent for treating diarrhea and

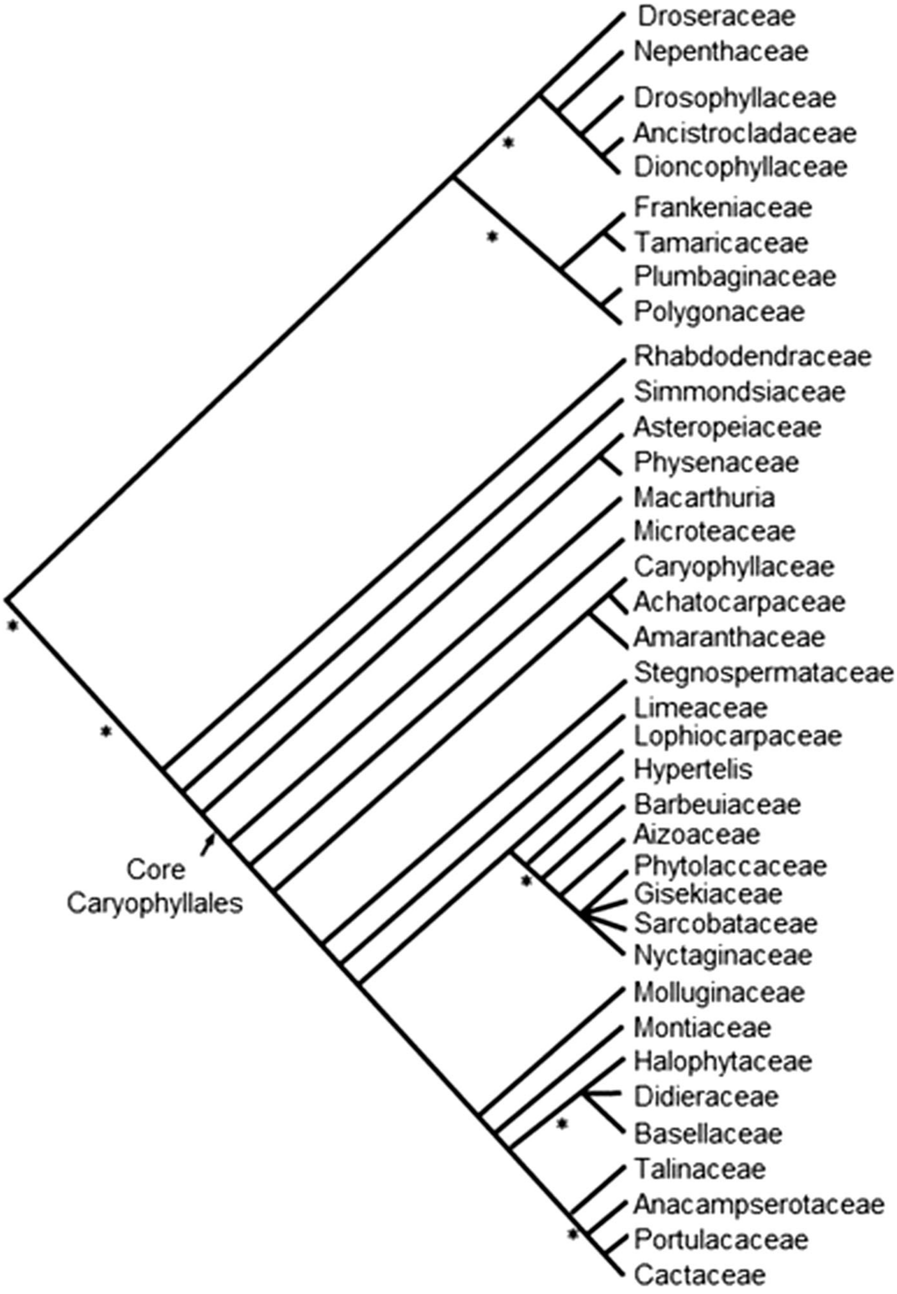

Fig. 2 Phylogenetic tree of the Order Caryophyllales (http://www.mobot.org/mobot/research/apweb/orders/Caryophyllalesweb.htm). * Denotes nodes with 50–80% bootstrap support; *unmarked nodes* have > 80% support

other diseases (Hurrell et al. 2004; Karlin et al. 2010). Tender branches and leaves provide forage to livestock particularly during the dry period (Karlin et al. 2010). *Tamarix* wood is used as fuel and to construct fences and cattle pens (Hurrell et al. 2004; Karlin et al. 2010).

Biological control of *Tamarix* resulted in tree mortality and facilitated the recruitment of other native plants in large areas of the western USA after the introduction of four species of *Diorhabda* beetles (Table 1) (Pattison et al. 2011; Hultine et al. 2015; DeLoach et al. 2014). However, the rate of weed suppression has raised some concerns in terms of conflicts of interest between land managers seeking control of the exotic plant and conservationists who seek to protect the southwestern willow flycatcher

Table 1 *Diorhabda* species released for biological control of *Tamarix* spp. in the western USA

Species	Common name	Origin	USA range
D. carinata	Larger tamarisk beetle	Qarshi and Buchara, Uzbekistan	Northern Texas
D. carinulata	Northern tamarisk beetle	Fukang and Turpan, China; Chilik, Kazakhstan; Buchara, Uzbekistan	Utah, Colorado, Nevada, Southern California
D. elongata	Mediterranean tamarisk beetle	Crete (nr Sfakaki) and Posidi Beach, Greece	Northern California, West Texas
D. sublineata	Subtropical tamarisk beetle	Sfax, Tunisia and southeast of Marith, Tunisia	South Texas

(*Empidonax traillii extimus*) (SWF), an endangered subspecies using this non-native plant as nesting habitat in some western riparian ecosystems (Dudley and DeLoach 2004; Sogge et al. 2008). The primary concern of USA wildlife agencies was that *Tamarix* defoliation by the *Diorhabda* biocontrol agents could reduce tamarisk canopy cover over the nest site, exposing the southwestern willow flycatcher birds in the nests to excessive heating and desiccation, particularly because this species breeds relatively late in the season (Sogge et al. 2008; Dudley and Bean 2012).

In Argentina, the crowned solitary eagle (CSE, *Buteogallus coronatus*), which inhabits semi-arid environments in the north central part of the country, is listed as one of the 18 endangered bird species (BirdLife International 2017) and was documented to nest on *Tamarix gallica* (Maceda 2007). The CSE nest is a large platform of sticks located on the top of larger trees with good access from the air (Maceda 2007). Nest records of CSE include an important diversity of native (e.g. *Prosopis*, *Aspidosperma Phyllostylon, Schinopsis*) as well as exotic trees (e.g. *Eucaliptus* sp. *Ulmus pumila*) and man-made structures (Maceda 2007).

Considering the plasticity of the CSE to building its nests, it seems unlikely that *Tamarix* bioncontrol using *Diorhabda* beetles and CSE conservation represents a conflict of interest in Argentina. However, the controversy between *Tamarix* biocontrol and the SWF in the USA emphasizes the need for a restoration plan to mitigate possible negative consequences of exotic plant decline when passive recruitment of native species is slower than desired (Dudley and Bean 2012). The *Tamarix* control pilot program within the NSIAS in Argentina foresees the implementation of mitigation measures by recruiting native plant species in the *Tamarix* control areas (FAO GEF 2017). In addition, installation of artificial platforms could also be considered as a tool for management and conservation of the CSE if the birds are reluctant to roost on defoliated plants.

Control methods

Many efforts have been committed in recent decades to control *Tamarix* in the western USA, where it is an important invasive alien weed of floodplains and wetlands (Dudley and DeLoach 2004). Conventional control methods for *Tamarix*, *i.e*. mechanical removal and chemical treatments, benefited native species in numerous locations, and promoted a return of surface flows in some cases (Egan 1997). Yet the benefits of these approaches did not provide a permanent control of the problem as *Tamarix* often grew back or reinvaded from surrounding areas (Carruthers et al. 2006). In addition, such control methods incur high financial expenditures and entail collateral damage to associated aquatic resources and non-target native riparian vegetation (Dudley and DeLoach 2004). Also, these labor and technology-intensive approaches are difficult to apply in remote or inaccessible habitats, and treated sites exhibit a high frequency of re-infestation (Shafroth et al. 2005). Hand removal by pulling seedlings effectively kills the plants and causes little damage to native plants but is labor intensive and too expensive except in small patches (Pasiecznik 2016).

In addition to the conventional control methods, a classical biological control program for *Tamarix* spp. was initiated in the 1960s in California and continued as a major US Department of Agriculture–Agricultural

Research Service program (USDA-ARS) in the 1980s and early 1990s with overseas explorations in France, Israel, Turkmenistan, China and Kazakhstan (DeLoach et al. 2000, 2014). Surveys of *Tamarix* natural enemies in the weed's native range resulted in the enumeration of over 100 associated herbivores (Carruthers et al. 2008) and various populations of what was considered the leaf beetle *Diorhabda elongata* (Brullé) were collected in Eurasia and North Africa between 1992 and 2002. More recently, however, a taxonomic revision by Tracy and Robins (2009) organized a complex of five fully diagnosable species of tamarisk beetles. Although the four closely related *Diorhabda* species used in the North American tamarisk biological control program (Table 1) were separable using molecular methods, hybrids could be formed by making interspecific crosses between these four species, particularly between the Mediterranean tamarisk beetle and the subtropical tamarisk beetle (Bean et al. 2013). Based on this revision, it is now understood that *Diorhabda carinulata* (Desbrochers) was imported to the USDA containment facilities in Temple, Texas and Albany, California for host specificity testing (DeLoach et al. 2003; Lewis et al. 2003a, b; Milbrath and DeLoach 2006; Herr et al. 2014). After seven years of study, *D. carinulata* was determined to be sufficiently host-specific for introduction into the US in July 1999 (Carruthers et al. 2008). Initial releases were made in 2001 in the states of California, Colorado, Nevada, Texas, Utah, and Wyoming (DeLoach et al. 2014). Although most of the beetle releases did not result in establishment (DeLoach et al. 2004), at some sites the beetle overwintered, dispersed, and the resulting defoliation of extensive *Tamarix* stands in select areas has been reported (Carruthers et al. 2008). By 2014 this species had controlled a total of 5335 stream km of *Tamarix* in Nevada, Utah, Colorado, north western New Mexico, and northern Arizona (DeLoach et al. 2014). Three other *Diorhabda* species have also been introduced into the USA: *D. sublineata* (Lucas), *D. carinata* (Faldermann) and *D. elongata*. *D. elongata* was released in California in 2003 and all three were released in west Texas since 2006. Releases of the *Diorhabda* spp. in California and Texas resulted in lower levels of control than *D. carinulata*, but included ca. 40% of the *Tamarix*-infested riparian areas in Texas and defoliation was observed over large areas for 2–4 consecutive years (Knutson et al. 2014). *Diorhabda* spp. adults and larvae feed on the foliage and sometimes also on the epidermis of young shoots of *Tamarix*. The larvae pupate under litter on the ground and the adults overwinter there (Lewis et al. 2003a, b). Day length appears to be the strongest factor inducing overwintering diapause for *D. carinulata*, and likely the other three sp. released in the USA (Bean et al. 2012; Dalin et al. 2010). The successful population buildup of *D. carinulata* and resulting damage to *Tamarix* in North America is influenced by adaptations to critical day lengths, with adults seeking overwintering sites when days are lower than 14 to 15 h for given latitudes (Bean et al. 2012).

In Argentina, attempts to control *Tamarix*, have focused on physical, mechanical and chemical methods (Sosa et al. 2006; Natale et al. 2014). In 2006, a *Tamarix* eradication program was implemented at the Llancanelo Lake Provincial Natural Reserve in Mendoza (Sosa et al. 2006). Small plants and shrubs of *Tamarix* were extracted by hand or with hand tools in an area of ca. 12 ha around the lake edge (Sosa et al. 2006). At the same lake, the municipality of Malargüe, Provincial Park Administration and local communities implemented a monitoring and control program for *Tamarix* that involves felling the trees with chainsaws (http://losandes.com.ar/article/view?slug=erradicaran-los-tamarindos-en-llancanelo). In addition, a pilot research program for *Tamarix* spp. is being implemented as part of the NSIAS in two natural protected areas of high conservation value in the Cuyo region (FAO GEF 2017). The objective of the research program is to implement a management strategy for *Tamarix* and restoration of biodiversity and ecosystem services in 180 ha (90 ha in the Llancanelo lake area and 90 ha in the area of the Guanacache, Desaguadero and Del Bebedero lakes) (FAO GEF 2017).

Potential for classical biological control of *Tamarix* in Argentina

A standard practice of a CBC programs involves documentation of herbivores attacking the target weed in its adventive range to determine if natural enemies must be introduced from the native range of the weed. A few generalist insect herbivores are known to be associated with *Tamarix* in Argentina: *Ceroplastes formicarius* Hempel, *Ceroplastes* sp., *Coccus hesperidum* (L.) (Hemiptera: Coccidae), *Automeris* *aspersa* (Felder), *A. melanops* (Walker) (Lepidoptera: Saturniidae), *Criptoblabes gnidiela* (Milliere) (Lepidoptera; Pyralidae), *Oiketicus kirbyi* Guilding, *O. platensis* Berg (Lepidoptera: Psychidae), *Tolype pauperata* (Burmeister) (Lepidoptera: Lasiocampidae), *Bostrichopsis uncinata* Germ. (Coleoptera: Bostrichidae), and *Praxithea deroudei* (Chabrillac) (Coleoptera: Cerambicidae) (Cordo et al. 2004; Pastrana 2004). In addition, the exotic leafhopper *Opsius stactogalus* Fieber (Hemiptera: Cicadellidae), which is specific to the genus *Tamarix,* has been found to be common and abundant in Argentina, but it is not reported to cause any significant damage to *Tamarix* (Virla et al. 2010). This leafhopper, which has also been recorded in the USA, can cause significant damage to *Tamarix* plants in a cage setting (Louden 2010). However, the impact of this species in the field for controlling the growth and spread of naturalized tamarisk is generally thought to be insignificant (DeLoach et al. 2004). Considering that insect species associated to *Tamarix* in Argentina do not suppress plant fitness, the introduction of additional host-specific insects or pathogens may be the only economically feasible method to control the density and spread of *Tamarix* spp. on a large scale.

However, biological control is not a panacea and risks of introducing an exotic species must be considered. Risk of damage to non-target plants is highest with plants that are most closely related to the target species (Pemberton 2000). The relative taxonomic isolation of *Tamarix* is an important aspect in evaluating the safety of *Diorhabda* in Argentina. Host specificity studies conducted in the USA determine that the *Diorhabda* beetles host range was restricted to plant species of Tamaricaceae (*Tamarix* and the old World genus *Myricaria*) and Frankeniaceae (*Frankenia*) (DeLoach et al. 2003; Milbrath and DeLoach 2006). No *Diorhabda* larvae completed development on any of the other 54 species of Caryophyllales tested (e.g. Amaranthaceae, Droseraceae, Plumbaginaceae, Polygonaceae, Portulacaceae, Simmondsiaceae). Other plant species unrelated to *Tamarix*, but that shared its habitat (e.g. Asteraceae, Fabaceae, Salicaceae), and commercial crop plants (e.g. *Vitis vinifera* L., *Helianthus annuus* L., *Juglans regia* L., *Lactuca sativa* L., *Cucumis sativus* L., *Prunus americana* Marshall, Prunus dulcis (Miller) D.A. Webb, *Lycopersicon esculentum* and *Triticum aestivum* L.) were also tested, with negative results (DeLoach et al. 2003; Milbrath and DeLoach. 2006).

Open-field studies indicated that *Diorhabda* beetles could not thrive on *Frankenia*, although some adult and larval damage was observed on *F. salina* when *Diorhabda* beetle densities were extremely high, and all of the surrounding *Tamarix* had been totally defoliated (Dudley and Kazmer 2005). An open review process involving scientific representatives from various stakeholder organizations (state, county, university, and environmental groups) supported the redistribution of *Diorhabda* beetles in California owing to its impact on *Tamarix* and its negligible non-target effects (Herr et al. 2014).

Shipments of *Diorhabda* beetles established in North America could be obtained through international cooperation with the USA (e.g. USDA-ARS) to start a colony on potted plants of *Tamarix* at the National Institute of Agricultural Technology (Instituto Nacional de Tecnología Agropecuaria, INTA) containment facility, in Castelar, Buenos Aires, Argentina. Ten species of *Frankenia* occur in southern South America, seven of which occur in Argentina (Zuloaga and Morrone 2009) and constitute the only plants in the continent that are somewhat related to *Tamarix*. A test plant list for Argentina should include all the *Frankenia* species present in the country. In addition, upon request of Argentine regulatory authorities, certain species within non-core Caryophyllales families (e.g. Plumbaginaceae and Polygonaceae) could also be included in the specificity tests.

Suitability of *Diorhabda* species to *Tamarix* invasion in Argentina

To investigate Argentina's climate suitability for colonization by *Diorhabda* species, we modeled the potential distribution and resulting overlap of *D. carinulata, D. sublineata, D. elongata,* and *D. carinata* with their host *T. ramosissima* using the software MaxEnt, version 3.3.3 k (Phillips et al. 2006, found at http://biodiversityinformatics.amnh.org/open_source/maxent/). Presence data (GPS coordinates) for the *Diorhabda* spp. were extracted from Tracy and Robbins (2009), Nagler et al. (2014), and Sánchez-Peña et al. (2016) (Table 2). Occurrence data for *T. ramosissima* in Argentina was acquired from Natale et al. (2008) along with data from the Global Biodiversity

Table 2 MaxEnt modeling results for the exotic weed *T. ramosissima* and candidate biological control agents based on environmental parameters of Argentina

Species	Occurrence points	AUC	Omission rate	Highest suitability value
T. ramosissima	1074	0.928 ± 0.007	0.084 ± 0.020	0.677
D. sublineata	118	0.970 ± 0.017	0.126 ± 0.121	0.681
D. carinulata	85	0.971 ± 0.015	0.114 ± 0.107	0.205
D. elongata	118	0.979 ± 0.005	0.108 ± 0.073	0.269
D. carinata	97	0.984 ± 0.007	0.124 ± 0.089	0.011

Occurrence points represent the number of unique coordinates for a given species that were used for modeling purposes. Area under the curve (AUC), omission rate, and highest suitability value are comparative metrics generated by MaxEnt. These metrics represent the mean (± SD) for ten simulations

Information Facility's website (http://www.GBIF.org).

Altitude and 19 bioclimatic variables were downloaded in 2.5 arc-minute resolution raster format from WorldClim's online database (Hijmans et al. 2005). These data are interpolated from weather station data, and are derivations of temperature and precipitation data considered to be biologically relevant (Hijmans et al. 2005). Default MaxEnt settings were used (Rinnhofer et al. 2012; Mukherjee et al. 2012), with 10,000 pseudo-absence points randomly selected from the model background. Models were run ten times, with 70% of the dataset randomly selected for training to build the models and the remaining 30% used for testing (Mukherjee et al. 2011). The continuous outputs were converted to the binary categories of suitable or unsuitable habitat to simplify comparison of the two species' ranges. The maximum sum of sensitivity and specificity of training data was used as a threshold to convert output of continuous to binary values (Liu et al. 2013). ArcMap's Raster Calculator tool was used to calculate the predicted range overlap of the two binary suitability outputs (ESRI 2014).

The resulting models were tested using one-tailed binomial t-tests to determine if modeled predictions were significantly better than random models with the same fractional predicted area. The omission rate, or percentage of test points that fell outside of the binary predicted range, was also tested within MaxEnt. Additionally, ENMTools' Range Overlap tool was used to compare the beetle's individual habitat suitability models with that of *T. ramossissima* (Warren et al. 2008, 2010).

Each species' model predictions proved to be significantly better than random, with all 50 replicates of binary predictions having p-values < 0.01. All area under the curve (AUC) values were > 0.9 and thus considered "good" (Pearson et al. 2006) (Table 2). Test omission rates were similarly small, indicating limited error in the models. The subtropical tamarisk beetle, *D. sublineata*, had a markedly higher suitability value across Argentina as compared to its congeners (Table 2; Fig. 3). Range overlap between *T. ramosissima* and *D. sublineata* is estimated to be 44.2%, (Fig. 4) while *T. ramosissima* and the other three beetles had a near 0% overlap. The model results for *D. carinulata*, arguably the most important biological control agent of *Tamarix* in the USA, failed to identify any areas in Argentina deemed suitable habitat for the beetle (Fig. 5).

These models comparing environmental suitability indicate that climatic factors may markedly influence the colonization of *T. ramosissima* by the *Diorhabda* beetles if released in Argentina. Models predict two regions—one on the eastern coast and one in the northwest region of Argentina—that are predicted to be more suitable for colonization by *D. sublineata* (Fig. 3). Data also indicate, however, that the remaining natural enemies are poorly adapted to conditions in Argentina generally. Graphical results are presented for *D. carinulata* (Fig. 5) but similar output was also observed for *D. elongata* and *D. carinata*. These findings are not unlike the realized allopatric distributions of *Diorhabda* spp. in North America, with *D. carinulata* occurring primarily within the Great Basin and now dispersing into southern California while *D. sublineata* is established in southern Texas and is dispersing south into Mexico (Estrada-Muñoz and Sánchez-Peña 2014; Sánchez-Peña et al. 2016).

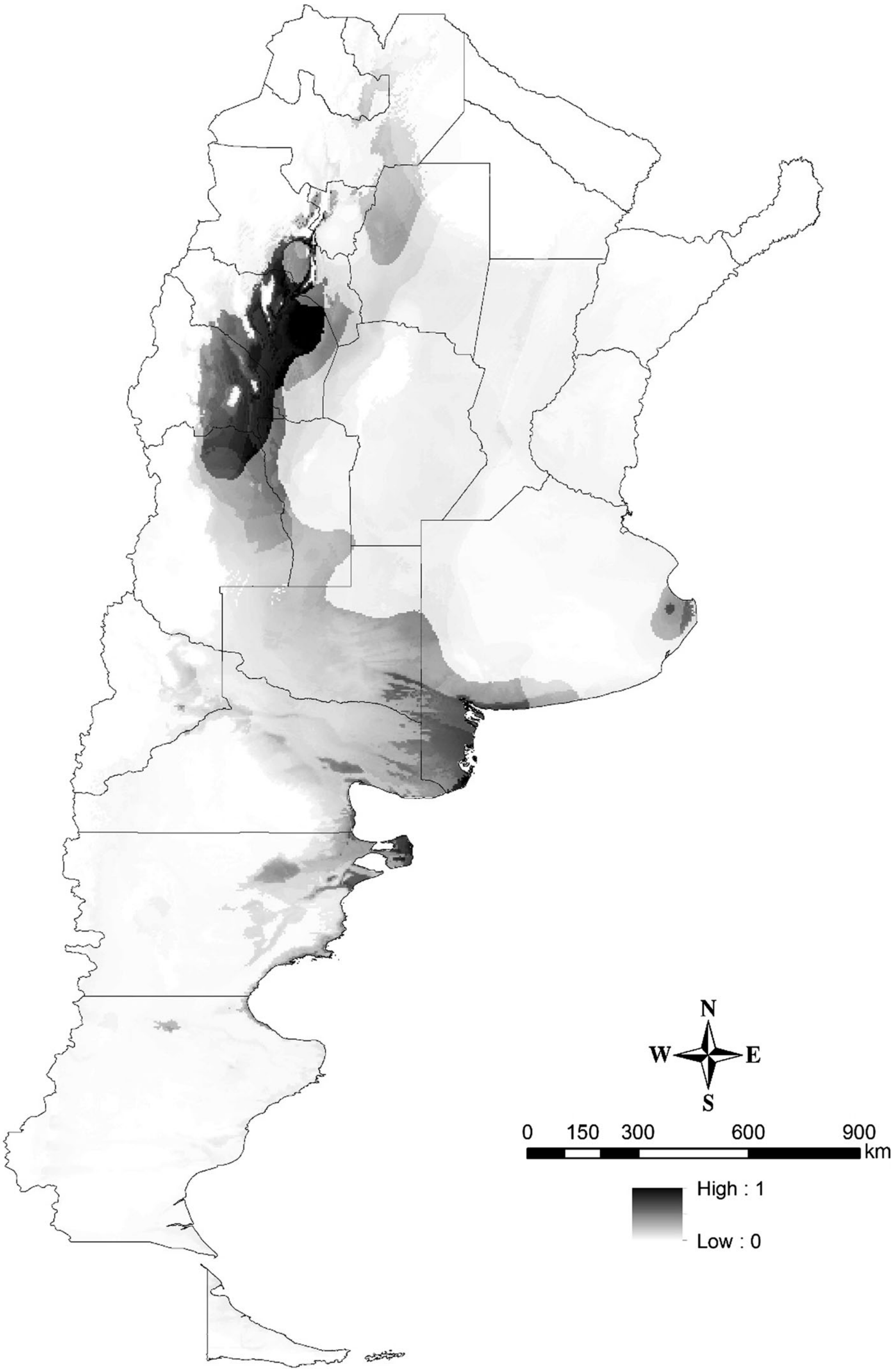

Fig. 3 Predicted geographic distribution of the candidate biological control agent *Diorhabda sublineata* across Argentina

It is clear that environmental factors will contribute to establishment and spread of the *Diorhabda* beetles in Argentina, but day length requirement is also a strong driver determining the suitability of beetles as biological control agents of *Tamarix*. As stated previously, populations of *Diorhabda* beetles in the USA respond to critical day lengths ≤ 14 h by switching from reproductive to overwintering strategies (Bean et al. 2012). In Cordoba, Argentina, a city near large stands of *T.*

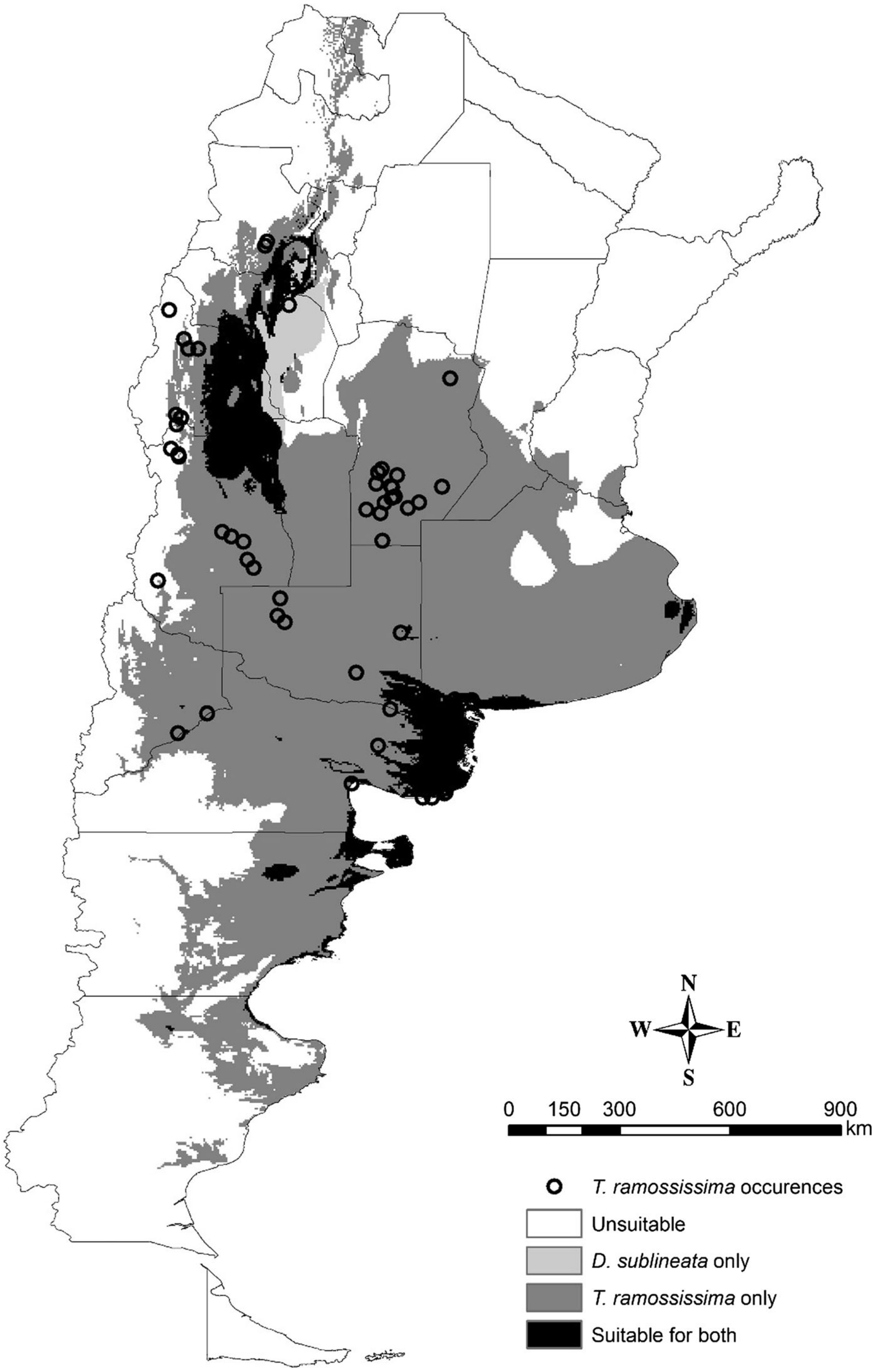

Fig. 4 Habitat suitability predictions for *Tamarix ramossissima* and the specialized herbivore *Diorhabda sublineata* for Argentina based on maximum entropy modeling

ramosissima, the longest day of the year experiences just 14 h of daylight. This indicates that current *D. carinulata* ecotypes present in the USA are poorly adapted to day length regimes in the weed's invaded range in Argentina, although in the USA *D. carinulata* is adapting to shorter critical

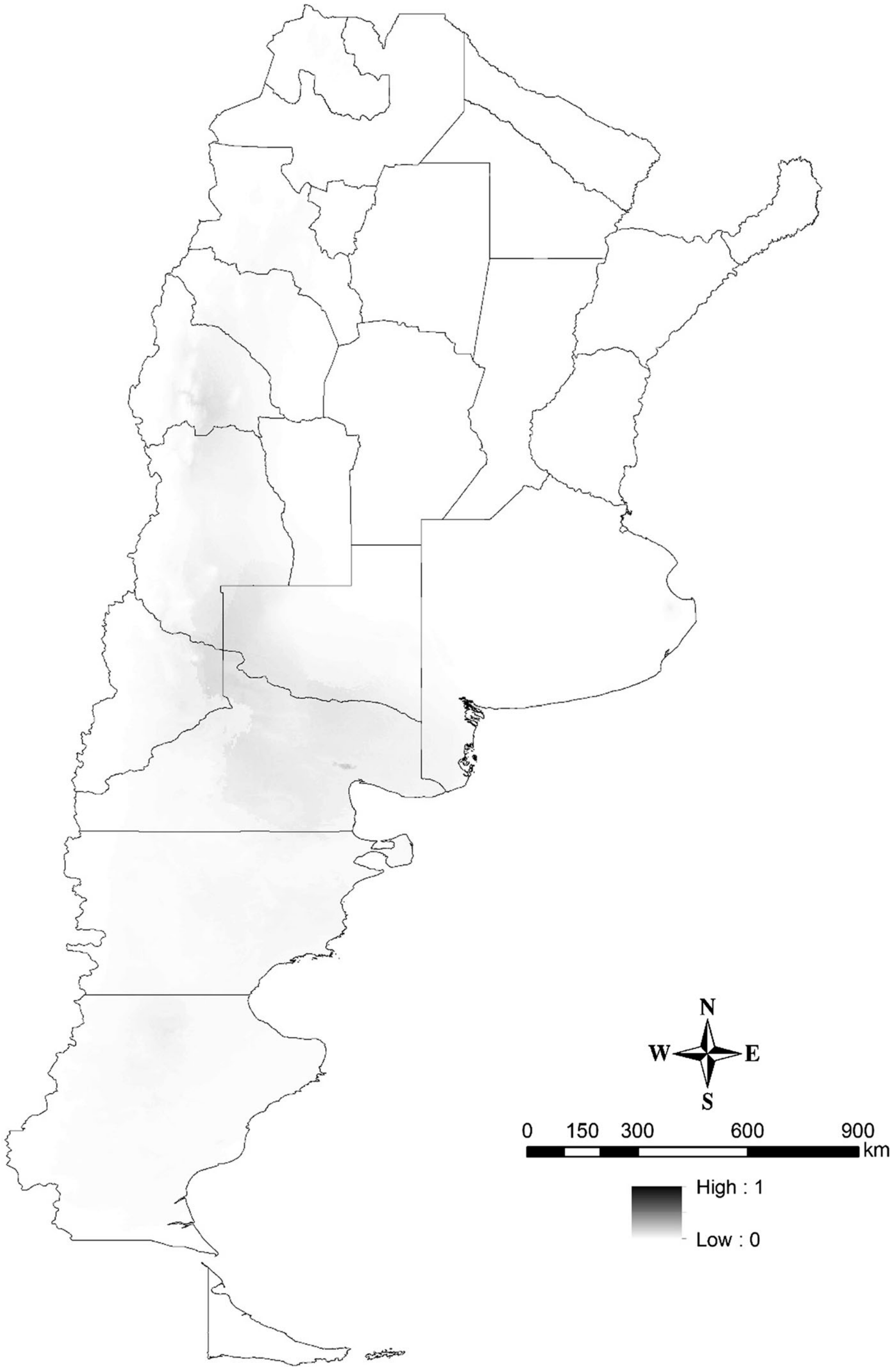

Fig. 5 Predicted geographic distribution of the candidate biological control agent *Diorhabda carinulata* across Argentina

day length over time (Bean et al. 2012). In contrast, *D. sublineata* appears to be better adapted to short critical day lengths in the USA and may be the best candidate for initial consideration for Argentina (Tracy and Robbins 2009).

Discussion

The taxonomic isolation of *Tamarix* spp. in Argentina, their widespread distribution, negative impact to natural areas and lack of impact from existing natural enemies all indicate that *Tamarix* is an ideal candidate for classical biological control in Argentina.

Piggybacking on the biocontrol program undertaken in the USA constitutes an opportunity for Argentina to reduce costs associated with the exploratory surveys, risk assessments and rearing procedures to implement biological control of *Tamarix* spp. in the country. Considering the host range tests performed in the USA and the taxonomic isolation of *Tamarix* spp. in Argentina, a minimal amount of additional host specificity testing would have to be conducted in Argentina to evaluate if *Diorhabda* beetles could be safely used as biological control agents against *Tamarix* spp. in Argentina.

Classical biological control implementation is often considered only after conventional control methods are deemed unsustainable or have failed to reduce weed population levels (Olckers 2004). However, high rates of success can be achieved by targeting weeds during the early stages of invasion (Olckers 2004). *Tamarix* spp. are widespread in Argentina, but its potential for invasion is probably at an early stage. *Tamarix* spp. have the potential to invade more than three quarters of the arid and semi-arid areas of the country (around 1.4 million km^2), constituting one of the main threats to biodiversity conservation (Natale et al. 2013). This implies that the problem could be attacked before it becomes even more widespread. Manual and herbicidal control can be effective in some areas, such as public parks and protected areas, but these approaches are not feasible at a landscape scale. In this context, it is proposed that integration of biological control with existing short-term control measures will reduce *Tamarix* abundance and spread. The implementation of a CBC program for *Tamarix* in Argentina is expected to contribute to the restoration of biodiversity and ecosystem services in protected areas of high conservation value and to the conservation of water resources in sensitive arid and semi-arid regions of Argentina.

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