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Potential Geographic Distributions and Successful Invasions of Parthenogenetic Broad-Nosed Weevils (Coleoptera: Curculionidae) Native to South America

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A. A. LANTERI,[1] N. V. GUZMÁN,[2,3] M. G. DEL RÍO,[1] AND V. A. CONFALONIERI[3]

ABSTRACT Ten species of parthenogenetic broad-nosed weevils (Coleoptera: Curculionidae: Entiminae) native to Argentina, southern Brazil, and Uruguay were selected for niche modeling analysis based on climatic data and altitude, to evaluate their potential range expansion inside and outside South America. The selected species belong to five genera of the tribe Naupactini affecting economically important crops. Until present, five of the 10 species analyzed here have invaded prairies and steppes of countries outside South America (Australia, New Zealand, Mexico, United States, and South Africa): *Aramigus tessellatus* (Say), *Atrichonotus sordidus* (Hustache), *Atrichonotus taeniatulus* (Berg), *Naupactus leucoloma* Boheman, and *Naupactus peregrinus* (Buchanan). Our niche modeling analyses performed with **MAXENT** demonstrated that these areas would be also suitable for *Aramigus conirostris* (Hustache), *Eurymetopus fallax* (Boheman), *Pantomorus auripes* Hustache, *Pantomorus ruizi* (Brèthes), and *Pantomorus viridisquamosus* (Boheman), consequently, they also have the potential to invade areas outside their native ranges, mainly in southeastern United States, some European countries (e.g., Portugal, France, and southern England), South Africa, New Zealand, and southeastern Australia. All the studied species share similar environmental requirements, the most important variables being the Mean Temperature of Driest Quarter, the Annual Mean Temperature and Isothermality. Long distance dispersal through commercial trade, and parthenogenetic reproduction would increase the threat of these weevils to crop production worldwide.

KEY WORDS parthenogenesis, invasive species, South American weevils, niche modeling, agricultural pests

The analysis of the potential geographic distributions of species is relevant to several disciplines, such as conservation biology and management of agricultural pests (Muirhead et al. 2006, Ferrer et al. 2007, Acosta 2008, Kumar and Stohlgren 2009). Invasive or introduced species are nonnative species accidentally or deliberately transported to new geographic areas where they subsequently establish breeding populations (Laverty and Sterling 2002, Kiritani and Yamamura 2003). They are considered the second most important threat to biodiversity after habitat loss (Giovanelli et al. 2007, Mercado–Cárdenas and Buddle 2007). In particular, the invasion of phytophagous insects through human activities (especially commercial trade) may increase the risk of establishment of new agricultural pests (Peterson and Nakasawa 2008). Phytosanitary policies against invasive agricultural pests and the appropriate management of their populations require information on habitat suitability (Baker et al. 2000).

Curculionoidea is the largest and most diverse lineage of Coleoptera, with ≈62,000 species (Marvaldi et al. 2002), several of which are economically important pests, for example, the "boll weevil" *Anthonomus grandis* Boheman, the "white-fringed weevils" of the *Naupactus leucoloma* Boheman species group, the "fruit weevil" *Naupactus xanthographus* (Germar), and the "fuller's rose weevil" *Naupactus cervinus* Boheman (Lanteri and Marvaldi 1995; Lanteri et al. 2002; Scataglini et al. 2006; Guzmán et al. 2007, 2012; Rodriguero et al. 2010b; del Río et al. 2010).

Apomictic (or ameiotic) parthenogenesis is quite common among the broad-nosed weevils of the subfamily Entiminae (Suomalainen 1962, Suomalainen et al. 1976, Smith and Virkki 1978, Lokki and Saura 1980, Normark 2003). This kind of reproduction, which is frequently associated with polyploidy and winglessness (Suomalainen 1969, Lanteri and Normark 1995), may increase the species' ability to establish in new areas because a single female at any stage of development has the potential to start a new population without male fertilization (Kearney 2005). Moreover,

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parthenogenetic weevils may have higher colonization abilities than their sexual counterparts, especially in areas of low biodiversity (Stenberg and Lundmark 2004). These weevils have generalized genotypes, allowing them to occupy more extreme environments and broader geographic distributions than their sexual relatives (Lynch 1984, Lanteri and Normark 1995, Guzmán et al. 2012).

Three parthenogenetic broad-nosed weevils of the genus *Otiorhynchus* have occasionally been introduced from the Old World into Argentina and Chile, damaging cherries and berries (cranberries, strawberries, etc.) cultivated in the Patagonian forests (del Río et al. 2010). Seven parthenogenetic species of the tribe Naupactini native to Argentina, southern Brazil and Uruguay, which belong to the *Pantomorus–Naupactus* complex (Scataglini et al. 2005), have become pests of pastures and several crops in Australia, New Zealand, and the United States. These species are the following: *Aramigus tessellatus* (Say), *Atrichonotus taeniatulus* (Berg), *A. sordidus* (Hustache), *Eurymetopus birabeni* Kuschel, *Naupactus leucoloma* Boheman, *N. minor* (Buchanan), and *N. peregrinus* (Buchanan) (Buchanan 1939, Chadwick 1965, Kuschel 1972, Lanteri et al. 2002).

The main objectives of this article are to assess the potential distributions of 10 weevil species belonging to five genera of the *Pantomorus–Naupactus* complex and to project the resulting models onto the whole world (map of global potential distribution), to predict future invasions into new environments and agroecosytems. These insects are native to Argentina, southern Brazil, Uruguay, and in some cases, to Paraguay; they are major pests of economically important crops, such as wheat (*Triticum aestivum*) and other cereals, lucerne (*Medicago sativa*), sunflower (*Helianthus annus*), and potato (*Solanum tuberosum*) (Lanteri 1994; Lanteri et al. 1997, 2002).

Materials and Methods

Species Analyzed and Their Geographic Distribution. The 10 weevil species selected for this study belong to the following taxa of Naupactini: *Aramigus* Horn (*A. conirostris* and *A. tessellatus*), *Atrichonotus* Buchanan (*A. sordidus* and *A. taeniatulus*), *Eurymetopus* Schönherr (*E. fallax*), *Naupactus leucoloma* species group (*N. leucoloma* and *N. peregrinus*), *Pantomorus auripes* species group (*P. auripes* and *P. ruizi*), and *Pantomorus viridisquamosus* species group (*P. viridisquamosus*) (Lanteri 1984, Lanteri and Loiácono 1990, Lanteri et al. 1991, Lanteri and O'Brien 1990, Lanteri and Díaz 1994, Lanteri and Marvaldi 1995). The remaining species of these taxa were not included in the current study because the small number of records available (<10 localities) precluded the analysis of potential distributions (Stockwell and Peterson 2002, Hernández et al. 2006, Lobo and Tognelli 2011, Pearson et al. 2007).

Samples were collected from natural vegetation (usually pastures) and crop fields, using sweeping entomological nets. Species' distribution records were derived from the following published sources: revisionary studies by Lanteri and colleagues (Lanteri 1984, Lanteri and Loiácono 1990, Lanteri and O'Brien 1990, Lanteri et al. 1991, Lanteri and Díaz 1994, Lanteri and Marvaldi 1995, Morrone and Lanteri 1991); literature documenting the occurrence of species outside their putative native range (Buchanan 1939, Chadwick 1965, Kuschel 1972, Elgueta 1993, Elgueta and Marvaldi 2006); and material collected and/or examined subsequent to the revisionary studies mentioned above (Guzmán et al. 2012), and deposited in different entomological collections: Charles W. O'Brien collection, Green Valley, USA (CWOB); Departamento de Zoología, Universidade Federal do Parana, Curitiba, Brazil (DZUP); Florida State Collection of Arthropods, Gainesville, USA (FSCA); Fundación e Instituto Miguel Lillo collection, Tucuman, Argentina (FIML); Museo de La Plata, Argentina (MLP); Museo Nacional de Historia Natural de Santiago, Chile (MNHS); Museu National de Histoire Naturelle, Paris, France (MNHN); Texas A and M University, College Station, USA (TAMU); Universidad de la República, Montevideo, Uruguay (URUC); and United States National Museum, Washington, DC, USA (USNM).

Tables of Supplementary Material (Tables 1–10 [online only]) provide information on the locations and geographic coordinates of the samples. The geographic areas where the studied species are native or were supposedly introduced and the main weevil species-host plant associations are detailed below.

Aramigus conirostris (Hustache) is found in central and northeastern Argentina (from Misiones and Salta to Buenos Aires provinces), Uruguay, and southern Brazil (Santa Catarina and Río Grande do Sul states) (Lanteri and Díaz 1994) (Supp. Table 1 [online only]). It is not frequently associated to crops, except lucerne, *Medicago sativa* (Lanteri et al. 2002).

Aramigus tessellatus (Say), like *A. conirostris*, is naturally distributed in Argentina, Brazil, and Uruguay, but with a wider and more southern distribution. In Argentina, it was recorded from Misiones and Jujuy in the north, to Rio Negro in the south; and in Brazil, from São Paulo to Río Grande do Sul (Lanteri and Díaz 1994). It is considered to have been introduced into central Chile (Araucania), Mexico (Chihuahua), and the United States, where it occurs from Nebraska, Iowa, and Illinois in the north, to Texas in the south (Buchanan 1939, Elgueta and Marvaldi 2006) (Supp. Table 2 [online only]). *A. tessellatus* is a pest of cereals such as wheat (*Triticum aestivum*), oat (*Avena sativa*), and barley (*Hordeum vulgare*) (Lanteri et al. 1997). It also attacks lucerne (Lanteri 1994), sunflower (*Helianthus annus*), and potato (*Solanum tuberosum*) (Lanteri et al. 2002). Lucerne is the main cultivated host in Chile and Uruguay (Alzugaray et al. 1998, Elgueta 1993). It is also associated with raspberries (*Rubus* spp.) and pears (*Pyrus* spp.) in Chile (Elgueta 1993) and wild pastures in the United States. Morphological and molecular analyses demonstrated that *A. tessellatus* forms a highly variable species complex with several morphotypes (Lanteri and Díaz 1994,

Normark and Lanteri 1998), each of which is probably adapted to a particular micro environment.

Atrichonotus sordidus (Hustache) is native to central–eastern Argentina, Uruguay, and southern Brazil (Rio Grande do Sul), and was introduced into Australia (New South Wales) along with crops (Chadwich 1965, Lanteri and O'Brien 1990) (Supp. Table 3 [online only]). In Australia, *A. sordidus* is associated with Iceland poppy (*Papaver nudicaule*), *Clerodendrum* spp., lily (*Allium* spp), clover (*Trifolium repens*), beans (*Phaseolus* spp), oat (*Avena sativa*), and rye (*Secale cereale*) (Chadwick 1965), but its occurrence in the wild is unknown. In Argentina it usually attacks pastures and cereals (Lanteri et al. 2002), and in Uruguay, clover (*Trifolium* spp.), lucerne and lotus (*Lotus* spp.) (Alzugaray et al. 1998).

Atrichonotus taeniatulus (Berg) is native to central–eastern Argentina and Uruguay and is thought to have been introduced in Chile (including Juan Fernández and Easter Islands), Australia (New South Wales and Western Australia), New Zealand (North Island), and the United States (southern states of Alabama, Florida, Georgia, Mississippi, and Texas) (Lanteri and O'Brien 1990) (Supp. Table 4 [online only]). It was first introduced into the United States in the early 1900s (Buchanan 1939) and into Australia and New Zealand during the 1960s (Chadwich 1965, Kuschel 1972). *A. taeniatulus* damages lucerne, sunflower, and pastures in Argentina (Lanteri and O'Brien 1990, Lanteri 1994, Lanteri et al. 2002); lucerne, lotus, and clover in Uruguay (Alzugaray et al. 1998); lucerne, pepper (*Capsicum annuum*), and bean in Chile (Elgueta 1993); ornamental plants and garden shrubs (dahlias, hibiscus, and roses) and *Eucalyptus* in Australia (Chadwick 1965); and lucerne, clover, and *Galega* spp. in New Zealand (Kuschel 1972).

Eurymetopus fallax (Boheman) was reported from several localities of north–central Argentina (from Tucuman and Santiago del Estero to Buenos Aires provinces), Uruguay, and southern Brazil (Santa Catarina state) (Lanteri 1984, Lanteri and Morrone 1995) (Supp. Table 5 [online only]). It attacks lucerne (Lanteri 1994), sunflower (Lanteri et al. 2002), and cereals (Lanteri et al. 1997).

Naupactus leucoloma Boheman is widely distributed in Argentina, from Jujuy and Salta provinces in the northwest to Chubut province in the southeast (Patagonia) and is also present in Uruguay and southern Brazil (Rio Grande do Sul). It was introduced in several provinces of Chile, in Peru, Australia, New Zealand, and South Africa, and in several states throughout the central Great Plains of the United States (Buchanan 1939, Chadwick 1965, Kuschel 1972, Sites and Thorvilson 1988, Hardwick et al. 1994, Lanteri and Marvaldi 1995, Voss and Poly 2002, Elgueta and Marvaldi 2006, Guzmán et al. 2012) (Supp. Table 6 [online only]). *N. leucoloma* infests >250 plant species all over its distribution range, especially Fabaceae (Lanteri et al. 2002). Lucerne is the main host in Argentina and Uruguay (Lanteri 1994, Alzugaray et al. 1998). This species also attacks lotus in Uruguay (Alzugaray et al.

1998) and soybean (*Glycine max*) in southern Brazil (Lanteri et al. 2013).

Naupactus peregrinus (Buchanan) occurs in north–eastern Argentina, Uruguay, southern Brazil (Rio Grande do Sul), and Paraguay, and was presumably introduced into United States around 1937 (Florida, Mississippi, and Texas) (Buchanan 1939, Lanteri and Marvaldi 1995) (Supp. Table 7 [online only]). This species is associated with pastures, Lucerne, and lotus (Alzugaray et al. 1998, Lanteri et al. 2002) and, in recent years, with soybean in southern Brazil (Lanteri et al. 2013).

Pantomorus auripes Hustache is endemic to Argentina, where it is distributed from Misiones to Río Negro provinces. It is quite abundant in mountains and valleys of Cordoba, San Luis, and Buenos Aires provinces (Tandil and Sierra de la Ventana mountain systems), between ≈800–1,700 m.a.s.l. (Lanteri et al. 1991) (Supp. Table 8 [online only]). This species is occasionally associated with lucerne, sunflower, and potato (*Solanum tuberosum*) in Argentina (Lanteri et al. 2002).

Pantomorus ruizi (Brethes) is widespread throughout Argentina, from Jujuy province in the northwest, to Santa Cruz province in the south, being particularly frequent in the central–western provinces. It is also found in Chile, from Antofagasta in the north to Valdivia in the south (Lanteri et al. 1991, Morrone and Lanteri 1991, Elgueta 1993) (Supp. Table 9 [online only]). Because it is uncertain whether *P. ruizi* is native to Chile, we decided to analyze its global distribution including and excluding this country. In South America it is the southernmost distributed species of the tribe Naupactini, with an altitudinal range extending from sea level to ≈1,000 m.a.s.l. *P. ruizi* is associated to native vegetation typical of the arid environments of Argentina and Chile, such as *Eupatorium* spp., *Baccharis* spp. (Asteraceae), *Larrea nitida* (Zygophyllaceae), and *Stipa* spp. (Poaceae) (Lanteri et al. 2002). It is also harmful for soybean and lucerne in both countries (Elgueta 1993, Lanteri et al. 2002), to *Vitis vinifera* and *Pyrus communis* in Chile (Elgueta 1993), and to *Pinus ponderosa* in Argentina (Gómez and Lanteri 2006).

Pantomorus viridisquamosus (Boheman) is present in most provinces of north–central Argentina, southern Brazil (Santa Catarina and Rio Grande do Sul states) and Uruguay, and it was occasionally found in Curepipe, Mauritius Island (Lanteri and Loiácono 1990) (Supp. Table 10 [online only]). This species is associated with lucerne in Argentina and Uruguay (Alzugaray et al. 1998, Lanteri 1994, Lanteri et al. 2002) and, in recent years, with soybean in southern Brazil (Lanteri et al. 2013).

Ecological Niche Modeling. To estimate the distribution probabilities of species occurrence we used MAXENT version 3.1, a machine learning approach based on maximum entropy (http://www.cs.princeton.edu/≈schapire/maxent/) (Phillips et al. 2006, Phillips and Dudik 2008). This program requires only species presence data and environmental variable layers for the studied area (Pearce and Boyce 2006). The estimated probability of species occurrence varies from 0 to 1, where 0 is the least suitable habitat and one is the
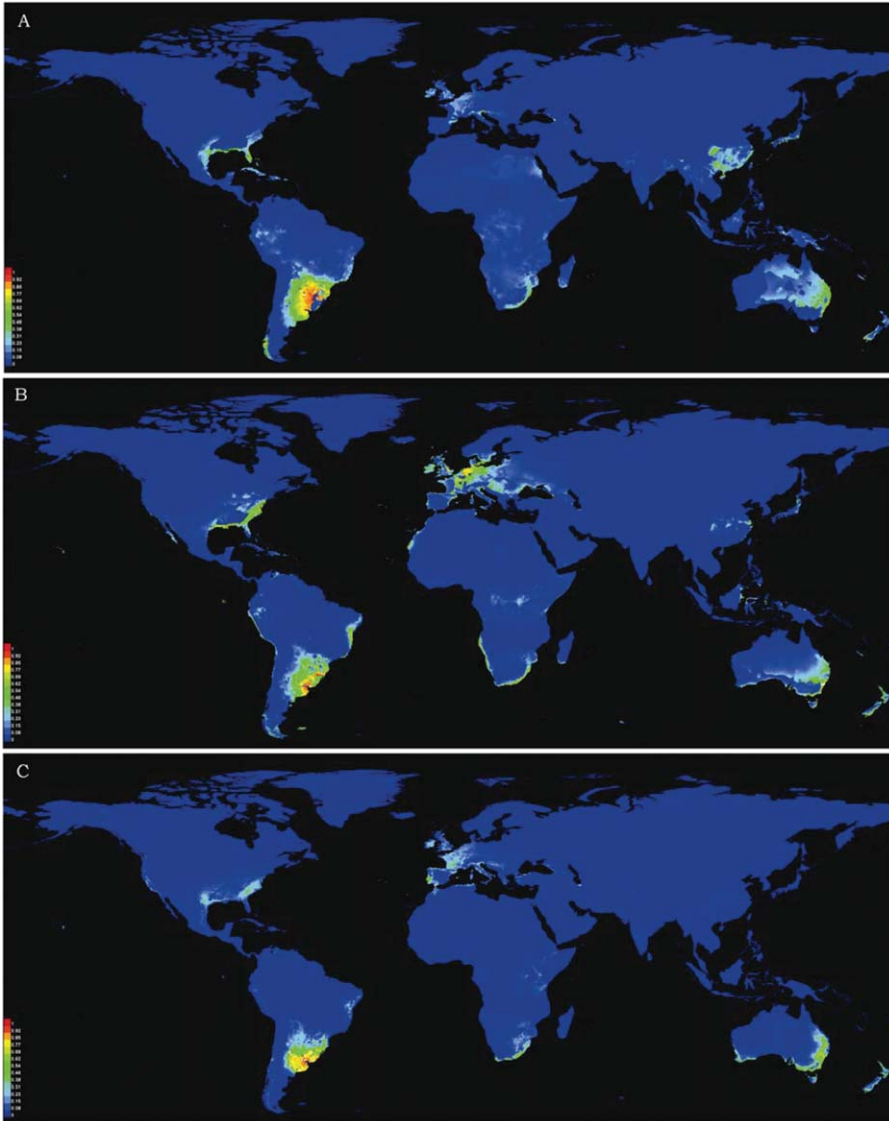
Fig. 1. Map of predicted global potential distributions from ecological niche modeling generated by MAXENT, using localities in South America for: (A) *A. conirostris*, (B) *A. sordidus*, and (C) *E. fallax.* Distributions are defined by probabilities of species occurrence above the minimum predicted probability (lower limit of the area shaded in blue). White dots indicate training locations and purple dots indicate test locations. The color code in the vertical bar on the lower right corner corresponds to the probability of species occurrence (from 0 to 1). (Online figure in color.)

most suitable habitat. To generate present-day ecological niche models for the whole world, we only included samples from the putative native areas in South America. Then, we checked if the species occupy suitable or unsuitable environments in non-native areas. We also generated niche models using all the records available for species which were undoubtedly introduced into countries abroad (native plus introduced); thus, allowing the prediction of the potential range expansion that can take place from established populations outside their native range.

The present locations of each species were plotted on distribution maps where the potential distribution is indicated with different colors (Figs. 1A–F, 2A–D, and 3A–D). Because MAXENT produces a continuous probability, we transformed the output to a map representing probabilities of occurrence. For a given species, the highest probability (ca. 1.00) is indicated with red color, a moderate probability (ca. 0.80) with orange color, a low probability (between 0.20–0.70) with green color, and an almost nil probability of occurrence (ca. 0.00) with blue color.

All environmental variables available (20 layers) were tested for multicolinearity by examining cross-correlations among variables (Pearson correlation co-
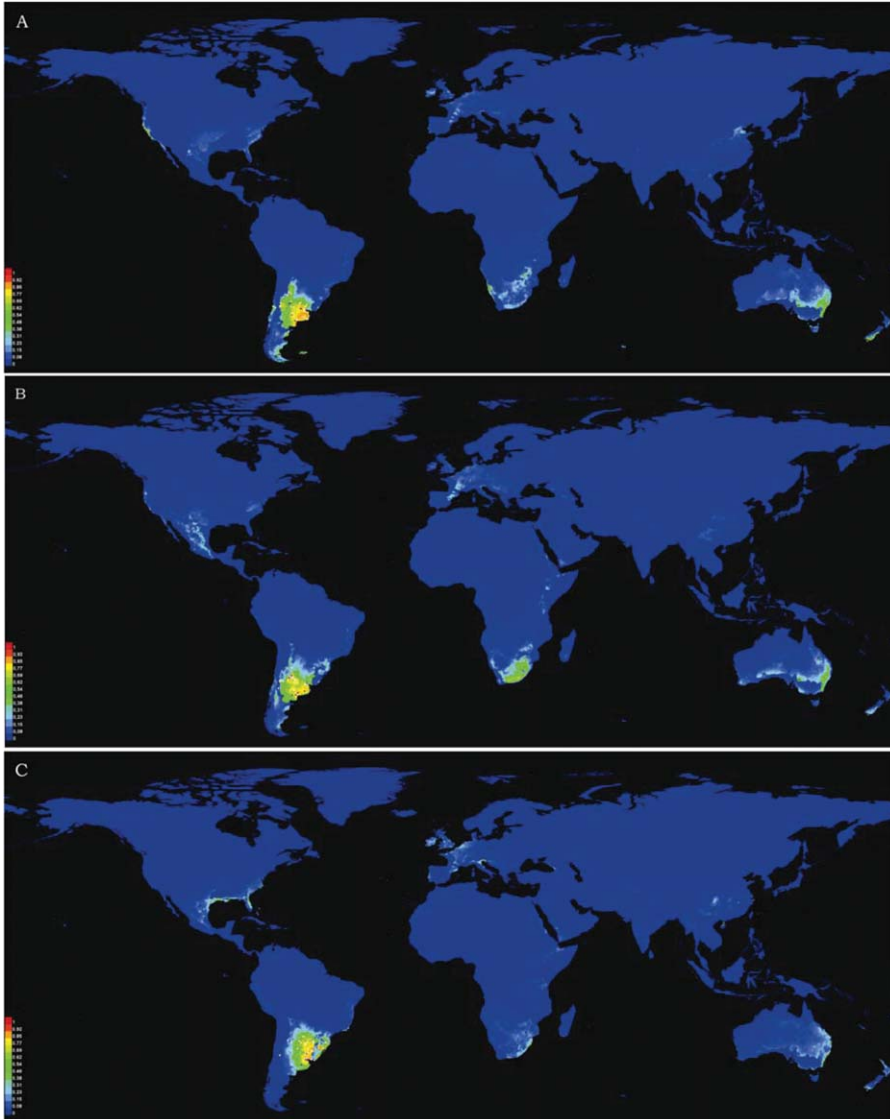
Fig. 2. Map of predicted global potential distributions from ecological niche modeling generated by MAXENT, using localities in South America for: (A) *N. leucoloma*, (B) *P. auripes*, and (C) *P. viridisquamosus*. Distributions are defined by probabilities of species occurrence above the minimum predicted probability (lower limit of the area shaded in blue). White dots indicate training locations and purple dots indicate test locations. The color code in the vertical bar on the lower right corner corresponds to the probability of species occurrence (from 0 to 1). (Online figure in color.)

efficient *r*) in geographical space, based on occurrence records of species.

Only one variable from a set of highly correlated variables was included in the analysis ($r \geq 0.80$), based on its potential ecological influence on species' distribution. Then, we selected the following 11 environmental variables: Annual Mean Temperature, Mean Diurnal Range (mean of monthly max temperature–min temperature), Isothermality, Maximum Temperature of Warmest Month, Temperature Annual Range, Mean Temperature of Wettest Quarter, Mean Temperature of Driest Quarter, Annual Precipitation, Precipitation of Wettest Month, Precipitation

of Driest Month, and Altitude. These were downloaded from WORLDCLIM version 1.4 (http://www.worldclim.org/) (Hijmans et al. 2005) and were combined and analyzed in a Geographic Information System (GIS) through DIVA-GIS v 7.1 (http://www.diva-gis.org/).

All environmental layers had a spatial resolution of 30 arc-seconds (1 km^2). The default convergence threshold of 10^{-5} was used in MAXENT, maximum iterations were increased to 1000, and regularization values and functions of environmental variables were selected automatically by the program. For each run, 75% of the localities were used to train the model and
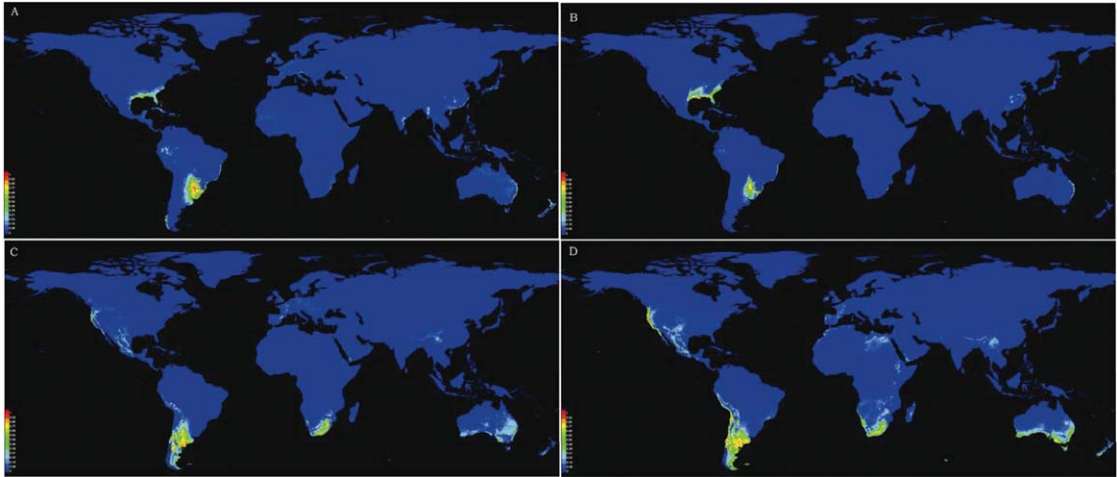
Fig. 3. Map of predicted global potential distributions from ecological niche modeling generated by MAXENT, using localities in South America for: (A) *N. peregrinus* and (C) *P. ruizi*; and localities throughout the species' distribution range for: (B) *N. peregrinus*, (D) *P. ruizi.* Distributions are defined by probabilities of species occurrence above the minimum predicted probability (lower limit of the area shaded in blue). White dots indicate training locations and purple dots indicate test locations. The color code in the vertical bar on the lower right corner corresponds to the probability of species occurrence (from 0 to 1). (Online figure in color.)

25% were randomly selected to test it. The model performance was assessed using a threshold independent method based on the Area Under the Curve (AUC) of Receiver Operating Characteristics Curve (ROC). The contribution of each explanatory variable to model performance was evaluated with a jackknife procedure implemented in MAXENT, where variables are successively omitted and then used in isolation to measure their relative, as well as their absolute contribution to the model. The most important variables are those that produce the highest training gains or reduce the training gain when left out of the model.

Results

General Patterns Across Species. According to AUC values, the ability of all models to distinguish presence from random background points is higher than 0.9, revealing a very good performance. Likewise, the analysis including all the data, which was performed only for species already introduced in countries abroad, indicates that models performed better than random predictions with high ROC (AUC) values (≥0.5).

An evaluation of the contribution of the environmental variables shows that Mean Temperature of Driest Quarter, Annual Mean Temperature, and Isothermality are the most important variables determining the distribution of almost all species, with the most useful information by themselves.

In South America, the most suitable environments or the areas with probability of occurrence >50% (i.e., red to green colors in Figs. 1A to 4D) for most species analyzed, are the prairies and steppes of central–eastern Argentina, Uruguay, and southern Brazil, which

are located close to the Parana, Uruguay, and La Plata rivers. The only exception is *P. ruizi*, whose potential distribution range extends throughout the Patagonian steppes (Fig. 3C). The current locations of most species coincide with the predicted suitable areas, except for a few sites corresponding to *N. leucoloma*, *P. auripes*, *P. viridisquamosus*, and *A. tessellatus* (Figs. 2A–C and 4A).

Outside South America, the invasive species *A. sordidus*, *A. taeniatulus*, *N. leucoloma*, *N. peregrinus*, and *A. tessellatus* are usually located in areas predicted as suitable by the niche modeling (Figs. 1B, 2A, 3A, and 4A).

Potential Distribution of Each Target Species. The niche model predicts that the area encompassing southern Brazil, northeastern Argentina, and western Uruguay (from north Parana river down to La Plata river, and between the Uruguay and Parana rivers), provides the most suitable environment for *A. conirostris* (Fig. 1A), while its probability of occurrence ranges from low to moderate in southeastern United States (mainly Florida state), southeastern Africa, Australia, and Asia, and coasts of northeastern Spain and Italy.

E. fallax has the highest probability of occurrence in the grasslands of central–eastern Argentina and Uruguay, in the vicinity of La Plata river system (Fig. 1C). Its probability of occurrence is low to moderate in southeastern United States (mainly Florida), central–northern Europe, and coasts of southeastern Africa, Australia, and New Zealand.

For *P. auripes,* the area with highest environmental suitability is located in central Argentina, close to the mountain systems of Cordoba province, with its range extended to the west of the country. The probability of occurrence is moderate in southern Africa and
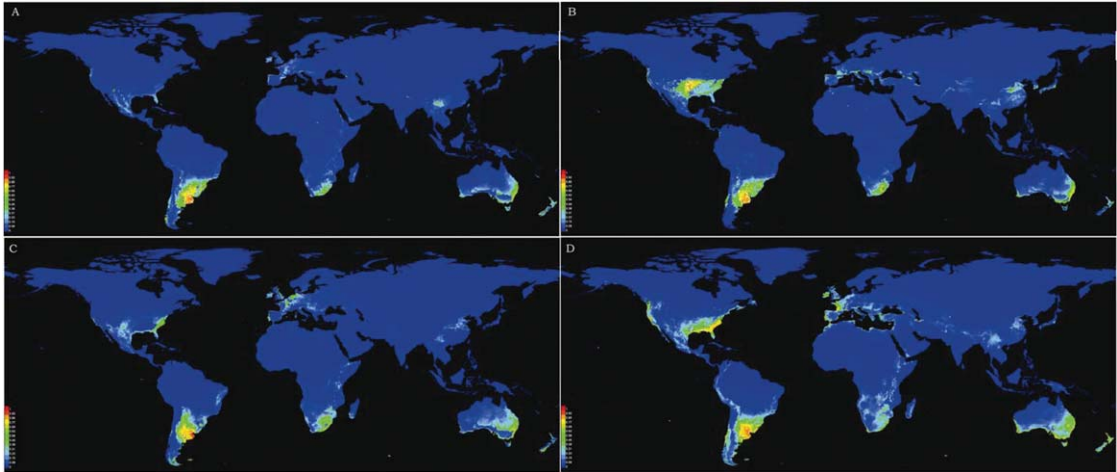
Fig. 4. Map of predicted global potential distributions from ecological niche modeling generated by MAXENT, using localities in South America for: (A) *A. tessellatus*, (C) *A. taeniatulus*; and localities throughout the species' distribution range for: (B) *A. tessellatus*, (D) *A. taeniatulus*. Distributions are defined by probabilities of species occurrence above the minimum predicted probability (lower limit of the area shaded in blue). White dots indicate training locations and purple dots indicate test locations. The color code in the vertical bar on the lower right corner corresponds to the probability of species occurrence (from 0 to 1). (Online figure in color.)

southeastern Australia, and low in southern New Zealand, the Mexican plateau, and central Europe (Fig. 2B). *P. viridisquamosus* is most likely to occur in central–eastern Argentina, mainly the Mesopotamia, along the banks of the Parana and Uruguay rivers. It shows a low to moderate probability of occurrence in southeastern United States (mainly Florida), southeastern Australia, and coasts of southeastern Africa (Fig. 2C).

The geographic regions predicted by niche modeling as suitable for species that successfully invaded countries outside their putative native distributions were similar as for noninvasive species. For instance, the most suitable areas for *A. sordidus* (Fig. 1B) are in Argentina and Uruguay, along the Uruguay and La Plata rivers, and southern Brazil. This species has a low to moderate probability of occurrence in southeastern United States (mainly Florida), northern Europe, and coasts of southern Africa, eastern Australia, and New Zealand.

A. tessellatus (Fig. 4A) is most likely to occur in Buenos Aires province, in the vicinity of La Plata river, and close to Tandilia and Ventania mountain systems, where most morphotypes of this species are found. Niche modeling also predicts low to moderate probabilities of occurrence, mainly in south and central Chile, southeastern Africa, southeastern Australia, coasts of New Zealand, southeastern United States (Florida), the Mexican Plateau, and southern Asia (Fig. 4A). South–central United States is not predicted as suitable, despite the species has been established there since the end of the 19th century (Buchanan 1939, Elgueta 1993). For *A. tessellatus*, the analysis of the whole current distribution suggests wide suitable areas in southeastern United States, and a higher probability of occurrence in southern Africa,

Australia, southeastern Asia, and Europe (Fig. 4B). There are some locality records in nonsuitable areas of the United States (Fig. 4B).

A. taeniatulus has the highest probability of occurrence in Buenos Aires province (Argentina), and low to moderate probabilities in central Chile, southeastern United States (mainly Florida), eastern Australia, southern Africa, New Zealand, and northern Europe (mainly France and The Netherlands) (Fig. 4C). This species was able to colonize most of these countries, except those of Europe and Africa. Niche modeling based on all records predicts moderate to high probabilities of occurrence in Chile, eastern Australia, southern Africa, and western Europe. In addition, there are moderately to highly suitable areas in the southeast and along the Pacific coast of the United States (Fig. 4D).

For *N. leucoloma*, the most suitable areas are in central Argentina (mainly in the vicinity of La Plata river), in the mountains of Cordoba province, and the pre-Andean mountains in Jujuy, Salta and Tucuman provinces (Yungas biogeographic province). However, there are some records in a nonsuitable area of northern Patagonia. Niche modeling predicts a moderate probability of occurrence in central Chile, the United States Pacific coast, South Africa, southeastern Australia, and New Zealand (Fig. 2A). The species is well established in all these countries, attacking several crops, especially cultivated legumes. When all the records were included in the analysis, the model predicts the occurrence of *N. leucoloma* throughout Chile, except for the Valdivian forest in the south, a broad area of southeastern United States, and a narrow strip along the Pacific coast of this country (see Fig. 2A in Guzmán et al. 2012).

N. peregrinus is most likely to occur in northeastern Argentina, mainly northern Mesopotamia, between the Parana and the Uruguay rivers, and in southern Brazil (Rio Grande do Sul). In addition, the model predicts its occurrence along the Mexican Gulf and the United States Atlantic coasts (Florida state) (Fig. 3A), and in a narrow strip along the eastern and western coasts of Australia and New Zealand, respectively. When all the records were included in the analysis, the model predicts the expansion of this species throughout those areas in the United States (Fig. 3B).

The niche model for *P. ruizi* excluding records from Chile identified three areas of highest suitability: the west side of the mountains in Cordoba province; southern Buenos Aires province close to the boundaries of Rio Negro and La Pampa provinces; and the eastern pre-Andean range in Mendoza and Neuquen (western Patagonia) (Fig. 3C). This analysis predicts the occurrence of *P. ruizi* in central Chile, the United States Pacific coast, the Mexican Plateau, southern Africa, and southern Australia. When all the records were included in the analysis, the model predicted the distribution of *P. ruizi* over almost all Chile, extending north to the coasts of Peru. The prediction for the Pacific coast of the United States is higher compared with the analysis based on the native records (Fig. 3D).

Discussion

The weevil species herein studied are native to the central Pampas of Argentina, Uruguay, and southern Brazil, a fertile plain of $\approx$750,000 km^2 only interrupted by the Ventana and Tandil hills (500–1,300 m.a.s.l.) in Buenos Aires province. The climate of the Pampa biogeographic province is temperate, with annual precipitations of 600–1,200 mm distributed fairly evenly through the year. These climate conditions together with soil characteristics make land appropriate for agriculture. There are almost no native trees, and the dominant vegetation types are grass prairies and grass steppes composed of several species of Gramineae belonging to the tribe Stipeae (*Stipa* and *Piptochaetium*) (Cabrera and Willink 1973). The environments of the Pampas are unsuitable for most Naupactini species living on trees and shrubs, except for those that became secondarily associated with grasses. On the contrary, the flightless Naupactini studied by us seem to be particularly adapted to these treeless plains, and parthenogenetic reproduction would have increased their potential for expansion all over the area (Lanteri and Normark 1995, Guzman et al. 2012). Range expansion to the open plains might have occurred during the Quaternary, when geological changes caused a retraction of the Subtropical and Chacoan flora and fauna (Ringuelet 1961), and it was probably favored by Pleistocene climate fluctuations (glacial-interglacial cycles) (Simpson–Vuilleumier 1971, Guzmán et al. 2012). In historical times, the range expansion of these species is probably taking place at higher rates, because of the extension of the agricultural frontier and the increase of commercial trade between distant countries.

Our niche model shows that the studied species are mainly influenced by the same three climatic variables. In addition, occurrence records are located in areas predicted as suitable by the model based on the species' native ranges, except for *N. leucoloma*, *P. auripes*, *P. viridisquamosus*, and *A. tessellatus* (Figs. 2A–C and 4A). This result is explained by a strong association between the latter species and different crops, mainly cereals, grasses, and lucerne (Lanteri et al. 2002). Agroecosystems provide protected environments and new food sources for weevil pests, especially those that are highly polyphagous such as the Naupactini. For example, *N. leucoloma* was first found in southern Argentina, Chubut province, about 10 years ago, in a new agricultural environment along the banks of the Chubut river, near Trelew city.

The state of Florida was consistently predicted for species with most suitable environments being in northeastern Argentina, Uruguay, and southern Brazil, because these areas have almost identical conditions of temperature and humidity. This is the case for two species of *Aramigus*, two *Atrichonotus* and *N. peregrinus* (Figs. 1A–B, 4A,C, and 3A). Until present, only three of them have been introduced in Florida (*A. tessellatus*, *A. taeniatulus*, and *N. peregrinus*). In contrast, Florida was not predicted as suitable for species distributed mainly along the western side of the Parana river (e.g., *N. leucoloma*, *P. auripes*, and *P. ruizi*), which seem to be adapted to lower temperature and humidity conditions (Figs. 1C, 2A, and 3C). Rather, they are most likely to occur in steppes of southern Africa and southeastern Australia, where only *N. leucoloma* has been detected so far.

Central Chile is not predicted as a suitable area for most Naupactini species studied by us, except for *N. leucoloma* and *P. ruizi*, which mainly occur in xerophytic environments such as those found in the dry Pampas, Espinal, and Monte biogeographic provinces, and also in the Patagonian steppe. However, central Chile has been invaded by these species, two other parthenogenetic weevils, *A. tessellatus* and *A. taeniatulus* (Figs. 4B,D and 4A,C) and by two sexual species associated with grape production, *N. xanthographus* (Germar) and *N. verecundus* Hustache (Lanteri et al. 2002, Guzman et al. 2012). This is probably because of the fact that the central area of Chile is the major growing region for crop and fruit production in this country (Elgueta 1993), and the commercial trade between Chile and Argentina is very frequent. Likewise, *E. fallax* shows a low probability of occurrence in central Chile, central Europe (mainly France and England), southeastern Australia, and New Zealand, but it could be introduced in these countries through commercial trade. Indeed, another species of *Eurymetopus*, *E. birabeni*, which has a similar native range as *E. fallax* (Lanteri 1984), has successfully invaded New Zealand (Kuschel 1972). The potential distribution of *E. birabeni* could not be modeled because of the low number of records, but it would be similar to that of *E. fallax.*

The wide range of host plants of *N. leucoloma* is the best explanation for its worldwide distribution. The closely related species *N. peregrinus* and *N. minor* are also established in the United States (Florida, Alabama, and Mississippi) but they show a more restricted distribution in both native and colonized areas (Buchanan 1939, Lanteri and Marvaldi 1995). *N. minor* is naturally found in Argentina (mainly Entre Rios province), Uruguay and southern Brazil (Rio Grande do Sul); it is associated with lucerne and lotus in Argentina and Uruguay (Alzugaray et al. 1998, Lanteri et al. 2002) and with soybean (*Glycine max*) in southern Brazil (Lanteri et al. 2013). Its potential distribution could not be modeled because of the low number of locality records, but it would be similar to that of *N. peregrinus.*

Summarizing, niche modeling based on locality records from South America clearly demonstrates that all the weevils studied have the potential to invade prairies and steppes outside their native range, mainly in southeastern United States, some European countries (e.g., Portugal, France, and southern England), South Africa, New Zealand, and southeastern Australia. This conclusion is drawn from the fact that the areas predicted as suitable have already been invaded by five of the species analyzed, thereby suggesting the invasive potential of the remaining species. Moreover, the colonization probability and potential expansion of the introduced species usually increase after they become established outside its native range (see potential distributions based on all records of *N. leucoloma* in Guzmán et al. [2012], *A. tessellatus* in Fig. 4B, *A. taeniatulus* in Fig. 4D, and *P. ruizi* in Fig. 3D). Indeed, the analyses based on all records (native plus colonized areas) correctly predicted the expansion of *P. ruizi* and *N. leucoloma* in Chile, and that of *N. leucoloma*, *A. taeniatulus*, and *A. tessellatus* in the United States. Similar global potential distributions have been predicted for other insect species native to South America and introduced in the United States (Peterson and Nakasawa 2008).

Only 8 of ≈200 species of Naupactini weevils inhabiting Argentina and neighboring countries have successfully established in overseas countries: *A. tessellatus*, *A. sordidus*, *A. taeniatulus*, *N. leucoloma*, and *N. peregrinus*, plus *E. birabeni*, *N. minor*, and *N. cervinus* Boheman, the latter being found in the five continents (Rodriguero et al. 2010 b). All of them are parthenogenetic, as well as most Naupactini established in Chile (*N. leucoloma*, *N. cervinus*, *P. ruizi*, *A. taeniatulus*, and *A. tessellatus*) (Lanteri and Normark 1995, Rodriguero et al. 2010a), except *Naupactus xanthographus* (Germar) and *N. verecundus* Hustache, which have sexual reproduction (Lanteri et al. 2002, Guzmán et al. 2012).

It is evident that parthenogenetic reproduction provides a great advantage for long-distance dispersal and further establishment of broad-nosed weevil populations; however, it does not guarantee by itself successful colonization of new lands. As a matter of fact, there are probably >30 parthenogenetic Naupactini in South America (see Lanteri and Normark 1995) and

less than one third invaded countries outside this continent or have been able to cross the Andes.

Species that are widespread in their native environment and/or are associated with commercially important crops have a greater chance of invading foreign countries. This is the case for the bisexual species *N. xanthographus* and *N. verecundus* introduced in Chile along with grapes, and for the parthenogenetic *A. tessellatus*, *A. taeniatulus*, and *N. leucoloma*, introduced into the United States, probably along with cereals and beans (Buchanan 1939). Other Naupactini that are less widespread over their native ranges, show a more restricted distributions in the newly invaded countries (i.e., *N. minor* and *N. peregrinus* introduced into the United States, *A. sordidus* into Australia, and *E. birabeni* into New Zealand) (Buchanan 1939, Chadwick 1965, Kuschel 1972); one possible explanation may be a limited degree of tolerance to low temperature and low humidity.

A. conirostris, *E. fallax*, *P. auripes*, and *P. viridisquamosus* have a low to moderate probability of colonizing some countries outside South America, while *P. ruizi* shows a higher probability of range expansion, especially along the Pacific coast of Chile, Peru, and the United States. However, the latter species is rarely associated with crops.

We conclude that niche modeling is effective in predicting the potential distribution of several parthenogenetic broad-nosed weevils indigenous to the South American Pampas, in both the native and invaded areas worldwide, at least on the basis of the climatic variables included in this analysis. However, overseas invasions also depend on external factors such as mode of reproduction, association with crops, extent of commercial trade among countries, and effectiveness of quarantine and other control measures implemented by the importing and exporting countries.

Acknowledgments

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