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The giant African snail, *Achatina fulica* (Gastropoda: Achatinidae): Using bioclimatic models to identify South American areas susceptible to invasion

Roberto E. Vogler^{1,2}, Ariel A. Beltramino^{1,3}, Mariano M. Sede^{2,4}, Diego E. Gutiérrez Gregoric^{1,2}, Verónica Núñez^{1,2}, and Alejandra Rumi^{1,2}

Correspondence, R.E. Vogler: robertovogler@fcnym.unlp.edu.ar; robertovogler@yahoo.com.ar

Abstract. The best way to reduce problems related to invasive species is by preventing introductions into potentially susceptible areas. The purpose of this study was to create distribution models for the invasive gastropod *Achatina fulica* Bowdich, 1822 in South America in order to evaluate its potential geographic distribution and identify areas at potential risk. This mollusc, considered one of the 100 world's worst invasive alien species, is the focus of intense concern due to its impact on agriculture, human health, and native fauna. We tested two commonly used ecological niche modeling methods: Genetic Algorithm for Rule-Set Prediction (GARP) and Maximum Entropy (MaxEnt). Models were run with occurrence points obtained from several sources, including the scientific literature, international databases, governmental reports and newspapers, WorldClim bioclimatic variables, and altitude. Models were evaluated with the threshold-independent Receiver Operating Characteristic (ROC) and Area Under the Curve (AUC). Both models had consistent performances with similar areas predicted as susceptible, including areas already affected and new potentially susceptible areas in both tropical and temperate regions of South America.

Key words: land mollusc, bioinvasion, distribution, GARP, MaxEnt

In recent decades, South America has been seriously affected by invasive mollusc species (Letelier *et al.* 2007, Gutiérrez Gregoric and Vogler 2010, Rumi *et al.* 2010). Some of these introductions have been the result of unintentional events, such as the cases of *Theba pisana* Müller, 1774 and *Melanoides tuberculata* Müller, 1774 (Rumi *et al.* 2010, Peso *et al.* 2011). In contrast, other introductions have been intentional as a consequence of diverse interests, including biological control and ornamental, medicinal, and economic purposes (Cowie and Robinson 2003, Fernandez *et al.* 2003). The giant African snail *Achatina* (*Lissachatina*) *fulica* Bowdich, 1822, native to eastern Africa, is an example of the latter.

Considered one of the 100 world's worst invasive alien species (Lowe *et al.* 2000, Raut and Barker 2002), *Achatina fulica* was first introduced in South America at an agricultural fair in Brazil in the late 1980's as a breeding animal in order to compete with *Cornu aspersum* (Müller, 1774), the "real" escargot (Teles and Fontes 2002, Thiengo *et al.* 2007). Due to the lack of snail-eating habits of the Brazilian population, facilities where the species used to be reared were abandoned and the animals were released into the wild (Teles and Fontes 2002, Thiengo *et al.* 2007, Zenni and Ziller 2010).

These events were followed by a rapid and expansive dispersal in Brazil with its occurrence confirmed in 25 of 26 states in the country (Maldonado Júnior *et al.* 2010, Salgado 2011).

Recent reports suggest that Achatina fulica has expanded its range and become widespread throughout several South American countries, including Argentina, Colombia, Ecuador, Paraguay, Peru and Venezuela (Correoso Rodríguez 2006, Martinez-Escarbassiere et al. 2008, Borrero et al. 2009, Correoso and Coello 2009, Paraguay Biodiversidad 2010, Gutiérrez Gregoric et al. 2011). This broad distribution may not only be attributed to active dispersal from established populations (Correoso and Coello 2009) but also to the repeated transportation opportunities provided by people, including fishing (i.e. using the individuals as bait), heliciculture, sold as a "pet", and the inadvertent transport of specimens (e.g., with waste, building materials, plants). Together these factors have contributed to a rapid geographical range expansion of this invasive species (Borrero et al. 2009, Colley 2010, Gutiérrez Gregoric et al. 2011). In this context, bioclimatic models (also known as species distribution models and ecological niche models; Jeschke and Stryer 2008) constitute important tools to predict future changes in the species geographic ranges,

¹ División Zoología Invertebrados, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, Paseo del Bosque s/n (B1900FWA), La Plata, Argentina

² Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Argentina

³ Agencia Nacional de Promoción Científica y Tecnológica (ANPCyT), Argentina

⁴Instituto de Investigaciones Biomédicas en Retrovirus y SIDA, Facultad de Medicina, Universidad de Buenos Aires, Paraguay 2155 (C1121ABG), Buenos Aires, Argentina

since they may be used to identify potential areas of suitable habitat where invasive species may actually be present but not yet detected and favorable regions where they may disperse in the future (Nyári *et al.* 2006, Baldwin 2009, Fukasawa *et al.* 2009, Robinson *et al.* 2010).

Predictive modeling characterizing the distribution of Achatina fulica in South America, especially in those countries where the species introduction has been recent, represents a valuable tool for developing effective control policy in order to manage the ongoing invasion. An extensive list of methods to generate spatial distribution models of plants, animals, and viruses at different geographical scales, have been described in the literature (see review by Elith and Leathwick 2009) and include GARP (Genetic Algorithm for Rule-Setting Prediction; Stockwell and Peters 1999) and MaxEnt (Maximum Entropy; Phillips et al. 2004, 2006). Using MaxEnt and 13 environmental variables, Borrero et al. (2009) developed a potential distribution model for the giant African snail in South America; however, this model focused on the Andean region. This model indicated low to medium probability that the species would occur in southern South America; however, due to recent findings of the species in subtropical areas of Argentina and Paraguay, we hypothesize that the potential southern distribution area would be larger than previously predicted. In this paper, we generate two high-resolution bioclimatic models using GARP and MaxEnt in order to re-evaluate threat of A. fulica in the southernmost region of South America. The models generated will be useful in planning control strategies, prioritizing areas for surveillance, and for taking preventive actions in order to limit the spread of A. fulica.

MATERIAL AND METHODS

Study area and species records

The study area included all South American countries. Presence data (N=490) for *Achatina fulica* were obtained from several sources, including the scientific literature, international databases, government reports and newspapers (Table 1). For those localities where coordinates were not provided by the source, a georeferenced position was obtained from the gazetteer GEOLocate Web Application (http://www.museum.tulane.edu/geolocate/web/webgeoref. aspx).

Environmental variables

Nineteen bioclimatic variables and a topographic variable (altitude) (Table 2), at a spatial resolution of 30 arc seconds (approximately 1 km²), were used as predictors. These data, obtained from WorldClim v. 1.4 (http://www.worldclim.org), were derived from weather station

data spanning 1950–2000 (Hijmans et al. 2005). Given the heterogeneous habitats that *Achatina fulica* can occupy and its polyphagous diet, we chose to not include vegetation cover in our models, as was done in De Meyer et al. (2008).

Modeling of susceptible areas

Models of the potential distribution of *Achatina fulica* were generated by using two algorithms: GARP (DesktopGarp v. 1.1.6; Stockwell and Noble 1992, Stockwell and Peters 1999, Scachetti-Pereira 2002, Scachetti-Pereira and Siqueira 2007) and MaxEnt (MaxEnt v. 3.3.3a; Phillips *et al.* 2004, 2006). These algorithms model the species' ecological niche (a set of ecological conditions habitable for a species) by examining the relationship between locations of known species presence and the environmental characteristics of that area and then extrapolating from this the areas where similar conditions occur in the study area (Paredes-García *et al.* 2011). In both models, 75% of presence records were randomly selected and used in the model training while the remaining 25% were used in the model testing.

For GARP, we generated 100 models with a convergence limit of 0.05, a maximum of 100 iterations, and all four rules (atomic, range, negated range, and logistic regression). The 20 best models were selected by hand following the recommendations of Anderson et al. (2003). The predictions of the best subset were arithmetically combined in ArcGIS v.9.1 (ESRI, Redlands, California) to create a composite prediction of the species potential distribution. This potential distribution was interpreted as a surface of densities related to the probability of suitable conditions for Achatina fulica. The consensus GARP map was reclassified into four categories: areas highly susceptible (pixels where the 20 models predicted presence), areas of susceptibility medium-high (pixels where 19/20 models predicted presence), areas of susceptibility medium-low (pixels where 18/20 models predicted presence), and areas of low susceptibility (pixels which converge up to 16 of the 20 models).

For MaxEnt, the model was computed as "logistic". This output returns a continuous map with an estimated probability of presence between 0 (no probability of the species presence) and 1 (high probability of presence), which permits fine distinctions between the suitability of different areas modeled (Giovanelli *et al.* 2008). All other parameters were used by default settings. Increased presence probability areas for *Achatina fulica* were considered to be more susceptible to invasion by the species.

To determine which variables contributed most to the development of the model, the MaxEnt program was configured to calculate the significance of variables using the jackknife procedure. This procedure produces three types of models: models created with an omitted variable and all other

Table 1. Sources of *Achatina fulica* occurrence in South America used in the two bioclimatic models.

Country	Consulted sources
Argentina	Gutiérrez Gregoric et al. (2011)
Brazil	Teles et al. (1997)
	Vasconcellos and Pile (2001)
	Teles and Fontes (2002)
	Carvalho et al. (2003)
	Barçante et al. (2005)
	Colley <i>et al.</i> (2005)
	Eston et al. (2006)
	Sacramento et al. (2006)
	Berto and Bogéa (2007)
	Oliveira et al. (2007)
	Paula and Lopes (2007)
	Thiengo et al. (2007)
	Agudo-Padrón (2008)
	Schiffler et al. (2008)
	Thiengo et al. (2008)
	Albuquerque et al. (2009)
	Colley and Fischer (2009)
	Ohlweiler et al. (2010)
	Thiengo et al. (2010)
	Web sites (November 2011):
	Base de dados sobre especies exóticas invasoras I3N-Brasil: http://www.institutohorus.org.br
	ClickSergipe (2010): http://www.clicksergipe.com.br
	Conquiologistas do Brasil (2010): http://www.conchasbrasil.org.br
	Gazeta do Triângulo (2010): http://www.gazetadotriangulo.com.br/novo/
	Injipa (2010): http://injipa.com.br
	Portal Agora Maranhão (2010): http://www.agoramaranhao.com
	Portal de São Francisco do Sul (2010): http://www.sfs.com.br
	Portal O Día (2010): http://www.portalodia.com
	Prefeitura de Aracruz (2010): http://www.aracruz.es.gov.br
	Prefeitura de Bela Vista (2010): http://www.belavista.go.gov.br
	Prefeitura de Jataí (2010): http://www.jatai.go.gov.br
	Rede Globo (2010): http://www.globo.com
Bolivia	Rondônia Digital (2010): http://rondoniadigital.com
Colombia	Correoso and Coello (2009) Borrero <i>et al.</i> (2009)
Colonibia	Correoso and Coello (2009)
	Base de datos sobre especies exóticas invasoras I3N-Colombia (November 2011): http://ef.humboldt.org.co.
Ecuador	Borrero et al. (2009)
	Correoso and Coello (2009)
Paraguay	Paraguay Biodiversidad (2010)
Peru	Borrero et al. (2009)
1 01 0	Correoso and Coello (2009)
Venezuela	Carvalho <i>et al.</i> (2003)
, chezuciu	Martínez-Escarbassiere et al. (2008)
	That the Doublete trus (2000)

variables included, models including only one variable, and a model created with all variables. The variables considered most important for model development are those reducing training gain when are not included in the model and show gain when the model is developed involving just the single

variable (Colacicco-Mayhugh et al. 2010, Torres and Jayat 2010).

Finally, comparison of the resulting models from both algorithms was done through Receiver Operating Characteristic (ROC curves analyses; Fielding and Bell 1997) representing

Table 2. Bioclimatic variables used in models development. Temperatures are expressed in °C *10, precipitations in mm, and elevation in m above sea level.

Variable	Description
alt	Altitude
bio1	Annual mean temperature
bio2	Mean diurnal range (monthly mean, To max-To min)
bio3	Isothermality (bio2/bio7) x 100
bio4	Temperature seasonality (standard deviation x 100)
bio5	Maximum temperature of warmest month
bio6	Minimum temperature of coldest month
bio7	Temperature annual range (bio5-bio6)
bio8	Mean temperature of wettest quarter
bio9	Mean temperature of driest quarter
bio10	Mean temperature of the warmest quarter
bio11	Mean temperature of coldest quarter
bio12	Annual precipitation
bio13	Precipitation of wettest month
bio14	Precipitation of driest month
bio15	Precipitation seasonality (coefficient of variation)
bio16	Precipitation of wettest quarter
bio17	Precipitation of driest quarter
bio18	Precipitation of the warmest quarter
bio19	Precipitation of the coldest quarter

the distribution predictions vs. independent presence and absence data and, by calculating the Area Under the Curve (AUC). The AUC is a threshold independent index commonly used to assess prediction maps (Pearce and Ferrier 2000, Giovanelli et al. 2008), which can take values between 0.5 (no predictability) and 1 (perfect prediction). According to Loo et al. (2007), a value above 0.8 indicates a strong prediction. For GARP it is only possible to calculate a single value of AUC due to the nature of the algorithm (Larson et al. 2010), whereas for MaxEnt two values, one for model training and one for model testing are calculated. However, since the strength of the predictions of both methods cannot be compared directly (Phillips et al. 2006), identification of areas susceptible to invasion by Achatina fulica in South America was interpreted separately but in a comparative manner. In addition, to increase the level of detail within each country, the primary political division (e.g., state, province) was incorporated into the models for a better interpretation of results.

RESULTS

In general terms, both models had very good performance and agreed that a large region of South America is highly susceptible to invasion by *Achatina fulica* (Fig. 1). The

AUC calculated from the ROC curve generated for GARP was 0.805. Meanwhile, MaxEnt showed the best performance for the analyzed dataset, with AUC values of 0.944 for training data and 0.921 for test data, with a standard deviation of 0.010. The MaxEnt model showed a larger area of susceptibility to invasion by the giant African snail, showing in all countries a greater number of affected states (also called departments, regions, provinces or districts according to the country) than GARP (Figs. 2–4, Table 3). According to GARP, countries such as Chile and Uruguay, would not be susceptible to invasion, but would be according to MaxEnt, although the area affected was small (Fig. 4).

The jackknife test of variable importance in MaxEnt showed that temperature seasonality (bio4) and mean temperature of coldest quarter (bio11) were the variables that most influenced the development of the model when these variables were used alone (Fig. 5). Temperature seasonality (bio4), isothermality (bio3), and altitude (alt) exhibited modest reductions in training gain when they were removed from the model, thus indicating that contain information necessary for the model (Fig. 5). The remaining variables contributed less to model development.

DISCUSSION

In this study, models generated with GARP and MaxEnt produced similar results and consistent prediction maps. Although the predictive power of both algorithms cannot be directly compared (Phillips *et al.* 2006), parallel interpretation of the graphical output was useful in identifying area susceptible to *Achatina fulica* invasion.

Our results are in agreement with other previous studies, which suggest that even though the species exhibits a wide environmental tolerance, it prefers warm habitats (Raut and Barker 2002, Albuquerque *et al.* 2009). Specifically, temperature seasonality and mean temperature of coldest quarter were identified as the two variables having the most important effect on the potential distribution of *Achatina fulica*. These findings would explain the absence of species in southern South America, which is characterized by marked seasonality and low temperatures.

Our models matched many of the predictions made by Borrero *et al.* (2009) and Correoso and Coello (2009) with susceptible areas identified in Guyana, French Guiana, Suriname, Peru, Venezuela, Ecuador and Colombia; however, by including the southernmost records of the species for model training and employing a higher spatial resolution, the potential distribution areas in the South America temperate regions were expanded. According to our results, Chile and Uruguay appear to be the least susceptible countries, with the exception of southern Chile, which might be susceptible to invasion

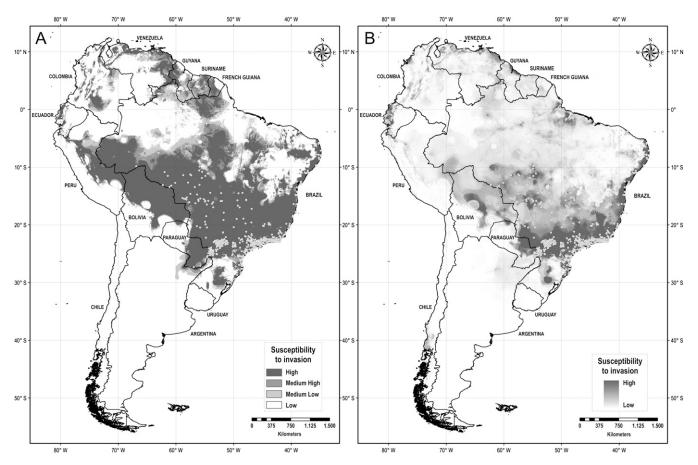


Figure 1. Bioclimatic models of susceptible areas: **A,** GARP and **B,** MaxEnt. Lighter areas indicate low susceptibility regions and darker areas indicate high susceptible regions. Points indicate occurrences records used in study.

due to the existence of favorable environmental conditions. Specifically, this region of Chile contains "Valdivian Temperate Rainforest", which has been reported to contain another exotic snail, *Cornu aspersum*, and an exotic slug, *Arion intermedius* Normand, 1852 (Cádiz and Gallardo 2007, Artacho and Nespolo 2009), suggesting that environmental conditions exist to support invasions of other mollusc species, including *Achatina fulica*.

In Argentina, the northeast region shows varying degrees of susceptibility but the overall trend is towards a medium susceptibility level. Even the north central area could be identified as susceptible, although with a low probability. Nonetheless, it is important to maintain vigilance of this area because it is comprised of Subtropical Cloudforest (Yungas), which shares some environmental conditions with the Paranaense Rainforest (located in northeastern Argentina, southern Brazil, and East of Paraguay), where the species is already present (Miranda and Cuezzo 2010, Gutiérrez Gregoric *et al.* 2011).

In Paraguay, despite the fact that the majority of the eastern portion of the country can be considered as a highly susceptible area, *Achatina fulica* has only been reported in the one southern location, the Ayolas (Table 1). Due to the large number of occurrences of *A. fulica* in Brazil along the Paraguay border (Thiengo *et al.* 2007, Colley and Fischer 2009), it can be assumed that the species may occur in other locations of Paraguay but its presence has not yet been reported.

The majority of Bolivia is highly susceptible to *Achatina fulica* invasion, with the exception of the southwest region where susceptibility appears to be low. We were unable to locate confirmed locations of the species presence; however, Correoso and Coello (2009) reported that the species was being commercialized in the city of La Paz. This fact, combined with the country's shared border with Brazil and Paraguay (Paula and Lopes 2007, Thiengo *et al.* 2007) suggests that the species is inevitably present in Bolivia but surveys are needed to confirm its distribution.

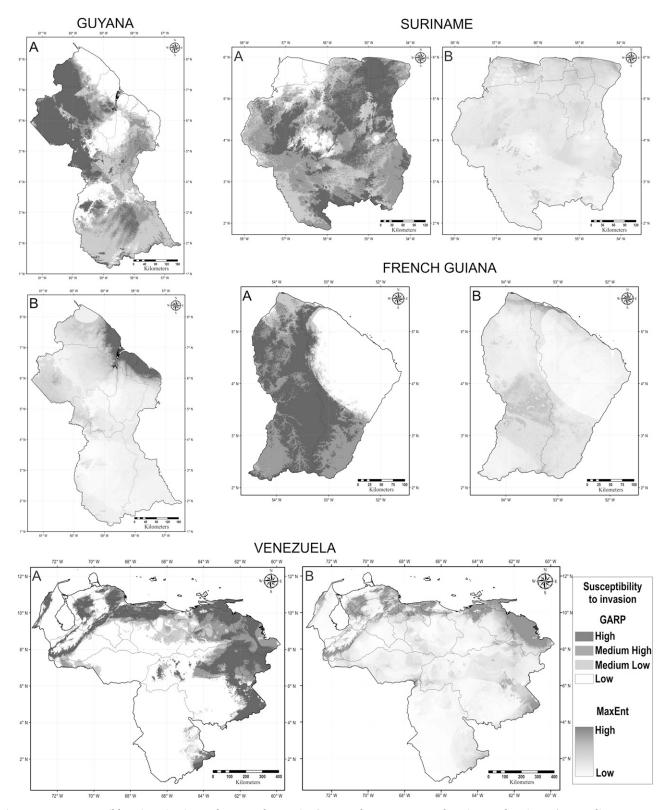


Figure 2. Areas susceptible to invasion in northern South America (Venezuela, Guyana, French Guiana and Suriname), according to **A,** GARP and, **B,** MaxEnt.

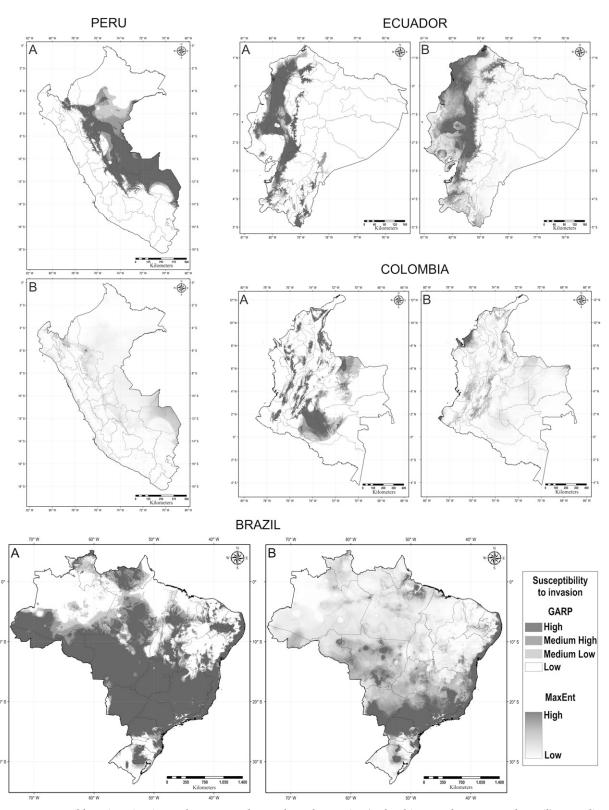


Figure 3. Areas susceptible to invasion in northwestern and central South America (Colombia, Ecuador, Peru, and Brazil), according to **A,** GARP and, **B,** MaxEnt.

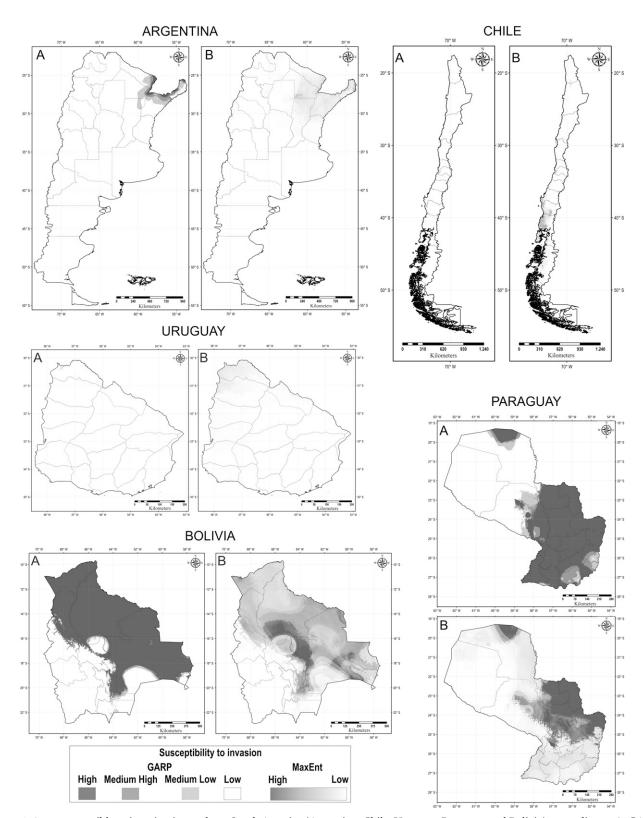


Figure 4. Areas susceptible to invasion in southern South America (Argentina, Chile, Uruguay, Paraguay and Bolivia), according to **A,** GARP and, **B,** MaxEnt.

Table 3. Primary political division of South American countries susceptible to invasion according to each model. The summary for each political division includes the total number of units per country, as well as the number of susceptible units identified with GARP and MaxEnt. † Total political units per country; ‡ Political units susceptible according to GARP; § Political units susceptible according to MaxEnt.

	Primary political division			
Country	Total†	GARP‡	MaxEnt§	
Argentina	23	6	15	
Bolivia	9	7	7	
Brazil	26	26	26	
Chile	15	0	13	
Colombia	32	29	31	
Ecuador	24	18	23	
French Guiana	2	2	2	
Guyana	10	10	10	
Paraguay	17	16	17	
Peru	24	17	24	
Suriname	10	10	10	
Uruguay	19	1	10	
Venezuela	24	24	24	

For Brazil, models indicate the area of highest susceptibility to occur between the midwest and Atlantic coast in a southeastward direction. Some areas of low susceptibility are noted in the northwest and northeast portions of the country. In 2005, in response to the invasive behavior of the giant African snail and its implications on health, biodiversity, and agriculture, IBAMA (Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis) forbad the sale and breeding of *Achatina fulica* (Carvalho-Junior and Nunes 2009). Remarkably, Brazil is the only South American country with *A. fulica* regulatory legislation.

We identified a larger area in South America that is climatically susceptible to be invaded by the giant African snail than that previously reported by Borrero et al. (2009). A comparative analysis of our models clearly indicates that several subcontinent temperate regions contain the minimal environmental conditions able to support an invasion of Achatina fulica. Several newly-predicted susceptible areas involve boundaries with countries where the invasive species is known to occur. This knowledge is especially useful to governmental authorities in countries where the invasive species was recently confirmed (e.g., a single location in Argentina that borders Brazil and Paraguay; Gutiérrez Gregoric et al. 2011) or where it is yet unreported (e.g., Chile and Uruguay). We expect that control and management authorities can use this information to establish priority areas for surveillance and to plan preventive actions aimed at limiting the spread of the species.

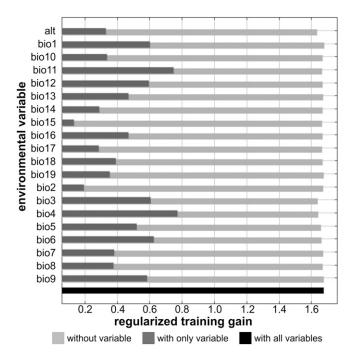


Figure 5. Jackknife test of training gain for the MaxEnt model. Abbreviations: **alt**, elevation, **bio1** through **bio19**, bioclimatic variables (Table 2).

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