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Seeking the flowers for the bees: Integrating biotic interactions into niche models to assess the distribution of the exotic bee species *Lithurgus huberi* in South America

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ABSTRACT

The wood-boring bee *Lithurgus huberi* Ducke (Apidae: Megachilinae: Lithurgini) is arguably an exotic species to South America. This solitary bee is the only representative in the Western Hemisphere of the Old World genus *Lithurgus*, and likely a conspecific with the Indo-Australian species *Lithurgus atratus*. *L. huberi* appears to have reached the continent at least 100 years ago, when it was discovered and described. Because this species seems to be oligolectic on pollen of Convolvulaceae flowers in South America, we attempted to integrate this biotic interaction (plant–bee relationships) to our species distribution model (SDM) procedures to predict its potential distribution in South America. The modeled distribution of seven *L. huberi*'s host plant species did not improve the algorithms' ability to predict its distribution, but it produced constrained ranges. These results suggest that our biotic variables are not independent of the abiotic variables used (mostly related to climate). We employed five modeling algorithms, Envelope Score, GARP, Mahalanobis Distance, Support Vector Machines, and MaxEnt, but only the former two showed a good performance when predicting the occurrence of both, the host plant species and *L. huberi*. Our results indicate that this exotic pollinator is mainly distributed in eastern, northeastern, central, and southwestern South America, with few suitable areas in the Amazon region. We also highlight suitable areas for future surveys and present new occurrence records.

1. Introduction

The world is undergoing fast and intense environmental changes caused, directly or indirectly, by human activities (MEA, 2005; Sala, 2000). Habitat loss and fragmentation, deposition of anthropogenic fixed nitrogenous substances, and the increasing atmospheric CO_2 concentration with its associated climatic changes, are considered to be worldwide drivers of environmental change (Tylianakis et al., 2008). Introduction of exotic species are also recognized as a major cause of environmental changes (Pejchar and Mooney, 2009; Tylianakis et al., 2008) and economic losses elsewhere (Pimentel et al., 2001, 2005). Therefore, practical tools to predict exotic species invasions are of the greatest importance for both science and society (Jiménez-Valverde et al., 2011; Thuiller et al., 2005), especially if we consider that human activities greatly increase species migratory abilities, allowing them to overcome their natural migratory barriers (Jiménez-Valverde et al., 2011).

The invasion of exotic species is often characterized by three stages (Richardson et al., 2000): species' introduction, naturalization, and spread. In the first stage, the species arrive within its new ranges. In the second, some individuals from self-sustaining populations arrive and establish other populations in the new geographic range. Given the appropriate conditions, such populations

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will increase the species' range, and eventually, in the third stage, they will spread, causing a new range expansion.

A wide array of environmental features may be changed after the establishment of exotic species in a new area, such as biogeochemical cycles (Ashton et al., 2005), which have inherent effects on important ecosystem processes (Bradley et al., 2010; Mangla et al., 2010; Pejchar and Mooney, 2009; Traveset and Richardson, 2006). Those changes may decrease the availability of important resources for native species (Asner et al., 2008; Iponga et al., 2008) and also affect species–specific interactions (Traveset and Richardson, 2006). Thus, cultural (*e.g.* tourism, aesthetic beauty), provisioning (*e.g.* food, fuel, water), and/or regulating ecosystem services (*e.g.* climate regulation, disease regulation, pollination) may be affected during the invasion process of exotic species.

In the context of pollination services, it is well known that many angiosperms rely on animal species for seed production (Herrera and Pellmyr, 2002; Traveset and Richardson, 2006). Depending on the degree of specialization, they may be generalists, which are visited by several pollinators, or extremely specialized species, which rely on a narrow suite of specific pollinators. In the latter case, the introduction of a pervasive exotic pollinator is expected to decrease the quantity and quality of pollen grains exchanged among different individuals, with subsequent fitness losses (Traveset and Richardson, 2006). Generalist invasive pollinators may easily become integrated to plant–pollinator systems in the exotic range (Traveset and Richardson, 2006) and may cause negative results for plant communities, given the establishment of fragile and loose interactions between invader pollinators and the plant species, but also for pollinator as well (Butz-Huryn, 1997; Santos et al., 2012).

When considering all factors determining either the success or failure of exotic species in new ranges, it is usually expected that the abiotic component of their ecological niche exerts a major effect on their distribution (Jiménez-Valverde et al., 2011; Soberón and Peterson, 2005; Soberón, 2007). However, while the biotic component of their niche is usually not considered in macroecological studies (Hortal et al., 2010; Pearson and Dawson, 2003), interspecific interactions with plant species are very important to pollinators, since they mainly depend on plants to survive in their environments. Therefore, the potential effects of such components, while determining the distribution of a given species, should be carefully considered whenever possible. Some attempts to contemplate interactions between pollinators and their specific host plants in macroecological scales have already been explored (Araújo and Luoto, 2007; Giannini et al., 2013a; Heikkinen et al., 2007; Meier et al., 2010; Preston et al., 2008; Rouget et al., 2001), however, as far as we know, no study has assessed the effects of the host plant species distribution on the distribution of an exotic species.

Other similar studies have already tried to include the biotic components of species niche while evaluating their distributions. Usually, biotic interactions between different species are considered by including them as predictor variables of the focus modeled species layers, corresponding to the modeled distribution of its interacting species (Giannini et al., 2013a; Heikkinen et al., 2007). Nonetheless, only the inclusion of known presence/absence data of interacting species (Araújo and Luoto, 2007; Giannini et al., 2013a), their abundances (Pellissier et al., 2010), or even land cover types (González-Salazar et al., 2013) may also be used as biotic predictor variables potentially determining the distribution of a species. Although such methods may seem simple at first, considering the broad spatial scale used in species distribution modeling, they can certainly provide us with a deeper understanding of important biological interactions occurring in local and/or regional scales, especially if we consider community ecology frameworks (Guisan and Rahbek, 2011; Meier et al., 2010; Pellissier et al., 2010). Considering the biotic portion of the species' niche, while dealing with their potential distributions, is of utmost importance, especially in a rapidly changing world (Adler and HilleRisLambers, 2008).

Herein, we constructed species distribution models to examine the potential distribution of the exotic bee species *Lithurgus huberi* Ducke (Apidae: Megachilinae: Lithurgini) in South America. Given the discovery of new occurrence records for this species (see below), the main goals in this study were: (1) to evaluate the capability of several species distribution modeling algorithms on predicting new occurrences using only the older ones; (2) to evaluate how the modeled distribution of its host plant species may affect the final distribution of *L. huberi*; and (3) to highlight unsurveyed but suitable areas for the occurrence of *L. huberi* in South America, with the aim of directing future studies.

2. Materials and methods

2.1. The modeled species

L. huberi was described by Ducke (1907) from Maranhão, Brazil, and is the only representative of this Old World genus of solitary bees in the Americas. The nesting biology, cocoon, and floral associations of *L. huberi* have been documented by Camillo et al. (1994, 1983), Mello et al. (1987), and Pick and Schlindwein (2011). The species is univoltine and, as in other members of the genus, *L. huberi* has a wood-nesting habit that facilitates dispersion across great distances. Nests are built inside dead dry logs, and are initiated between March and June (Camillo et al., 1983, 1994; Gonzalez et al., 2013a,b; Michener, 1965, 2007; Snelling, 1983). Also, as in other *Lithurgus*, it appears to be oligolectic on plants with large pollen grains. While it has been observed to collect pollen from Asteraceae, and especially Malvaceae, in its natural range (Michener, 2007), in its invaded range, this species has been collected on flowers of Convolvulaceae (particularly on *Ipomoea* and *Merremia*) and Malvaceae (*Sida* sp. and *Gossypium* spp.; Camillo et al., 1983, 1994; Pick and Schlindwein, 2011). Given morphological similarities with *Lithurgus atratus*, an Indo-Australian species presumably composed of at least eight species that have been suggested to represent a single taxonomic unit (Michener, 1965), Snelling (1983) was the first to hypothesize that *L. huberi* was exotic to South America. Nonetheless, a recent study by Gonzalez et al. (2013b) suggested that those species are in fact two independent taxonomic units, a classification that has also been previously adopted by other authors (*e.g.* Moure and Melo, 2007). Following Colautti and MacIsaac (2004), *L. huberi* can be classified as a widespread but locally rare exotic species (Stage IVa species).

2.2. *L. huberi* and host plant species occurrences dataset

To predict the potential distribution of *L. huberi* in South America, we gathered a total of 56 occurrence records for this species from the following sources: (1) literature records (see Supplementary Material for complete list of published papers holding *L. huberi* occurrence information), (2) online databases such as CRIA Species Link (http://splink.cria.org.br) (the only institution in CRIA Species Link bearing *L. huberi* occurrences was Coleção Entomológica da Universidade Federal do Pernambuco), Global Biodiversity Information Facility (http://www.gbif.org), Inter-American Biodiversity Information Network (IABIN; http://iabin.databasin.org), and Discover Life Bee Species Guide and World Checklist (http://www.discover-life.org), and (3) museum collections [(i) Coleção Entomológica Padre J.S. Moure, Universidade Federal do Paraná, Curitiba, PR, Brazil; (ii) Coleção Entomológica Paulo Nogueira-Netto, Universidade de São Paulo, São Paulo, SP, Brazil;

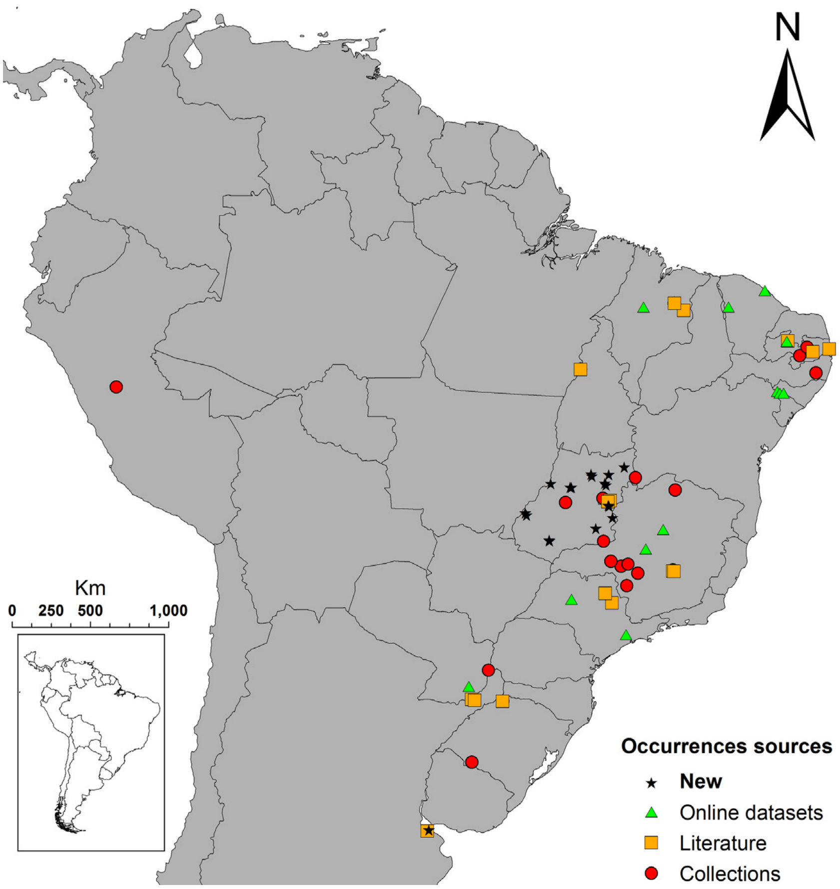

Fig. 1. Occurrence records for *Lithurgus huberi* in South America, including data sources and new records reported in this study.

(iii) Coleção Entomológica da Universidade Federal do Pernambuco (retrieved from CRIA Species Link)]. Additionally, we gathered 18 new occurrence records taken from field surveys in the Brazilian state of Goiás and in Argentina (Table S1). In some localities in Brazil, more than 30 individuals of *L. huberi* were sampled, thus suggesting high density populations of this species (DPS, pers. obs.). All *L. huberi* occurrences are depicted in Fig. 1.

To evaluate how the modeled distribution of *L. huberi* is affected by the distribution of the host plant, we gathered data on the occurrences of all plant species recorded to be used by *L. huberi* as pollen resources in South America (Camillo et al., 1983, 1994; Pick and Schlindwein, 2011). All available information for *Ipomoea nil* (L.) Roth, *Ipomoea bahiensis* (L.) Roth, *Ipomoea purpurea* (L.) Roth, *Ipomoea indica* (Burm. F.) Merril, *Ipomoea cairica* (L.) Sweet, *Ipomoea asarifolia* (Desr.) Roemer & Schultes, and *Merremia aegyptia* (L.) Urban were gathered from CRIA Species Link and GBIF. We disregarded those obtained both for *Sida* spp. and *Gossypium* spp. because the species–specific relationships of the bee with these plants are unspecific and were not fully addressed in the literature, as far as we are aware of. The complete list of institutions holding occurrences for these plant species can be found in the Supplementary Material.

We used Google Earth (Google Inc., 2013) to acquire proxy geographical information from city hall coordinates for those records of bees and flowers that did not have exact geographical information. Given the grid resolution used in this study (see below), of the initial 56 old occurrences gathered for *L. huberi*, only 48 remained as unique. All 18 new occurrences for *L. huberi* remained when considering this grid resolution. The amount of unique occurrences for all modeled host plant species are listed in Table S2.

2.3. *Modeling algorithms as predictive tools*

Species Distribution Models (SDM hereon) are considered good tools for predicting the distribution of exotic species (Araújo and Peterson, 2012; Jiménez-Valverde et al., 2011). Based on the observed occurrences of the modeled species, these tools correlate the environmental variables of these known locations to create a multidimensional environmental space. Then, based on such environmental space and the known species location, niche parameters can be estimated and the species potential distribution can be projected into the geographical areas with environmental features similar to those of the observed occurrences (Araújo and Guisan, 2006). These tools have also been widely used to predict the distribution of species unknown to science (Raxworthy et al., 2003), predict new records for rare ones (Almeida et al., 2010; De Siqueira et al., 2009; Silva et al., 2013), guide and optimize future surveys (Raxworthy et al., 2003), and to indicate areas with high predicted species richness as priority targets for future conservation actions (Loyola et al., 2012; Nóbrega and De Marco Jr., 2011).

2.4. *Environmental layers, modeling procedures, distribution thresholds, and evaluation*

We used all 19 available layers from WorldClim's climatic variables dataset (Hijmans et al., 2005) to derive principal components (PCs hereon) that we employed as environmental layers during the modeling procedures. From the 19 PCs produced, we selected seven, which accounted for more than 98% of the variation on the original environmental variables set (Table 1), and used them as new variables. This method is recommended to decrease

Table 1
Summary of the Principal Component Analysis which generated the principal components (PC) used as environmental layers. Each cell value represents the individual loadings of each variable in each of the PCs. The PCs, individual, and accumulated proportions of each PCs are also shown.

Environmental variables	Principal components						
	PC1	PC2	PC3	PC4	PC5	PC6	PC7
Annual mean temperature	0.271	0.225	−0.130	0.043	−0.054	−0.018	0.019
Annual precipitation	0.262	−0.221	−0.025	−0.214	0.174	0.089	−0.095
Isothermality	0.237	0.011	0.345	−0.074	−0.232	−0.493	−0.217
Maximum temperature warmest period	0.194	0.316	−0.345	−0.017	0.134	−0.076	−0.043
Mean diurnal range	−0.179	0.219	−0.075	−0.541	0.039	−0.474	−0.320
Mean temperature coldest quarter	0.286	0.183	−0.006	0.037	−0.097	−0.028	−0.040
Mean temperature driest quarter	0.277	0.160	0.013	0.162	0.020	−0.021	−0.112
Mean temperature warmest quarter	0.232	0.262	−0.305	0.076	0.049	−0.006	0.090
Mean temperature wettest quarter	0.234	0.255	−0.234	−0.057	−0.119	−0.023	0.189
Minimum temperature coldest period	0.294	0.123	−0.007	0.165	−0.060	0.013	0.024
Precipitation coldest quarter	0.202	−0.222	0.068	0.101	0.604	−0.288	0.129
Precipitation driest period	0.143	−0.397	−0.227	−0.019	−0.130	−0.325	0.272
Precipitation driest quarter	0.154	−0.396	−0.221	−0.023	−0.099	−0.296	0.231
Precipitation seasonality	−0.039	0.328	0.409	−0.328	0.069	−0.053	0.749
Precipitation warmest quarter	0.155	−0.211	−0.199	−0.502	−0.430	0.323	0.072
Precipitation wettest period	0.267	−0.082	0.124	−0.274	0.298	0.249	−0.103
Precipitation wettest quarter	0.268	−0.090	0.113	−0.278	0.294	0.246	−0.129
Temperature annual range	−0.250	0.118	−0.315	−0.258	0.216	−0.090	−0.076
Temperature seasonality	−0.250	−0.009	−0.389	0.024	0.245	0.049	0.193
Proportion explained by each PC	0.554	0.197	0.092	0.059	0.039	0.026	0.015
Accumulated variation proportion	0.554	0.751	0.843	0.902	0.941	0.966	0.981
Principal Components eigenvalues	55.356	19.750	9.203	5.905	3.888	2.558	1.481

the collinearity among environmental variables, but also to avoid model overfitting that may result in biologically unreliable species potential distributions (Jiménez-Valverde et al., 2011). The grid of all variables was 2.5 arc-min resolution (0.041 ≈ 4 km). We also used *L. huberi*'s host plant distributions as environmental layers (see below).

Given the overall biases and uncertain nature of species distribution models, different algorithms may result in different patterns of species distribution (Barry and Elith, 2006; Diniz-Filho et al., 2009; Rocchini et al., 2011). In order to provide the most reliable potential distribution possible, we evaluated *L. huberi* and its host plant species distributions considering five different modeling algorithms: (1) Envelope Score, a quantitative version of BIOCLIM (Nix, 1986; Piñero et al., 2007); (2) GARP with best subsets (Stockwell and Peters, 1999); (3) Mahalanobis Distance (Farber and Kadmon, 2003); (4) Support Vector Machines (SVM hereon; Schölkopf et al., 2001; Tax and Duin, 2004); and (5) Maximum Entropy (Phillips and Dudik, 2008; Phillips et al., 2006). While Envelope Score and Mahalanobis distance are simpler models that usually need presence data only to produce the species' potential distributions, MaxEnt, SVM, and GARP are artificial intelligence methods that are generally more complex, and correctly predict the species known occurrences more often (Rangel and Loyola, 2012). We used the software MaxEnt to run Maximum Entropy (Phillips et al., 2006), and openModeller Desktop for the other four modeling algorithms (Muñoz et al., 2011).

In our first modeling experiment, we divided the occurrences of all host plant species into ten 75–25% training–testing subsets. With the training subsets, we produced distributions of all host plant species using all modeling algorithms. With the testing subsets, the distributions predicted by each algorithm were evaluated. With the two best modeling algorithms, we used all available occurrences for each host plant species to produce their final distributions. Here, we considered as the host plants distributions the binary maps of presence/absence generated by each modeling algorithm. Later, we used these distributions obtained from each modeling algorithm to produce a summed distribution map for each plant species. In addition to the individual host plant distribution, we also created a stacked layer where the resulting individual host plant distribution for each host plant species were summed up. We used either all single or stacked host plant distribution layers (SEP and STK treatments, see below) in different treatments to determine *L. huberi*'s potential distribution (see Fig. 2A).

As we did for the host plant species distributions, we randomly divided all *L. huberi*'s old occurrences into ten 75–25% training–testing subsets. We used the training subsets with the previously selected PCs to produce *L. huberi*'s distributions with the four modeling algorithms. Then, we evaluated the resulting distributions with the testing subsets. Additionally, using a paired *t*-test, we assessed what proportion of the 18 new occurrences for *L. huberi* was predicted with each of the two best modeling algorithms. As a second independent model evaluation procedure, we pooled all old *L. huberi*'s occurrences to obtain its potential distribution according to the two best modeling algorithms, and evaluated these distributions using all new *L. huberi*'s occurrences as a testing subset. We used the two best modeling algorithms in all the following modeling experiment (see Fig. 2B).

In the second modeling experiment, all available *L. huberi* records were divided into ten 75–25% training–testing subsets. For the first treatment, we only used the PCs as environmental layers (PCONLY hereon) and we evaluated the resulting *L. huberi*'s distributions produced by the two best modeling algorithms with the testing subsets. Finally, we used all available *L. huberi* records with the same two best algorithms to produce the *L. huberi* final distribution and its summed final distribution. Our second and third treatments for this second modeling experiment were similar to the first one, except for slight differences. For the second treatment, we used all separated distributions of *L. huberi*'s host plant species as environmental layers, along with the PCs already used in the first treatment (SEP treatment hereon). For the second treatment, we only used the stacked host plant species layer as an environmental predictor, along with the PCs as environmental variables (STK treatment hereon), as already used for both PCONLY and SEP treatments. During all modeling procedures the algorithms were trained for the entire South American continent. Although the resulting host plant species distribution are very similar and consequently collinear, the different treatments used to predict *L. huberi*'s potential distribution (PCONLY vs. SEP vs. STK) would allow us to account for the effects produced by different environmental variables with different similarity levels.

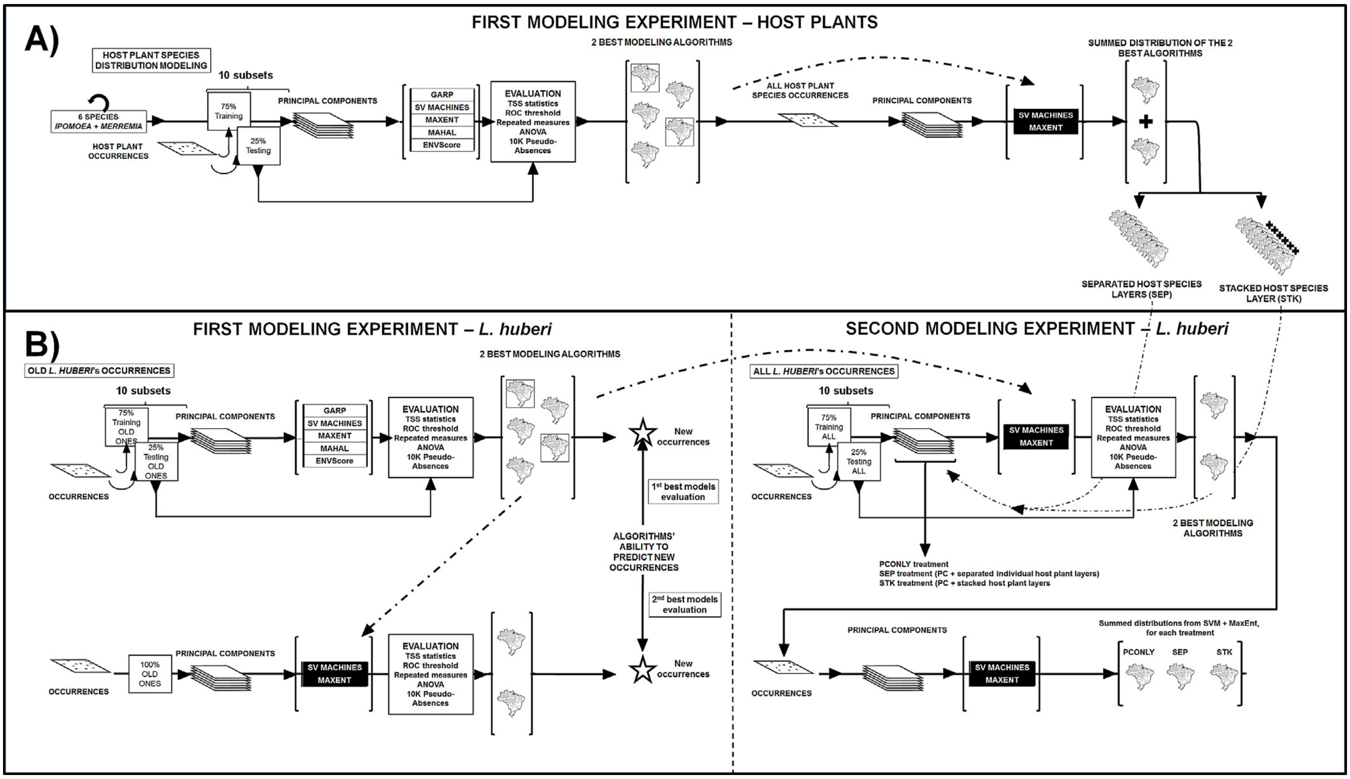

Fig. 2. Flowchart of all modeling procedures performed on this study. (A) Modeling procedures used to determine the host plant species distributions; (B) Modeling procedures used to determine *L. huberi*'s distribution in both the first and second modeling experiments. Black boxes are those algorithms which performed better during the first modeling experiment.

Despite the usual recommendation of using the LPT threshold (Pearson et al., 2007) to generate the presence/absence distribution matrices of the modeled exotic species (Jiménez-Valverde et al., 2011; Pearson et al., 2007), we chose to cut the modeled suitability matrices using the ROC threshold, which balances both omission and commission errors while determining the modeled distribution ranges. However, for comparison purposes, we also showed its current distribution considering the LPT threshold for all algorithms used to determine its final distribution under the ROC threshold in all modeling experiments. Following Liu et al. (2011), we only used True Skilled Statistics (TSS; Allouche et al., 2006) values to assess model performance. The TSS is a threshold-dependent statistics that varies from −1 to +1, where negative and around zero values regard distributions no better than a random distribution, while values near +1 represent perfect agreement between the observed and the modeled distributions. Acceptable models considering this statistics are those which reach at least 0.5, and excellent TSS values reaching a minimum of 0.7, an interpretation somehow similar to that employed with the *Area Under the Receiver-Operator Curve* statistics (AUC; Fielding and Bell, 1997). In all model evaluation procedures we used 10,000 random pseudo-absences (PAs hereon). We used repeated measures ANOVAs (Fig. 2A and B) to determine the two best modeling algorithms while modeling the host plant species distributions and during the evaluation of the best environmental layer in predicting *L. huberi* distribution.

3. Results

In the first modeling experiment, TSS values for Envelope Score always showed the lowest values, independent of the species considered. The TSS values for all other modeling algorithms, for all species including *L. huberi*, were always higher than 0.5 (Fig. 3A), except for the modeled distributions of the host plants *I. nil* and *I. purpurea* obtained with Mahalanobis distance and GARP, which had TSS values below 0.5, under the ROC threshold. Despite a few exceptions (*e.g. I. asarifolia*, *I. bahiensis*), for which only SVM showed higher predictive performance, both SVM and MaxEnt were the algorithms that obtained the highest TSS values (Fig. 3A). Therefore, we selected them to model both the host plants' and *L. huberi*'s final distributions in South America. In general, considering the ROC threshold, all host plant species distributions were frequent in northeastern and southeastern South America, with a few species also showing suitable areas in central and northwestern South America (Bolivia, Paraguay, Peru, Ecuador, Colombia, and Venezuela). Suitable areas for the occurrence of those host plant species were not observed in core Amazonian areas (predicted distributions are depicted in Figure S1).

Under the ROC threshold, no differences in the algorithms' ability to predict the 18 new occurrences for *L. huberi* were observed between SVM and MaxEnt (paired *t*-value: 0.138; d.f.: 9; *p*-value: 0.892; MaxEnt: 0.594 ± 0.187, mean ± standard error; SVM: 0.605 ± 0.193). In the second independent model evaluation, while SVM predicted all new occurrences, MaxEnt only predicted half of them, similar to what was predicted in the first model evaluation procedure. Nonetheless, this bigger proportion of occurrences correctly predicted by SVM was mainly caused by a model overprediction of the species potential distribution in South America (TSS values for SVM and MaxEnt were 0.356 and 0.385, respectively in the independent model evaluation).

Considering the different treatments used to determine *L. huberi*'s distribution in the second modeling experiment, MaxEnt showed a constant performance with no substantial increase/decrease in TSS values in all procedures, with values around 0.5 and 0.7 (Fig. 3B). Such variation in TSS values is

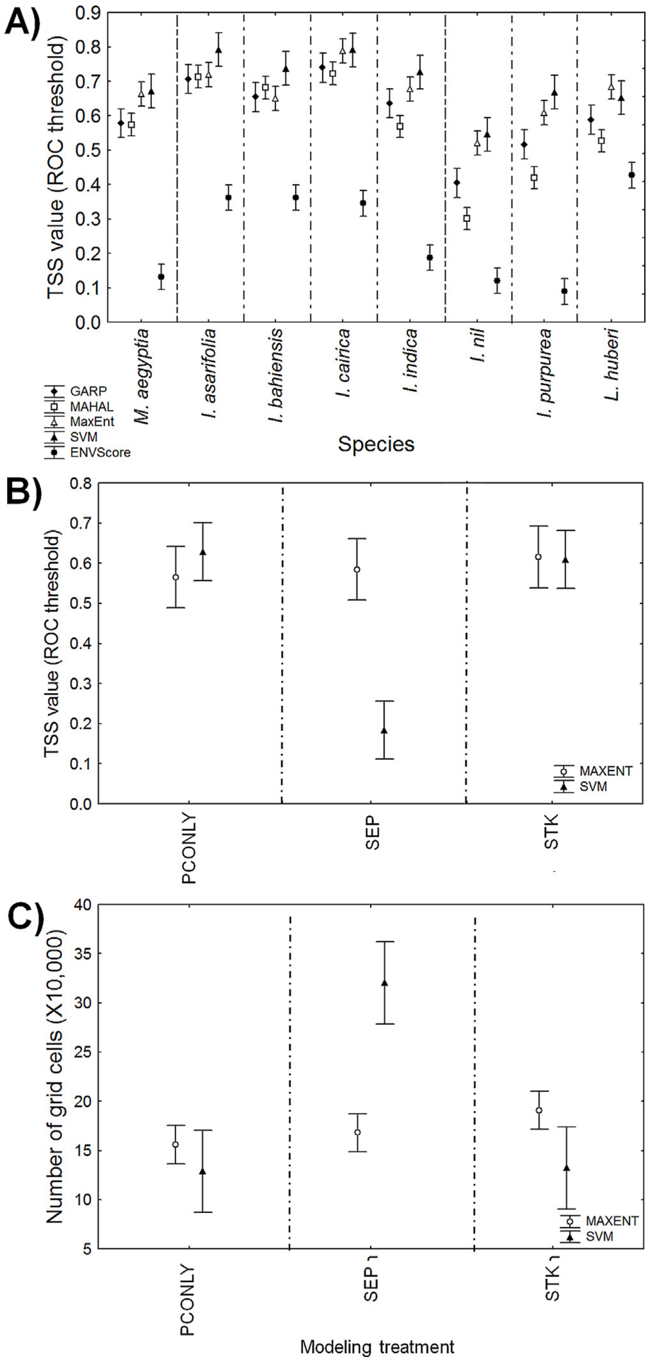

Fig. 3. Results of the second modeling experiment. (A) Evaluation of the four algorithms used to determine the distribution of the seven host plant species as well as of *L. huberi* in the first modeling experiment; (B) Evaluation of both MaxEnt and Support Vector Machines (SVM), the chosen algorithms to determine the final distributions for *L. huberi*, in the second modeling experiment. (C) *L. huberi*'s range sizes according to each algorithm in the second modeling experiment. Mid-points refer to means and bars represent 95% confidence intervals.

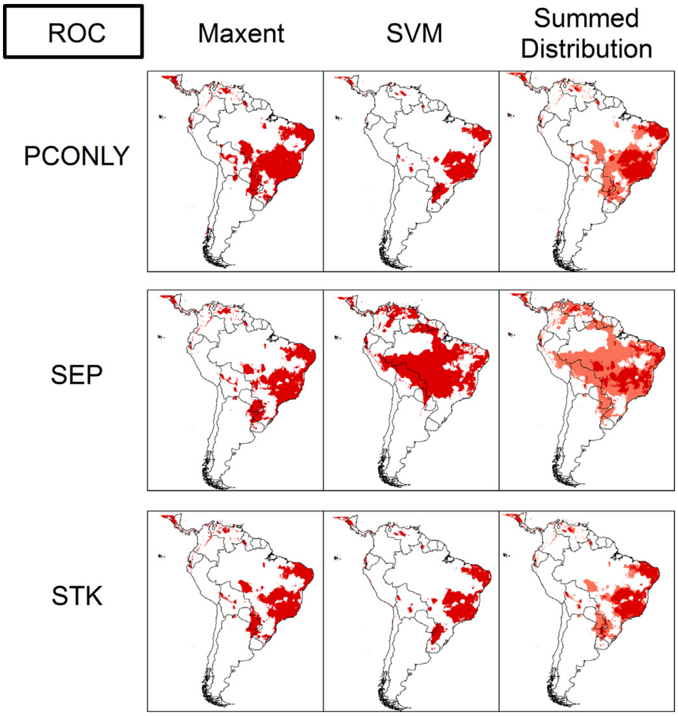

Fig. 4. Final individual distributions for *Lithurgus huberi* produced by each modeling algorithm according to each modeling treatment and its related summed distributions, considering the ROC threshold.

not negligible, and may have been caused by the use of all the different 10 random subsets of *L. huberi* occurrences used during the modeling procedures. Nonetheless, the algorithm SVM also showed a similar trend, at least for both the PCONLY and STK treatments. However, its performance showed a substantial decrease for the SEP treatment, with TSS values ranging between 0.1 and 0.3 (Fig. 3B). Although the total size of *L. huberi*'s resulting distributions were larger for both SEP and STK treatments, when compared to those produced with the PCONLY treatment, those distributions produced with MaxEnt were more cohesive, with less dispersed suitable patches for *L. huberi* occurrence in South America (Figs. 3C and 4, first column). We observed a similar trend for SVM in the STK treatment (Figs. 3C and 4, second column). On the other hand, the SEP treatment showed a substantial increase in range size (Figs. 3C and 4).

Fig. 4 shows the resulting final distributions for *L. huberi* produced by each modeling algorithm under each treatment, as well as, their summed distributions under the ROC threshold. In general, *L. huberi* distribution was mainly predicted to occur in northeastern and southeastern South America, similar to the predicted distribution of its host plant species. Even so, for both modeling algorithms used, we observed disjunct distributions in central, southern, and northern areas of South America. As observed for its host plant species, *L. huberi* was not predicted to occur in core Amazonian areas. The only distribution that showed different results was that produced with SVM in the SEP treatment, which had a greater predicted range for *L. huberi* than that observed for MaxEnt (Fig. 4, second row). Finally, *L. huberi* distribution determined by the LPT threshold (Figure S2), especially when considering the SVM algorithm, showed a large increase in its predicted range, which certainly does not correspond to its distribution in South America. Based on a 350 km buffer around the known occurrences predicted by our models from the STK treatment, we suggest that future sampling efforts should be focused on: (1) Brazilian states of Goiás, Minas Gerais, and São Paulo in central-eastern South America; (2) Brazilian states in northeastern South America, and (3) southern Brazilian regions, Paraguay, and some areas in northern Argentina (Fig. 5).

4. Discussion

In this study, we attempted to integrate biotic interactions (plant–bee relationships) to our SDM procedures when predicting the potential distribution of *L. huberi* in its invaded range in

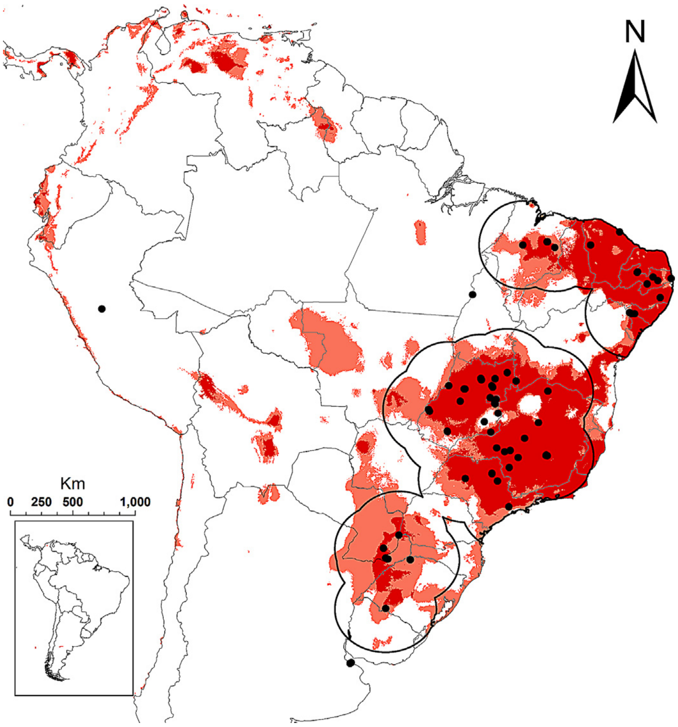

Fig. 5. Areas suggested for future surveys of *Lithurgus huberi* in South America, according to the summed distribution of MaxEnt and SVM algorithms considering the stacked modeled distribution of host plants produced by the STK treatments (Fig. 4, third column, last map). Known records for *L. huberi* are depicted as black circles.

South America. We also presented new occurrence records for *L. huberi* in Brazil ($n = 17$) and Argentina ($n = 1$). Of the five initial modeling algorithms, SVM and MaxEnt showed a good performance when predicting the occurrence of both, the host plant species and the bee. The inclusion of the host plant species distributions as variables when modeling the distribution of *L. huberi* did not increase the algorithms ability to predict its distributions, and in fact, for the SVM algorithm, model performance decreased. Nonetheless, when considering the STK treatment, both algorithms produced more constrained distributions, with lesser amounts of scattered suitable patches for *L. huberi* occurrence in South America. Our modeling procedures show that this exotic species is mainly distributed in eastern, northeastern, central, and southwestern South America, with a few suitable areas in the Amazon region. Such distribution pattern resembles that obtained from modeling all seven host plant species considered in the present study.

Generally, species distribution is determined by the intersection of the biotic, the abiotic, and the historic/migration elements that are available for the species (the BAM diagram; Soberón and Peterson, 2005; Soberón, 2007). However, biotic interactions are usually disregarded in macroecological analyses as effective variables determining the distributions of modeled species because they are assumed to exert only local effects (*e.g.* community assembly rules). This contrasts with abiotic variables (*e.g.* climate), which are thought to be the main responsible factors for determining species distribution at broader scales (Hortal et al., 2010; Pearson and Dawson, 2003; Willis and Whittaker, 2002). Nonetheless, the omission of biotic interactions from the SDM does not necessarily mean that they do not have any role in determining species distribution at broader scales (Meier et al., 2010).

Given such concerns and criticisms regarding the true effects of biotic variables at broader scale analyses (Guisan and Rahbek, 2011; Wisz et al., 2013), several studies have improved the models' ability to predict the species distribution. These studies have considered different kinds of biotic variables and different biological scenarios into the modeling procedures (Araújo and Luoto, 2007; Heikkinen et al., 2007; Meier et al., 2010; Preston et al., 2008; Rouget et al., 2001). In general, the contribution of biotic predictors on models' performance of focus species final distributions also varied. For instance, Heikkinen et al. (2007), Araújo and Luoto (2007), and Meier et al. (2010), found positive effects by including biotic variables in determining the target species' potential distribution. Pellissier et al. (2010) obtained results which ranged from highly positive, mildly positive, no effect, to even negative effects while evaluating the effect of including the abundance of *Empetrum hermafroditum* as a predictor variable affecting the distribution of other 34 subordinate species. Our results indicate that the biotic variables we used (the distributions of host plant species) are not independent of the abiotic variables (mostly related to climate) considered in the modeling procedures, as they did not improve the algorithms' ability to determine the modeled distribution of *L. huberi*. Nonetheless, our results are different from those found by other studies (Araújo and Luoto, 2007; Giannini et al., 2013a; Heikkinen et al., 2007; Meier et al., 2010), which indicated that biotic interactions are important variables determining the distributions of several target species.

In our case, given the dependency of insects and plants on climate conditions (Chown and Terblanche, 2006; Hutchinson, 1957), such variables would be the main factor responsible for both known and modeled distributions of *L. huberi* and its host plant species. Additionally, because *L. huberi* seems to be oligolectic on the pollen of those plants, the observed occurrences that we obtained for both, the bee and the host plant species, might already be the resulting intersection of the abiotic and biotic components regulating their niche (Soberón and Peterson, 2005; Soberón, 2007). Consequently, even though the use of the host plant species distribution to determine *L. huberi*'s distribution may produce a more concise distribution, may not necessarily improve the algorithm's prediction ability. At least for *L. huberi* and its host plant species, our results agree with the widely established theory that climate is the main variable determining the species distribution at a broad scales (Hortal et al., 2010; Pearson and Dawson, 2003). Such influence of climate on the distribution of both plant species and pollinators has also been shown for other intimate bee–plant species systems, namely between *Curcubita* (Curcubitaceae) plants and *Peponapis* bees (Apinae: Eucerini) (Giannini et al., 2011, 2010) and *Centris* (Apinae: Centridini) bees and oil-producing plants (Giannini et al., 2013b).

Exotic species may experience niche shifts after establishing in a new area (Broennimann et al., 2007; Da Mata et al., 2010; Fitzpatrick et al., 2007; Mukherjee et al., 2012), with a tendency to occupy regions that are climatically different from those where they naturally occur. However, a study involving another invasive megachiline species, *Anthidium manicatum* Linnaeus, showed that its invasive range seems to be restricted to areas environmentally similar to its original Eurasian range (Strange et al., 2011). The niche similarity in South America, when compared to its native distribution range, is smaller than that observed for North America, which suggests ongoing niche shifts. The relationship of *L. huberi* with species of Convolvulaceae species seems to have emerged only after its arrival in South America, since species of *Lithurgus* are known to visit only flowers of Asteraceae and, especially, Malvaceae as pollen sources in their native ranges (Michener, 2007). Such new relationship seems possible given that oligolectic bees can shift hosts (*e.g.* Wcislo and Cane, 1996; Williams, 2003), and it may also indicate that this species is becoming naturalized in South America after more than 100 years when it was first detected. However, our understanding on the floral preferences of *L. huberi* are limited to a few observations in Brazil (Camillo et al., 1983, 1994; Pick and Schlindwein, 2011; Pires et al., 2006), and to properly answer the question whether *L. huberi* suffered niche shift or not, further macroecologic analyses on its distributional patterns in both native and invaded ranges are required (*e.g.* Broennimann et al., 2012; Warren et al., 2008).

The use of additional flower resources not accounted in this study as important biotic predictor variables may exert significant effects in the determination of *L. huberi*'s distribution in its invaded range. Thus, given its putative relationships with species of Malvaceae in its original range, further natural history and ecological studies across its South American range might be necessary to determine whether this bee also rely on such sources of pollen in its invaded range, as scarce observations from its native range suggest. In the event *L. huberi* is observed collecting pollen from other plant species not considered here, the methods we used here should be reconsidered, with the inclusion of these new biotic interactions as a potential new predictor variables determining its distribution in South America. Other possible determinants of *L. huberi* distribution not considered here are the plant species it uses as nesting substrate, namely *Euphorbia carinatum*, *Euphorbia pulcherrima* (Euphorbiaceae), *Spathodea campanulata* (Bignoniaceae), and *Eucalyptus* sp. (Myrtaceae) (Camillo et al., 1994). Particularly important is the later species, which is now widely planted in Brazil for timber and charcoal. The abundance of *Eucalyptus* in Brazil, as well as other nesting substrates and also pollen from other sources not considered in our study, might also affect the distribution of *L. huberi*, especially in areas not predicted as suitable in our models.

Different species distribution models have different mechanistic features, and usually tend to produce results with inherent peculiarities (Diniz-Filho et al., 2009; Rangel and Loyola, 2012), and such difference may be observed even for the models we considered as the best ones to represent a given species potential distribution. Although both MaxEnt and SVM showed some differences while representing *L. huberi*'s distribution, with only a ~60% prediction rate of the bee's known occurrences, in general they were the algorithms that attained the best predictions of both the bee's and its host plant species' distributions, when compared to the others. Considering the fact the insect species' known distributions usually lack deep distributional knowledge, especially in the neotropical region (Ballesteros-Mejia et al., 2013; Kamino et al., 2011; Soberón et al., 2007), even algorithms that reached only a 60% prediction rate may generate interesting and useful species distributions to be evaluated in new field surveys. Using known occurrences for some leaf-tailed geckos in Madagascar allied with SDM procedures, Raxworthy et al. (2003) were able to find both new occurrences for the known modeled species, as well as, new-to-science leaf-tailed geckos species. In a similar way and given new distributional information on the orchid bee *Aglae caerulea*, Silva et al. (2013) pinpointed suitable areas for future surveys of the species in the Brazilian Cerrado Savanna.

Given the modeled distribution of *L. huberi* in South America, based on both SVM and MaxEnt algorithms, the areas depicted in Fig. 5 are suggested as suitable for future surveys. These areas correspond to northeastern Brazil, southeastern Brazil, and northeastern Argentina/southern Brazil. Although the third region was not predicted as suitable, according to the SVM algorithm, many of its known occurrences were located in this third area, and, therefore, it should be considered in future surveys. Similar approaches have been used before and yielded fruitful results. Eventually, in case future occurrences for *L. huberi* are obtained, especially in areas not predicted as suitable for species in this study, new distribution evaluation for *L. huberi* are advised (Guisan et al., 2006). The main justifications to be considered for such process are threefold: (1) optimization to a larger extent of the resources invested in field surveys, (2) the discovery and improvement of *L. huberi* known and potential distribution, and (3) the proper evaluation of the modeling methods employed in the present study.

5. Conclusions

In this study we modeled the distribution of seven host plant species recorded in the literature for *L. huberi* and used them as a biotic variable in determining the potential distribution of this exotic pollinator in South America. We also presented new occurrence records for this species in Brazil and Argentina, some of which appear to support high population densities of *L. huberi* (DPS, pers. obs.). Although the modeled host plant distributions did not improve the algorithms' ability to predict the distribution of *L. huberi*, similar studies with other host plants as well as with other biological contexts should be sought to properly evaluate biotic variables on SDM procedures. The modeled distribution of *L. huberi*, either using ROC or LPT thresholds, suggests that this species is able to colonize most of South America. Future surveys should focus on some of the areas indicated in Fig. 5 to evaluate the true invasive potential of this species. Biological studies across the invaded range of this species are also suggested to improve our knowledge of the documented floral association with Convolvulaceae as well as to detect any host shift.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolmodel.2013.11.016.

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