

Presence of the *Eucalyptus* snout beetle in Ecuador and potential invasion risk in South America

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Abstract

Eucalyptus snout beetles (Curculionidae: *Gonipterus scutellatus* complex), native to mainland Australia and Tasmania, defoliate *Eucalyptus* trees and are considered important pests. Since the 19th century, species of the *G. scutellatus* complex have been introduced to other continents. Here, we document the presence of *Eucalyptus* snout beetles in Ecuador and use ecological niche models to analyze their potential distribution in South America. Phylogenetic analyses of DNA sequences unambiguously demonstrated that the Ecuadorian specimens belong to the species *G. platensis*, which has low genetic diversity compared with other species in the complex. Ecological niche models revealed several areas of high to intermediate climatic suitability for the pest in South America, even in countries where it has not been registered, like Peru and Bolivia. Accurate identification of species in the *Gonipterus scutellatus* complex and understanding of their potential distribution are essential tools for improved management and prevention tactics.

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Abstract

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Key words

Ecological Niche Model, Forest pest; *Gonipterus platensis*; invasive species

Introduction

Eucalyptus trees (Myrtaceae) were initially introduced in South America in the early and mid-19th century to meet increasing demands of wood, coal, and firewood in the region (FAO, 1981). Commercial plantations of *Eucalyptus* have rapidly expanded in the last three decades and together with pine trees, today they constitute the base of forestry development in many countries of South America (Estay, 2020). In Ecuador, several species of *Eucalyptus* (mostly *E. globulus*) were first introduced in 1865 largely for firewood and construction materials (FAO, 1981). They have also been extensively planted for reforestation and erosion control programs, making them very common and even dominant in many landscapes of the Ecuadorian Andes (Granda, 2006). Although *Eucalyptus* trees mainly occur in the inter-Andean valleys of the country, a massive plantation program to produce wood chips for paper pulp was established in the early 2000 in the coastal province of Esmeraldas. Today, *E. globulus* is one of the most important tree species in the Ecuadorian forestry sector, which directly employs more than 230 000 people (c.a. 5.5% of the economically active population) and contributes around 2 to 3% to Ecuador's GDP (Grijalva et al., 2015).

Eucalyptus snout beetles are a complex of cryptic species (*Gonipterus scutellatus* complex) that feed on *Eucalyptus* leaves (Schröder et al., 2020). These beetles are native to Eastern Australia and Tasmania. Species of the complex have been accidentally introduced into Western Australia (at an unknown date), New Zealand in 1890, Africa in 1916, South America in 1925, Europe in 1975 and North America in 1994. In South America, they have been introduced in Argentina in 1925, Uruguay in 1937, Brazil in 1955, Chile in 1998 (Estay, 2020; González et al., 2010; Marelli, 1927), and more recently, Colombia in 2016 (Madrigal-Cardeno, 2019; Schröder et al., 2020). The morphological similarity between the species of the *Gonipterus scutellatus* complex has led to uncertainty and confusion regarding the identity of introduced populations (Mapondera et al., 2012; Schröder et al., 2020). According to the most recent taxonomy (Mapondera et al., 2012), two species of the complex are invasive in South America: *G. platensis* in Argentina, Brazil, Chile, Colombia and Uruguay, and *G. pulverulentus* in Uruguay. Correctly identifying newly introduced populations of *Eucalyptus* snout beetles is a first essential step towards effective management strategies.

In areas outside of their native range, *Eucalyptus* snout beetles cause severe damage to *Eucalyptus* trees, with both adults and larvae feeding on leaves and producing important economic losses (Mapondera et al., 2012). Damage includes crown defoliation, stag-horned or witches' broom appearance, epicormic and stunted growth, reduced tree vigor, and loss of apical dominance (CABI, 2021; Lanfranco & Dungey, 2001), all of which make the trees more susceptible to attack by other organisms (Fiorentino & Medina, 1991). Indeed, *Eucalyptus* snout beetle infestations were projected to produce between 20 to 85% losses in wood production over a 10-year growth period (Reis et al., 2012). These impacts have raised repeated concern and motivated the development of control programs with the parasitoid *Anaphes nitens* (de Souza, 2016; González et al., 2010; Hanks et al., 2000; Reis et al., 2012). However, biological control strategies have not always been successful, mainly due to geographical or seasonal mismatch between host and parasite (Mapondera et al., 2012; Reis et al., 2012). This highlights the need for further study of the ecology, taxonomy and life history of the beetles and their natural enemies, such as *A. tasmaniae*, *A. inexpectatus* (Hymenoptera: Mymaridae), *Entedon magnificus* (Hymenoptera: Eulophidae), and even entomopathogenic fungi that could potentially be used in biological control programs (de Souza, 2016; Garcia et al., 2019; González et al., 2010; Gumovsky

et al., 2015; Lobos Peirano, 2018). Finally, given that these beetles are listed as quarantine pests by several plant protection agencies (e.g., EPPO, CPCC, NAPPO) (CABI, 2021), and the long-term presence and uses of this tree in forestry in South America, countries that export *Eucalyptus* products should strive to detect, adequately manage or prevent the introduction and spread of these insects.

Identifying potentially suitable environments where introduced species may thrive can help in mitigation and conservation planning efforts. Potential distributions of alien species into new geographic areas can be estimated with ecological niche models. These predictive models provide estimates of species' potentially occupied environmental niches based on the relationship between their occurrences and the environmental characteristics of the landscapes where they occur (Jiménez-Valverde et al., 2011; Peterson et al., 2011; Soto-Centeno & Steadman, 2015). Such procedures enable the construction of risk maps that identify areas suitable for invading or potentially invasive alien species and may aid in the implementation of successful biosecurity strategies (Pili et al., 2020).

In this study, we report for the first time the presence of the *Eucalyptus* snout beetle in the city of Quito, Ecuador (Fig. 1). We suspected that these beetles belong to the species *G. platensis* due to its presence in several other countries of South America (as opposed to *G. pulverulentus* that is only present in Uruguay) and its recently reported presence in the neighboring country of Colombia (Schröder et al., 2020). To confirm this identification, we sequenced the COI gene of nine specimens collected in different sites in Quito and inferred a phylogeny using additional published sequences. Additionally, under an ecological niche modeling approach, we determined areas of suitable habitat in South America, with a focus on Ecuador, to set a baseline for possible areas at risk of invasion.

Methods

Specimen collection, DNA extraction, PCR and sequencing

Specimens of the *Eucalyptus* snout beetle were collected by hand in various sites in the city of Quito. We removed three legs of the same side of nine individuals for molecular analyses. Voucher specimens were deposited in the invertebrate collection of the Zoology Museum (Quito Católica Zoología Invertebrados, QCAZ I) of Pontificia Universidad Católica del Ecuador (PUCE), Quito, Ecuador.

For DNA extraction, we left the legs in 500 µL of TE buffer for 24 hours at 4 °C. After rehydration, each softened leg was crushed with a pestle for 15 minutes, then 500 µL of CTAB-PVP and 16 µL of Proteinase K were added to each sample and left shaking at 56 °C for 24 hours. We then added 650 µL of chloroform to each sample and mixed them to form an emulsion; subsequently, samples were centrifuged for 10 minutes at 13000 rpm. We removed the supernatant from every sample and saved each in different 1.5 µL tubes. Around 600 µL of 100% Isopropanol were added to every sample for DNA precipitation, and then centrifuged for 10 minutes at 13000 rpm. The pellet was then washed with 70% ethanol and centrifuged again for 10 minutes at 13000 rpm. The pellet was left to dry, and then resuspended in 25 µL of 0.1X TE Buffer. DNA concentration was quantified using a Nanodrop 1000 from Thermo Scientific.

We amplified two fragments of the mitochondrial gene COI with the following pairs of primers: the forward primer Jerry (5'- CAA CAT TTA TTT TGA TTT TTT GG-3') and the reverse primer Pat (5'- TCC AAT GCA CTA ATC TGC CAT ATT A-3') (Simon et al., 1994) and the forward primer dgLCO1490 (5'- GGT CAA CAA ATC ATA AAG AYA TYG G-3') and the reverse primer dgHCO2198 (5'- TAA ACT TCA GGG TGA CCA AAR AAY CA-3') (Meyer et al., 2005). Each Polymerase Chain Reaction (PCR) contained 13 µL total volume: 2.5 µL of 10x PCR Rxn Buffer, 3 mM MgCl₂, 0.2 µM of dNTPs, 0.2 M of forward primer, 0.2 M of reverse primer, 1 unit of Taq Platinum DNA Polymerase 5000U Invitrogen and 20 ng of DNA. Conditions for PCR amplification using the first pair of primers were the following: initial denaturation at 95 °C for 2 min; 40 cycles of 95 °C for 2 min, annealing at 46 °C for 1 min, and extension at 72 °C for 1 min; final extension at 72 °C for 5 min. Conditions for PCR amplification using the second pair of primers were the following: initial denaturation at 94 °C for 3 min; 35 cycles of 94 °C for 45 sec, annealing at 47 °C for 30 sec, and extension at 72 °C for 1.5 min; final extension at 72 °C for 10 min. The results were confirmed through an agarose gel electrophoresis. The amplifications were then treated with ExoSAP before being sent

to Macrogen Inc. for sanger sequencing.

Phylogenetic analyses

Phylogenetic analyses were conducted with the COI fragments amplified with the Jerry and Pat primers—GenBank accession numbers: MW041883-MW0441891. The sequences obtained with the primers dgLCO1490 and dgHCO2198 correspond to the COI fragment traditionally used in DNA barcoding efforts (Waugh, 2007) and are available as references for further comparisons—GenBank accession numbers: MW0441892-MW0441898. Our newly generated DNA sequences were aligned with previously published sequences (Garcia et al., 2019; Mapondera et al., 2012) and with other sequences available in GenBank for the *G. scutellatus* species complex using the Geneious Alignment tool in Geneious Prime 2020.0.3 (<https://www.geneious.com/>). This alignment tool is versatile because it can detect, and automatically transform, the direction of the sequences. The final matrix consisted of 152 sequences, including two sequences of *Oxyops* sp. as outgroups, and it had a length of 420 bp. We used IQ-Tree 1.6.12 (Nguyen et al., 2015) to determine in the same analysis the best-fitting evolutionary model, the best maximum likelihood tree, and three measures of nodal support. With the option ModelFinder (Kalyaanamoorthy et al., 2017), we selected the best-fitting model of codon substitution (MGK+F3X4+G4), because codon substitution models are more realistic than other types of substitution models (i.e., nucleotide, amino acid) in protein-coding sequences (Gil et al., 2013; Seo & Kishino, 2009). Nodal support was estimated with the SH-like approximate likelihood ratio test (SH-aLRT), using 1000 bootstrap replicates (Guindon et al., 2010), the aBayes test, which is a Bayesian-like transformation of aLRT (Anisimova et al., 2011), and the ultrafast bootstrap approximation, using 1000 replicates (Hoang et al., 2018; Minh et al., 2013). For the six *Eucalyptus* snout beetle species with most samples ($n \geq 10$), we calculated haplotype diversity (H) and nucleotide diversity (π) with the functions hap.div and nuc.div from the package *pegas* in R v3.6.3 (Paradis, 2010; R Core Team, 2022). H is the probability that two randomly drawn DNA sequences from the sample would be different; thus, the values of H range from 0 to 1, with 0 indicating that all sequences are identical and 1 corresponding to a highly diverse sample because all sequences are different. π is the average number of differences per nucleotide site, among pairwise comparisons of DNA sequences of the sample; thus, larger values indicate greater nucleotide diversity (Nei, 1987).

Occurrence data mining

After confirming the records in Ecuador as *Gonipteris platensis*, we generated a database of 347 occurrence records of this species available in the Global Biodiversity Information Facility (GBIF.org, 2022; www.gbif.org; <https://doi.org/10.15468/dl.8mwph7>). The occurrence dataset included few records from the native range of *G. platensis* in Australia ($N = 9$; GBIF.org, 2022; www.gbif.org; <https://doi.org/10.15468/dl.26tsqw>). Therefore, we focused on characterizing the potential distribution of the species only using records from the invaded range in South America. Occurrence records were then verified to ensure georeferencing accuracy, first, by excluding localities without spatial reference and duplicates, and then, by visual examination mapping using the packages *sp* (Pebesma & Bivand, 2005) and *maptools* (Bivand & Lewin-Koh, 2022) in R v3.6.3 (R Core Team, 2022). Finally, occurrences were rarefied to an extent of >5 km spatial distance from each other using the R package *raster* (Hijmans, 2023). The 5 km spatial buffer matched the resolution of the environmental data (see below), and thinning occurrence datasets helps reduce bias when modeling the distribution of invasive species (Elith et al., 2010). The final species occurrence dataset of *G. platensis* included 52 unique localities that were used for modeling. Data are available for download in Zenodo (doi.org/10.5281/zenodo.7818068).

Predicted distribution of suitable habitat

We used presence only data analyzed under a maximum entropy approach to develop present day ecological niche models (ENMs). Our goal was to evaluate the predicted distribution of *Gonipteris platensis* in its introduced range throughout South America, with a focus on Ecuador. We used climate data from 19 WorldClim variables summarizing temperature and precipitation features (Fick & Hijmans, 2017) and elevation. Environmental data was trimmed to the regional extent of South America using the R package *raster* (Hijmans, 2023). The choice of environmental background can influence the predictive ability in ENM

(Elith et al., 2010). Therefore, we created a background extent to calibrate the ENM by generating a buffer of 500 km around each observed locality of *G. platensis*, and sampling 10 thousand random points within that environmental extent. Final models were then projected onto the regional extent of South America.

ENMs were generated using Maxent v3.4.1; this method is widely used and shows high predictive performance compared to other modeling methods (Elith et al., 2006; Phillips et al., 2006). Species localities were randomly partitioned into 75% training and 25% testing datasets, and model calibration followed a cross-validation approach with $k = 5$. We evaluated a range of regularization values from 1–5 and combinations of up to four feature classes (i.e., L, Q, H, LQ, LQH, and LQHP) in the R package *ENMeval2.0* (Kass et al., 2021). The best tuning parameters for modeling were then selected using Akaike Information Criterion (AIC; Appendix, Table A1). Maxent uses regularization to reduce model complexity and included variables contribute differentially to the final model (Phillips & Dudík, 2008). Thus, we included all 19 WorldClim variables and elevation in the model and allowed the algorithm to converge onto the variables with the greatest contribution. The final model was calibrated using the background extent and the best tuning parameters (i.e., $fc = LQH$ and $rm = 2$) and was projected on South America and Ecuador. This approach allowed us to evaluate the predicted distribution of *G. platensis* across the introduced range.

Model performance was assessed using the area under the receiving operating characteristic curve (AUC). AUC is a threshold-independent measure that varies from 0 to 1, where a score of 1 represents perfect discrimination and a score of 0.5 represents a model no better than random (Peterson et al., 2011). We considered an AUC score greater than 0.7 to represent good model predictions (Peterson et al., 2011). Given that AUC has been deemed unreliable for estimating performance of presence-background models (e.g., Lobo et al., 2008) we separately calculated the Boyce Index (BI) to assess model prediction in the R package *ecospat* (Di Cola et al., 2017; Hirzel et al., 2006). The BI uses a Spearman rank correlation coefficient, which varies from -1 to 1 (Hirzel et al., 2006). A positive BI value approaching one indicates that model predictions are consistent with the evaluation dataset, zero indicates random performance, and negative values indicate a poor match with the evaluation dataset (Hirzel et al., 2006).

Because *G. platensis* is invasive in South America, the final projected model implemented a lowest presence threshold of 95% (LPT95, equivalent to the Minimum Training Presence threshold) obtained from the model estimated by the Maxent cloglog output (Soto-Centeno & Steadman, 2015). Under this rule, prediction pixels with equal or higher values than the LPT95 were scored as suitable conditions where *G. platensis* could sustain viable populations in the introduced range. We chose LPT95 to provide a conservative prediction where model datasets contained at least 95% of locality points within suitable habitat (i.e., a theoretical expectation of 5% omission rate of the training data; Pearson et al., 2007). This threshold also helped us determine visually if our ENMs allowed enough sensitivity to examine novel areas of environmental suitability where *G. platensis* could establish populations in South America.

Characterization of climate envelopes

We examined the range of conditions where *G. platensis* is found throughout South America (i.e., their “climate envelope”; Hijmans & Graham, 2006). These ranges were compared to the conditions where the species is found in Ecuador. This helped us define whether conditions in Ecuador differ from those in the rest of the continent. Climate envelopes were constructed using data from the top four environmental variables with highest contributions (i.e., $> 10\%$) in the Maxent models and elevation. In order of importance, the variables included temperature seasonality (bio 4), annual mean temperature (bio 1), precipitation of the coldest quarter (bio 19), and mean temperature of the coldest month (bio 6). While elevation did not have a high contribution to the model, we used it here to broadly discuss areas of predicted suitable habitat of *G. platensis*. From these data, we determined the climate and elevation profiles for all localities where *G. platensis* was documented by extracting environmental information across all localities and directly comparing the range of conditions individually in Ecuador vs. the rest of South America. These data were not normally distributed; thus, Wilcoxon rank sum tests followed by a Bonferroni correction for multiple comparisons were used to examine the differences between conditions in Ecuador vs. the rest of South America. This framework allowed us to better understand the variation in environmental niche occupancy

in the introduced range of *G. platensis* across the continent.

Results

Phylogeny and molecular identification

The gene tree of the mitochondrial COI gene of species of the *Goniapterus scutellatus* complex (Fig. 2) showed that the Ecuadorian samples are nested within the clade of *Goniapterus platensis*. The Ecuadorian samples were identical among them and showed no variation with most of the other *G. platensis* in the clade. In fact, across the dataset, *G. platensis* was one of the least genetically diverse species (see nucleotide diversities, π , in Fig. 2), despite being the one with the most representation of DNA sequences. On the other hand, *G. notographus* and *G. sp. 2* were the most genetically diverse species. Note that one sample, FJ888583_co58, here designated as *G. aff. notographus*, was placed outside the *G. notographus* clade.

Predicted distribution and climate envelope comparison

The distribution of *G. platensis* in South America could be driven by an expansion into novel environments. Thus, our ENM approach focused on evaluating areas of potentially suitable climate that the species could invade. This model had good performance and obtained a true positive fraction of 98% across all known unique localities of the invaded range (AUC = 0.956, BI = 0.883; Fig. 3). Notably, the ENM predicted highly suitable climates for *G. platensis* in the Andes of Colombia, Ecuador, and Northern Peru. The coastal portion Chile, from Santiago to Puerto Montt, also showed high suitability, whereas areas at the southeast of Brazil and Uruguay, east Argentina and the Andes of Bolivia showed intermediate suitability. In Ecuador, we found three areas of high suitability in the northern (where we collected the specimens analyzed in this study), central and southern parts of the Ecuadorian Andes. Comparison of climate envelopes of the four top contributing climatic factors and elevation for Ecuador and the rest of South America highlighted some variation in the occupied niches (Table 1; Fig. 4). For example, the range of *G. platensis* in Ecuador revealed significant climate envelope differences related to seasonality and elevation (Table 1; Fig. 4). Across South America, these beetles occupy a wide breadth of climatic conditions and elevations. They exist in elevational ranges spanning low and high altitudes, from 7 m to 3351 m above sea level (a.s.l.). In Ecuador, *G. platensis* occupies the highest elevational range with a mean of ca. 2600 (2233–3351) m a.s.l. (Fig. 4). The lowest elevation ranges were found in Argentina, Chile, and Uruguay, generally found from 7 to 327 m a.s.l.

Discussion

We aimed to document the introduction of the *Eucalyptus* snout beetle in Ecuador, determine its taxonomic placement, and model potentially suitable habitat throughout South America. With this framework, we provide the first genetic evidence for the presence of *Goniapterus platensis* in Ecuador. Furthermore, our ecological niche model analysis suggests areas of suitable habitat throughout a broad range of climatic and elevational regimes that may have played a role in the establishment of populations of *Eucalyptus* snout beetles in South America and could promote its future expansion into new areas.

The phylogenetic analysis we showed herein highlighted large genetic variation across the *Goniapterus scutellatus* species complex. However, most of the samples analyzed in this study came from Australia and Tasmania, with few samples coming from Portugal, Spain and South Africa (Mapondera et al., 2012), and only the nine samples we collected coming from South America. DNA barcoding data (mitochondrial COI sequences) clearly resolved the identity of the beetles found in Ecuador as *G. platensis*, which has also been documented in other South American countries (i.e., Argentina, Brazil, Colombia, Chile, and Uruguay) (Garcia et al., 2019; Mapondera et al., 2012; Schröder et al., 2020). The genetic diversity of *G. platensis* was one of the lowest among the species analyzed in this study (see values of π for each clade in Fig. 2), which coincides with the results found by Mapondera et al. (2012) for this species in Western Australia. In fact, the Ecuadorian samples share the same haplotypes with individuals from Tasmania (Garcia et al., 2019), which suggests that the Ecuadorian population could have originated from a Tasmanian source. Notwithstanding, an analysis including genetic samples from Colombia and other South American countries is needed to thoroughly examine whether the Ecuadorian samples were a product of a direct introduction from the

native range or if they were secondarily introduced from another South American country. An introduction from Colombia seems plausible given geographical proximity and the continuity of suitable climatic habitat predicted by our model (Fig. 3). Moreover, our phylogeny suggested that there are at least three different geographical origins of the *G. platensis* specimens found outside Australia. Indeed, two different sequences of this species from Spain and Portugal (JN391479_ESP and JN391480_POR) are the most different compared to the sequences of South America and Tasmania, as evidenced by their long branches in the phylogeny (see *Gonipterus platensis* clade in Fig. 2). Additional sampling and genetic analysis are necessary from *Eucalyptus* snout beetle populations from Southeastern Australia and from other South American countries to truly pinpoint the origin of invasive populations.

Two main challenges have been identified when producing ecological niche models (ENM) for invasive species (Lake et al., 2020). First, invasive species are often in disequilibrium with the novel environment they occupy, and second, generating ENM projections from native to invaded ranges may be problematic for correlative model approaches (Elith et al., 2010). We followed an ENM approach at the species level, including all unique localities of *G. platensis* in South America available in GBIF (GBIF.org, 2022; www.gbif.org; <https://doi.org/10.15468/dl.8mwpht>). This approach is justifiable because few records were available in open-source databases from the native range of Australia ($N = 9$). Such a low number of occurrences would bias ENM predictions, particularly when projected from native ranges into novel environments where the species was introduced. Furthermore, using only the native range to estimate the potential suitable habitat of a species may result in misrepresentation of predictions, particularly if the colonization into the invaded range is characterized by niche expansion (Broennimann et al., 2007). To mitigate the spatial data bias, we rarefied records and used a background extent that included only potentially reachable areas (following Elith et al., 2010). This choice of background would reduce the degree of model extrapolation (Elith et al., 2010). Despite the uneven sampling, our approach allowed us to produce estimates of the areas where *G. platensis* occurs, but also assess regions of suitable habitat where these beetles could potentially be found or invade (Fig. 3).

The ENM predictions presented herein attained a high true positive fraction for the currently known observations (Appendix, Fig. A1). Notably, the westernmost locality in the Buenos Aires province of Argentina showed the lowest predicted distribution values and was excluded by the LPT95 threshold. This inland locality of Argentina was characterized by a narrow range of high temperatures (i.e., little variation in temperature seasonality) and generally dry conditions (i.e., lowest precipitation of coldest quarter) that were unique compared to all other occurrences. Despite the lack of observation records from GBIF, model predictions showed that suitable habitat for *G. platensis* exists in southeastern Brazil in the city of Curitiba, PR, where the beetle was first documented as invasive for the country (Fig. 3; op. cit. *G. scutellatus* in Freitas, 1979). This region of suitability in Brazil spans from the state of Espírito Santo, south through Rio Grande do Sul, and west into Mato Grosso do Sul, in which *G. platensis* is widely recognized as a pest of *Eucalyptus* forests (de Souza, 2016; Wilcken & Oliveira, 2015).

In the northwestern parts of South America, ENM predicts suitable habitat across the Andes from Colombia to Bolivia at high elevations (Fig. 3). In Ecuador, *G. platensis* was predicted to have significantly higher elevations than elsewhere in the continent (Fig. 4; Table 1), with highly suitable habitat existing in and around the cities of Quito, Ambato, and Cuenca and with at least moderately suitable habitat occurring all along the Ecuadorian Andes (Fig. 3). Suitable habitat at high elevations was also predicted throughout Perú, which may represent potential areas for invasion (Fig. 3). In the southern countries, the model resulted in high to moderate values of suitability at lower elevations in Chile, Argentina, and Uruguay, respectively (Fig. 3). Examination of the climate envelopes revealed that *G. platensis* in Ecuador occupies significantly less seasonal and drier conditions than in other parts of the invaded range at similar elevations (Fig. 4; Table 1). Nonetheless, when considering the entire distribution, this beetle occurs across a wide elevational range and a variety of suitable environmental conditions where it could potentially sustain long term populations. The sampling bias, which likely excluded areas occupied by *G. platensis* but not included in GBIF or not yet documented across South America, renders our ENM predictions somewhat exploratory. Nonetheless, these results combined with climate envelope analysis highlights the potential of *G. platensis* to occupy a broad

range of environmental conditions, which may allow it to become highly invasive in different parts of South America.

Finally, we make a call to study the ecological and economic impacts of the invasion of *Eucalyptus* snout beetle and its hosts (e.g., *Eucalyptus globulus*) in South America, particularly in Colombia and Ecuador. In northern South America little research has been conducted on forestry of *Eucalyptus* species, whereas in Brazil and Chile, forestry research is quite active. In the particular case of Ecuador, *Eucalyptus* trees were planted in the late 19th century, mainly in volcanic soils, known as ‘cangagua’, in the inter-Andean valleys (FAO, 1981). These valleys have had human influence for millennia (Bush et al., 2022; Young, 2009), so perhaps these degraded environments have lost natural enemies that could exploit these insects as new hosts. We thus recommend extensive sampling of *Eucalyptus* snout beetles and potential controllers in Ecuador to test this hypothesis. Also, as far as we know and according to records in GBIF, *Gonipteris platensis* remains concentrated in a couple of areas of the Ecuadorian Andes (around the city of Quito in the North and in the city of Loja in the South, Appendix, Fig. A1), but our model predicts the whole range as climatically suitable for invasion. In fact, climatic suitability expands across the border to the Peruvian Andes, within the area of distribution of *Eucalyptus* spp. plantations (Castillo Vera et al., 2019; Luzar, 2007), where no reports of the insects have been made so far. All this highlights the urgency of conducting more studies on the invasion of this pest to design effective control and/or prevention measures.

Competing interests

The authors have declared that no competing interests exist.

Data accessibility

DNA sequences: Genbank accession numbers MW041883-MW0441898

Files and scripts used to run phylogenetic analyses are publicly available at Zenodo: doi.org/10.5281/zenodo.7823745

Records of *Gonipteris platensis* used for our models and R scripts for Ecological Niche Modeling are publicly available at Zenodo: doi.org/10.5281/zenodo.7818068

Author contributions

Verónica Crespo-Pérez: conception and design (lead), data curation (equal), writing original draft (lead), project administration (lead)

J. Angel Soto-Centeno: conception and design (supporting), data curation (equal), data analysis (equal), methodology (equal), writing original draft (supporting)

C. Miguel Pinto: conception and design (supporting), data analysis (equal), methodology (equal), writing original draft (supporting)

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Claudia Terán: methodology (supporting), writing - review and editing (equal)

Álvaro Barragán: conception and design (lead), data curation (equal), writing - review and editing (equal), project administration (supporting)

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Table 1. Environmental comparison of climate envelopes for *Gonipterus platensis* in South America. All values represent means (range) for the following environmental features: Temperature seasonality (st.dev. x 100; bio 4), annual mean temperature (bio 1), precipitation of the coldest quarter (bio 19), mean temperature of coldest month (bio 6), and elevation (in m a.s.l.). *P* values adjusted using a Bonferroni correction; values with an asterisk (*) indicate statistical significance at the 0.05 level.

Locality	n	bio 4	bio 1	bio 19	bio 6	Elevation
Ecuador	23	18.3 (11–44)	14.2 (10–16)	288 (103–363)	7.8 (4–10)	2666 (2233–3351)
South America	29	310 (31–581)	14.1 (10–21)	473 (76–993)	5.5 (2–13)	566 (7–2657)
	<i>P</i>	< 0.005*	> 0.5	0.265	< 0.005*	< 0.005*

Figure legends

Figure 1. Adult of *Gonipterus platensis* collected by VC-P and CMP in the city of Quito. Photo by VC-P with an Olympus Tough TG6 digital camera.

Figure 2. Maximum likelihood tree of a fragment of the COI gene of species of the *Gonipterus scutellatus* complex. Numbers at the nodes indicate support values from the SH-like approximate likelihood ratio test (SH-aLRT), the Bayesian-like transformation of aLRT (aBayes test), and the ultrafast bootstrap method. Terminal labels indicate the GenBank accessions, followed by sample codes. Clade classification follows Mapondera et al. (2012). Values of nucleotide (π) and haplotype (H) diversity for each of the six species examined are indicated below the species names.

Figure 3. Predicted distribution of *Gonipterus platensis* in its introduced range of South America. The inset shows a focus on Ecuador. Each model was calibrated to the local environmental conditions of the introduced

range. Warmer colors of predicted distribution (i.e., red) indicate higher environmental suitability. Niche model predictions including occurrences are included in the Appendix, Fig. A1.

Figure 4. Boxplots showing the distribution for environmental features characterizing the introduced ranges of *Gonipterus platensis*. Brown = Ecuador and teal = South America. Median: heavy line; 25% and 75% quartiles: edges of box; 5% and 95% quartiles: whiskers; observed values included as points to help visualize density.

Appendix

Table A1: Parameter tuning results from ENMeval (Kass et al. 2021) for *Gonipterus platensis* throughout South America. fc = feature classes (i.e. L = linear, Q = quadratic, H = hinge, P = product), rm = regularization (beta) multiplier, tune.args = parameter tuning to implement in Maxent, AICc = corrected Akaike Information Criterion, delta.AICc = deviation from the smallest AICc value (set at zero and arranged in ascending order), ncoef = number of coefficients.

fc	rm	tune.args	AICc	delta.AICc	ncoef
LQH	2	fc.LQH_rm.2	1083.09907	0	19
LQHP	3	fc.LQHP_rm.3	1086.08195	2.98288597	16
H	2	fc.H_rm.2	1094.32451	11.2254442	19
LQHP	2	fc.LQHP_rm.2	1095.95112	12.8520564	22
H	3	fc.H_rm.3	1096.50915	13.4100852	14
LQHP	4	fc.LQHP_rm.4	1100.32847	17.2294029	15
LQHP	1	fc.LQHP_rm.1	1103.75876	20.6596915	28
LQH	1	fc.LQH_rm.1	1107.2177	24.1186367	28
LQHP	5	fc.LQHP_rm.5	1107.68961	24.5905466	13
H	4	fc.H_rm.4	1110.39672	27.2976525	13
H	1	fc.H_rm.1	1112.79687	29.6978034	27
LQH	3	fc.LQH_rm.3	1113.34805	30.2489781	19
LQ	1	fc.LQ_rm.1	1119.77007	36.6710077	16
LQH	5	fc.LQH_rm.5	1121.3233	38.2242347	12
LQH	4	fc.LQH_rm.4	1125.6363	42.537234	17
H	5	fc.H_rm.5	1126.60636	43.5072975	12
LQ	2	fc.LQ_rm.2	1134.2499	51.1508365	14
LQ	3	fc.LQ_rm.3	1151.56173	68.4626582	12
LQ	4	fc.LQ_rm.4	1172.08359	88.9845189	12
LQ	5	fc.LQ_rm.5	1194.0281	110.929032	12
L	1	fc.L_rm.1	1314.40165	231.302579	15
L	2	fc.L_rm.2	1315.73578	232.636713	10
L	3	fc.L_rm.3	1331.31237	248.213307	9
L	4	fc.L_rm.4	1351.63307	268.534007	10
L	5	fc.L_rm.5	1356.33024	273.231173	8

Figure A1. Predicted distribution of *Gonipterus platensis* in its introduced range of South America with a focus on Ecuador (inset). Each model was calibrated to the local environmental conditions of the introduced range. Warmer colors of predicted distribution (i.e., red) indicate higher environmental suitability. Occurrences used for modeling are represented by green circles.







