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ANIMAL SCIENCE

Improving geographic distribution data for a putatively extinct species, a test case with a disappeared fly

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Abstract: Global biodiversity loss by anthropogenic impacts is an under-recognized form of global environmental change. Global defaunation is still poorly documented in the case of insects, showing a significant decrease in populations and diversity. The blowfly Neta chilensis (Walker 1837) is poorly known and presumed to be confined to southern-South America, with an unclear distributional pattern. It was last collected in 1984. We aimed, through Ecological Niche Models, to identify regions highly suitable for N. chilensis; to test the suitability of regions with doubtful records; to understand the impact that climatic change and human activities have had; and to identify regions with high chances to find it. We compiled 130 presence records from Argentina and Chile and 117 localities where it was sought but not found between 1987 and 2018. Results indicate that suitable conditions are restricted to southern and central Chile and to southwestern Argentina, that doubtful records are predicted in unsuitable areas, that N. chilensis occupies a narrow niche and that its decline is not mainly caused by climate changes but more probably to habitat loss and to the biological invasion. We identified two regions where the chances of finding the species are higher in the case that it is not extinct already.

Key words: climatic change, Ecological Niche Modeling, *Neta chilensis*, population decline, threatened.

INTRODUCTION

Limited description of ecological patterns and processes and gaps in accurate biodiversity data are the most frequent scenario for most taxa. This occurs while the world is facing a growing and accelerating mass extinction event caused by human action (Erwin 1991, Purvis & Hector 2000). Insects are the most diverse and numerous of all living organisms and a major part of the global biodiversity, representing an irreplaceable proportion of functional diversity and provision of ecosystem services (Kim 1993). Nevertheless, insects have largely been neglected in conservation studies and are poorly represented in threatened species lists (Kremen et al. 1993, Zamin et al. 2010, Cardoso et al. 2011a).

The uncertainty about the extinction of a species is common because rare or highly threatened species are intrinsically difficult to detect (Ladle et al. 2011). This problem is exacerbated in the case of insects because there are general biological data shortages that often neglect conservation efforts such as the so-called Linnean, Wallacean, Prestonian, Darwinian, Eltonian, Hutchinsonian , and Raunkiaerian shortfalls (knowledge gaps in taxonomy, in distribution, in abundance, in evolutionary patterns, in biotic interactions, in knowledge of species ecology and sensitivities to habitat change or in the ecological functions of species respectively), among others (Cardoso et al. 2011b, Hortal et al. 2015). The rediscovery of a species presumed to be extinct or unrecorded for a long period of time improves geographical knowledge and helps to address the Wallacean shortfall (Riddle et al. 2011). However, the rediscovery of a putatively extinct species depends on several factors such as the state of knowledge of species loss; the availability of resources, skills and technology to find suitable target areas; the accessibility of the areas, habitats or sites where the species are thought to survive; and the ease with which a species can be located when it is present within a habitat (Ladle et al. 2011).

In this study we focused in *Neta chilensis* (Walker 1837), a Calliphoridae endemic to southern South America. It is a very characteristic and stout fly species with conspicuous hairy legs and large hairy male genitalia. Little is known about this blowfly even about its basic life history characteristics. The life cycle and breeding preferences of the species remain unrecorded in the field, though successful laboratory rearing suggests it is truly necrophagous (Mariluis 1980, Reyes & Almonacid 1984).

Although this species seems to be confined to the southern part of South America, its actual distribution is not clear. Bibliographical references to *N. chilensis* distribution are quite vague and even contradictory. James (1970), in his "Americas South of the United States" catalog of Calliphoridae, mentioned *N. chilensis* to be distributed in "Bolivia, Peru, Chile and Argentina south to Straits of Magellan", based on the information provided by Shannon (1926) and Smart (1937). Years later, Dear (1979) regarded *N. chilensis* distribution to be restricted to southern Chile and central Argentina between the latitudes of 30° and 45° S and longitudes of 70° and 73° W. However, Dear (1979) did not include the distributions of the types of *Calliphora peruviana* Macquart and *Phryssopoda splendens* Macquart labelled from Paita (Peru) and Cobija (Chile) respectively, although he considered them junior synonyms of *N. chilensis*. Both records belong to localities far north from the distribution explicitly indicated. Subsequently, several authors followed one of these two criteria, replicating this information (see Lopes & Albuquerque 1982, Mariluis 1982, Mac-Lean & González 2006, Kosmann et al. 2013). Consequently, the distributional pattern of *N. chilensis* remains incompletely defined.

Considering the number of voucher specimens deposited in entomological collections, and published information, N. chilensis is a rare species. It was collected most recently in 1984 in the locality of Bariloche (Río Negro province, Argentina) and in 1982 in the Araucanía Region (Chile). Since then, many entomological surveys have sought N. chilensis in southern Andean Areas of South America. without success. It has not been collected in southern Argentina and Chile during the last 30 years (Mariluis et al. 1999, Olea et al. 2017). Moreover, most of these field trips occurred in regions where several of the known records had been collected. Possible explanations for the absence of N. chilensis could include a change in its distribution, a reduction and decline of its populations, or its extinction.

The development of ecological niche modeling has allowed new insights, and is widely used in ecology, biogeography, evolution, conservation biology and the effects of climate change on species (Guisan & Thuiller 2005). Ecological Niche Models (ENM) estimate the ecological requirements of a species by relating its known occurrences to a set of environmental variables and identifies other regions, or future, or past climatological reconstructions with analog ecological conditions (Soberon & Peterson 2005). Applications of ENM have included guiding field surveys to accelerate detection of unknown distributional areas of rare species (Pearson et al. 2007) or the recognition of areas where the environmental conditions appear highly suitable, so the chances of finding the species are also high. In summary, when the information on natural history, ecology, and behavior is essentially unknown, valuable information can be inferred from ENM. One of the most interesting aspects of ecological niche modeling is that species data sources can be simple presence observations, such as that information provided by specimens and their label data housed in natural history collections or records available from the literature. Hence. despite their limitations, the innovative use of such museum data integrated to spatial modelling methods is often justified by the lack of systematic survey data, coupled with widespread demand for mapped predictions (Elith & Leathwick 2009). These models have been widely used to improve biogeographic information in the case of insect species (e.g. Escalante et al. 2009, Hawlitschek et al. 2011, Lecheta et al. 2017, Montemayor et al. 2017). and particularly for conservation efforts (e.g. Verovnik et al. 2014, Nasser et al. 2019).

The habitat loss due to conversion of wild lands for intensive agriculture and urbanization, species invasion, soil and water pollution, the increase in CO₂ emissions and their related climate changes are believed to be the top drivers of insect species loss throughout the world, although scarce studies exist for most Diptera (Sánchez-Bayo & Wyckhuys 2019). Previous studies have demonstrated that increasing areas of Southern Andean ecoregions are being deeply impacted by human transformation of landscape (Echeverría et al. 2006, Lara et al. 2012). Recent evaluations have also assessed that insect with a narrow niche that inhabit these Andean areas will be severely impacted by future climate warming (Montemayor et al. 2016).

A crucial aspect of the knowledge needed to find 'lost' species is the availability of reliable biogeographic information on where to search for the species. In this study we aimed, through the development of ENM, to improve the biogeographical information of N. chilensis and to evaluate two potential drivers possibly affecting this species, climatic change and human activities. Our specific objectives were to 1) test the suitability of the surveyed locations where the species was not found; 2) identify the regions with environmental conditions highly suitable for the survival of *N. chilensis*; 3) investigate the suitability of the regions with doubtful records; 4) understand the impact that climatic change and human activities could have had in the distribution of the species; and 5) identify target regions with high chances to find the species.

MATERIALS AND METHODS

Species data

Three datasets were compiled (Supplementary Material - Figure S1, Tables SI-SIII). A first dataset comprised 286 specimens and 130 records, collected between 1918 and 1984, of *N. chilensis* with information of the localities and the years in which the specimens were collected (referred to hereinafter as historical dataset) (Table SI). This information was gathered to track when the species had been collected in a given locality.

A second dataset, constituted by 57 records, was compiled to build the ENM for *N. chilensis* (referred to hereinafter as ENM dataset) (Table SII). In the ENM dataset the spatial correlation between records has been

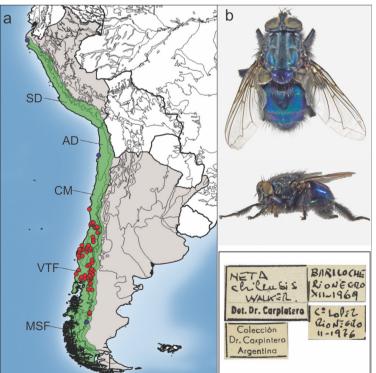
minimized by performing a Moran's I test at multiple distance classes using SAM, version 4.0 (Rangel et al. 2010). Significance was determined by permutation tests. The distance where spatial autocorrelation was minimal and with a sufficient number of records was determined to be 18 km. Three doubtful records from Nueva Oriental (Argentina), Cobija (Chile) and Paita (Peru), were excluded from the dataset used to build the model to test if these localities are predicted as climatically suitable in the model.

The records from the historical dataset and from the ENM dataset belong to bibliographical information or to specimens deposited in the following institutions (acronyms in parentheses): Fundación de Historia Natural Azara, Argentina (AZARA); Natural History Museum, London, United Kingdom (BMNH); Museo Entomológico Luis Peña, Facultad de Agronomía, Universidad de Chile (CUdeChile); Instituto y Fundación Miguel Lillo, Tucumán, Argentina (IFML); Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina (MACN); Museo La Plata, Argentina (MLP); Museo Nacional de Historia Natural de Santiago, Chile (MNHN); Museu Nacional, Universidade Federal do Rio Janeiro, Rio de Janeiro, Brazil (MNRJ); Instituto de Entomología, Universidad Metropolitana (UMCE); Museo de Zoología, Universidad de Concepción (UdeC) and National Museum of Natural History, Washington D.C., USA (USNM) (Figure 1a).

Finally, a third dataset (referred to herein after as absences dataset) was compiled for the localities where *N. chilensis* was extensively sought but not found (between 1987-2018) (Table SIII). This last dataset is constituted by 117 localities and was used to identify regions where the species was present but later disappeared. Among the 117 localities the ones closer than 15 km from a site were *N. chilensis* had been previously collected (40 localities) were identified assuming that in these localities *N. chilensis* is no longer present.

Information regarding climatic suitability (obtained from the ENM herein developed) and human influence (obtained from the Global





Human Footprint index v.2 1995-2004) were analyzed for these localities to evaluate if climate or anthropogenic impacts could be the cause of the disappearance of *N. chilensis*. The Global Human Footprint Index (GHFI) expresses as a percentage the relative human impact on global surface. Human impact is rated on a scale of 0 (minimum) to 100 (maximum) for each terrestrial biome. The index combines data sets representing human population density, land transformation, human access, and presence of infrastructures.

Ecological Niche Model (ENM)

The ENM was performed using Maxent v3.4.1k (Phillips et al. 2019). To build the model we used the bioclimatic variables available at WorldClim (http://www.worldclim.org) with a resolution of 30 seconds (Fick & Hijmans 2017). To avoid multi-collinearity, we performed a Principal Component Analysis (PCA) of the 19 Worldclim variables clipped to the extent of a polygon that encompassed all the ecoregions where the range of distribution of *N. chilensis* is hypothesized (i.e. Valdivian Temperate Forest, Chilean Matorral, Magellanic subpolar Forest, Atacama Desert and Sechura Desert) with a buffer of 50 km to include all the records (Figure 1a). The delimitation of this region was based on terrestrial ecoregions (Olson et al. 2001) as they have been identified based on climate, fauna, flora, and physiography. The PCA was performed using the "PCARaster" function of the 'ENMGadgets Rpackage' downloaded in R version 3.6.1 (Barve & Barve 2014) and it had a cumulative variation of >95% for the first four principal components, so we used them as climatic predictors. To avoid over-parameterization, models were tuned by exploring the performance of different betaregularization multiplier values (0.5 to 4) and of different feature classes (L, H, Q, LQ, LH and LQH). These models were tested in ENMTools

1.4 (Warren et al. 2010). Models with the lowest Akaike's Information Criteria corrected (AICc) scores were selected (Warren & Seifert 2011). Optimal model complexity was with a regularization multiplier of 0.5 and the feature classes LQ. We used a 4-fold cross validation, which leaves out 25% of the data as a testing set at each of 4 iterations, building the model on the remaining 75% of the data in each iteration.

The model was validated through the partial ROC procedure (pROC). To validate the model, 1000 random iterations with 50 % sub-sampling were performed to test if the real model is statistically significantly better than random (higher than 0.5) (P < 0.005) (Peterson et al. 2008). These evaluations were carried out in Niche Toolbox (http://shiny.conabio.gob.mx:3838/ nichetoolb2/) (Osorio-Olvera et al. 2018). Discriminatory ability was measured through threshold independent metric, the area under the curve of the receiver operating characteristic plot (AUC/ROC), it varies between 0 and 1. Values closer to 1 indicate better prediction, values of 0.5 correspond to a prediction equal to random and values lower than 0.5 correspond to a performance worse than random.

The niche breadth of the ENM was calculated in ENMTools 1.4 (Warren et al. 2010) through the Levin's concentration metrics. This index ranges from 0 (narrow niche breadth) to 1 (broad niche breadth) (Peers et al. 2012). Niche breadth is the suite of resources and environments that a species can inhabit or use (Slatyer et al. 2013). This analysis was performed to test if *N. chilensis* species can maintain viable populations within a wide or a narrow array of resources and conditions.

The ENM was converted in a binary map. Values above the threshold of 'Minimum Training Presence Logistic threshold' (MTP) were considered as presence, below this Threshold as absences. The MTP indicates values above which the climate conditions are suitable for the survival of the modeled species and guarantees that all presences of the target species are predicted as suitable.

To assess survival prospects of the species considering future scenarios, the model was trained using the PCA for current climate and was projected to a PCA performed for the climate of the 2040-2069 period, referred to as 2050. To perform the PCA for future climate three Global Climate Models (GCM) were used, CCSM4, GISS-E2-R and MIROC5, and two Representative Concentration Pathways (RCP), 2.6 and 8.5 (http:// www.worldclim.org/cmip5_30s). A RCP consider a wide range of possible changes in future climates depending on how much greenhouse gases (GHG) are emitted in the years to come. The RCP that predicts milder changes is 2.6, it assumes that global GHG emissions will peak between the year 2010-2020 and then emissions will decline substantially while RCP 8.5 predicts the most catastrophic scenario, and emissions will keep on rising during the current century. Future projections were represented as the average values of the continuous maps of the three GCM considered for the two RCPs.

Areas where the chances of finding *N*. chilensis are higher were identified following three criteria. The area should have a high climatic suitability (\leq 0.5), numerous records collected over several different years, and it should be farther away from 15 km to localities with absences. The first two criteria were chosen to ensure that, at least in the past, the species had been well established in the region. A polygon was drawn to delimit the areas limited by the more marginal presence records with a buffering zone of 15 km.

RESULTS

Historical dataset of Neta chilensis

Neta chilensis is distributed between the latitudes of 30° S and 46° S, in Neuquén, Río Negro, Chubut and Santa Cruz provinces in Argentina and in the Coguimbo, Valparaiso, Metropolitana, O'Higgins, Maule, Biobío, Araucanía, Los Ríos, Los Lagos and Aysén regions in Chile. This is the first time that the species is mentioned for the province of Santa Cruz in Argentina and for the Aysén region in Chile expanding its distribution toward more southern areas. All the records of the historical dataset are distributed in three different ecoregions: 97 are from the Valdivian Temperate Forest (collected between 1925-1984), 24 are from the Chilean Matorral (collected between 1918-1976) and 6 are from the Patagonian Steppe (collected between 1942-1980) but from ecotonal areas near the boundaries with the Valdivian Temperate Forest. and the Magellanic Subpolar Forest (Table SI). The records considered as dubious are located isolated to the core data of *N. chilensis*. namely Cobija (North of Chile), Paita (North of Peru) and Nueva Oriental (Southern Argentina).

When the absences-dataset was compared with the historical-dataset (Table I) we found that 39 of the localities where the species had been collected in the past are in localities closer to 15 km to one or more of the localities where the species could not be found. Consequently, 35 of these localities are in the Valdivian Temperate Forest, one in the Chilean Matorral, and three in the Patagonian Steppe.

The GHFI of the localities, close to areas where the species could not be found, of the Valdivian Temperate Forest rank between 7 and 65, of the localities of the Patagonian Steppe is 35, 45 and 46 and of the Chilean Matorral is of 40. The suitability scores of these sites are quite high for the Valdivian Temperate Forest ranging **Table I.** Localities where the species has been collected that are closer to 15 km to localities where *N. chilensis* could not be found (1987–2018). Information regarding locations, Global Human Footprint Index (GHFI), dates of collection, ID of the localities where it could not be found (further information in Supp. Mat 3) are provided. Abbreviations: Global Human Footprint Index: GHFI; VTF: Valdivian Temperate Forest; CM: Chilean Matorral; PS: Patagonian Steppe.

Longitude	و المنطقة ال	CUE	Colloction data	Absence	Absence years	Ecoregion	suitabilities
	Latitude	GHFI	Collection date	locality ID			
-71.71	-46.54	36	1973	19	2005	PS	0.16
-71.32	-42.92	46	1942	18	1993	PS	0.41
-71.07	-39.94	45	1957	31	2013	PS	0.53
-71.67	-30.67	10	1967	13, 14	2008	CM	0.19
-71.36	-39.77	40	1968	32, 33	2013	VTF	0.66
-71.71	-42.83	12	1962	34, 37, 39	2013/14	VTF	0.69
-71.83	-42.83	12	1959/72	35	2013	VTF	0.62
-71.71	-42.83	12	1962	35, 36, 38, 39	2013/14	VTF	0.69
-71.74	-42.74	18	1980	35, 36, 38, 39	2013/14	VTF	0.66
-71.83	-42.83	12	1959/72	36, 38, 39	2013/14	VTF	0.62
-71.63	-42.11	7	1975	26, 27, 28, 29, 30	2011/12	VTF	0.74
-72.45	-41.17	28	1968	11	2000	VTF	0.03
-71.43	-41.08	53	1930/37/55	17	1992	VTF	0.64
-71.31	-41.13	65	1934/49/57/67/69/84	17	1992	VTF	0.62
-71.37	-41.12	53	1943	17	1992	VTF	0.64
-71.43	-41.23	28	1949/66	17	1992	VTF	0.63
-71.45	-41.18	21	1962	17	1992	VTF	0.37
-71.82	-41.03	21	1962	16	1992	VTF	0.55
-71.8	-41.05	21	1966	16	1992	VTF	0.56
-71.65	-40.76	42	1946	15	1992	VTF	0.67
-73.71	-40.53	28	1967	1	1982	VTF	0.24
-71.47	-40.36	20	1949	23	2011	VTF	0.6
-71.36	-40.15	39	1949/57	21, 22, 24, 25	2011	VTF	0.59
-71.63	-40.16	20	1949/52	20	2011	VTF	0.72
-71.66	-40.11	26	1957	20	2011	VTF	0.71
-71.64	-40.16	20	1971/73	20	2011	VTF	0.72
-71.71	-40.16	14	1981	20	2011	VTF	0.69
-71.28	-38.81	17	1973	40	2014	VTF	0.66
-72.8	-36.14	34	1968	7, 8, 10	1996, 2000	VTF	0.61
-70.44	-34.24	34	1967	6	1995	VTF	0.52
-70.45	-33.59	34	1970	2, 5	1988/95	VTF	0.47
-70.4	-33.58	39	1970	3, 4, 5	1990/95	VTF	0.46
-70.51	-33.5	40	1953/69	3, 4	1990	VTF	0.45
-70.52	-33.52	40	1956	3, 4	1990	VTF	0.45
-70.52	-33.5	40	1965	3, 4	1990	VTF	0.44
-70.45	-33.59	34	1970	3, 4	1990	VTF	0.47
-70.47	-33.35	53	1970	12	2004	VTF	0.4
-71.27	-33.02	54	1918	9	1999	VTF	0.43
-71.15	-32.99	51	1963	9	1999	VTF	0.47

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between 0.3 and 0.74, most of them being higher than 0.50, for the Patagonian Steep scores are 0.16, 0.41 and 0.53, and for the Chilean Matorral of 0.19 (Table I).

The GHFI of the 40 localities where *N*. *chilensis* could not be found rank between 1 and 66, the majority having indices higher than 20. The suitability scores of these localities rank between 0.02 and 0.76, the majority were higher than 0.50 (Table SIII).

Ecological niche modeling

The ENM was validated by the pROC analysis, yielding predictions better than random (AUC ratios 1.58) and high discriminatory ability (AUC 0.91). The niche breadth of the ENM calculated by Levin's concentration metrics was 0.28 therefore, the species occupies a narrow climatic niche. According to our model, suitable climatic conditions for the survival of *N. chilensis* are found in southern and central Chile and in southwestern Argentina (Figure 2). Higher suitability values are mainly found in the Valdivian Temperate Forest towards the west on its coastal sides and towards the east in its Andean sides and in the most southern region of the Chilean Matorral ecoregion. These locations correspond in Argentina to the south of Neuquén, Río Negro and Chubut provinces and in Chile to the west of the Maule, Biobío and Araucania regions.

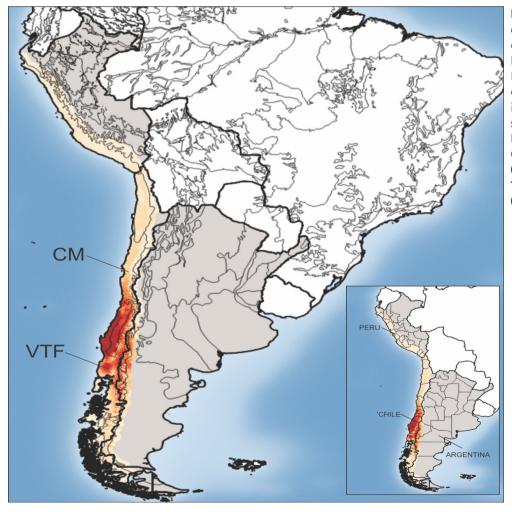


Figure 2. ENM of *N.* chilensis, darker colors represent higher suitability. In the larger map ecoregions are indicated, in the smaller map political limits. References: Chilean Matorral (CM) and Valdivian Temperate Forest (VTF) ecoregions. The three doubtful records were predicted in unsuitable areas by our ENM. The Cobija record in Chile is in a large unsuitable area in the Atacama Desert ecoregion which prevents the species from dispersing naturally from its core distribution in southern and central Chile and in southwestern Argentina. The record from Paita in Peru is in the Sechura Desert ecoregion approximately 2,500 km from areas predicted as suitable. The record from "Estancia Nueva Oriental" is predicted in an unsuitable area but is surrounded by patched suitable areas that are not too far away (the nearer is approximately 40 km away). Given its proximity to suitable areas this location probably represents the southernmost record available for *N. chilensis* (Figure 3).

The future projections developed with the three GCM and under the two RCP scenarios (2.6 and 8.5) showed very similar patterns (Figure 4ab). In all future projections a shift of the suitable areas towards the north and east of the Chilean Matorral ecoregion is predicted. All the localities where the species was collected are predicted with a lower climatic suitability (Table SIV).

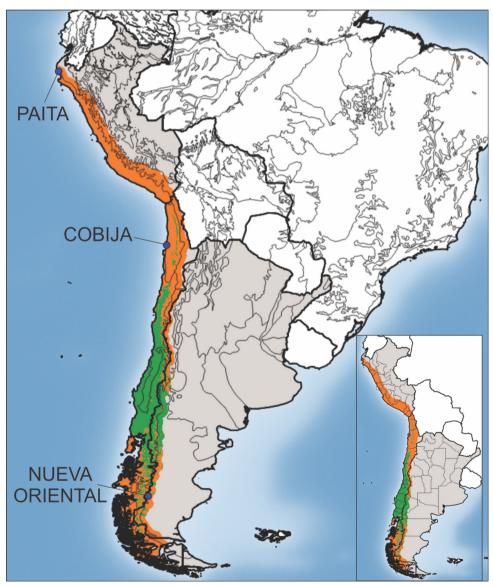


Figure 3. Binary map of ENM, presence areas are indicated in green and absence areas in orange. Countries with records of *N. chilensis* in gray. Blue dots represent the doubtful records. Smaller map indicates the political division of the region for an easier location of the areas. Two areas matched with the criteria selected to define areas were the chances of finding *N*. *chilensis* should be higher. A small one located in the southwest of the Biobio Region and a larger one located through the Biobio and Maule regions. In the first area *Neta chilensis* has been collected between 1925 and 1980 and in the second area between 1956 and 1981 (Figure 5).

DISCUSSION

Neta chilensis was collected in several years from the Metropolitana Region (Chile) and provinces of Chubut, Neuquén and Río Negro (Argentina). It is difficult to determine when *N*. chilensis declined but it seems to have occurred sometime around the 1970s to early 1980s when it was last observed in these provinces/regions. Data obtained from the labels of museum specimens (data not included in the table of SI) indicate the presence of *N. chilensis* from early spring (September) to autumn (April) with most of the specimens collected between December and February. This pattern represents the typical period of high activity of Calliphoridae in the Valdivian Forest (Figueroa Roa & Linhares 2002) and probably reflects the seasonal occurrence of the species. However, the frequency of samples and collecting effort is usually concentrated in summer months, and may not reflect the complete seasonal abundance pattern of the species.

Ecological niche models based on climatic parameters do not take into consideration features that can be crucial for the establishment of a species, as biotic interactions (i.e. predators, competitors, or presence of host plants) or if a region is reachable for the species but mainly

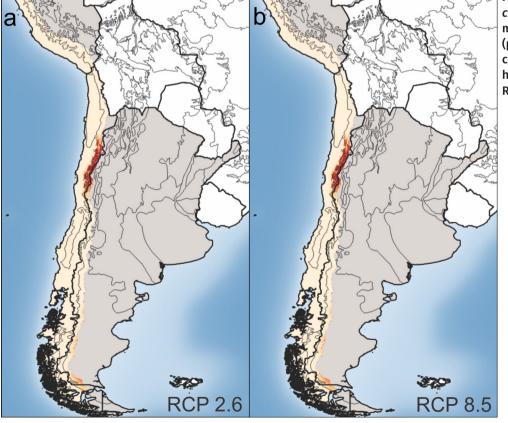


Figure 4. Neta chilensis average map of the three GCM (period 2050), darker colors represent higher suitability. a. RCP 2.6; b. RCP 8.5. estimate the complete set of abiotic conditions under which a species can persist, namely the fundamental niche of a species (Soberon & Townsend 2005, Soberon 2007). Therefore, ENM should be cautiously interpreted.

Our results indicate that *N. chilensis* occupies a narrow climatic space. The climatic suitability is high in several of the localities where *N. chilensis* was recorded in the past but is no longer present. Likewise, several of the localities from the absence dataset are close to localities where the species has been previously found and are geographically distributed in areas with high suitability. Absence data must

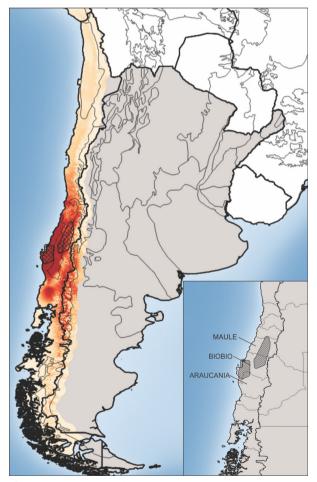


Figure 5. Cross-hatching indicates areas where the chances of finding *N. chilensis* are higher. In the smaller political map are indicated the Regions where these areas are located.

be carefully considered because the absences may be due to the facts that either the species is not present (true absence) or to insufficient exploration. However, our data suggests that a strong decline of *N. chilensis* population has occurred in the fundamental niche of the species.

A potential contributing factor in the absence of N. chilensis in recent surveys is biological invasions, recognized as primary threats to local biodiversity (Chornesky & Randall 2003). The dominance of the invasive blowfly species Calliphora vicina and Lucilia sericata over native species in the southernmost part of South America is well documented (Patitucci et al. 2011) and may have had a negative impact on N. chilensis through competition. On the other hand, the introduction of Vespula germanica (Fabricius) (Hymenoptera) could have had a negative impact on the populations of N. chilensis through predation since this wasp has been documented feeding on Calliphoridae (Magunacelaya et al. 1986). Vespula germanica was first recorded in Chile in 1970s and in Argentina a decade after (Masciocchi & Corley 2013). Based on the available data, N. chilensis populations declined around the same period when, the expansion of V. germanica began into Chile and Argentina.

Habitat loss and fragmentation should also be considered as a possible cause of the decline of *N. chilensis*. The replacement of the native forests to pasturelands, shrublands, agricultural land, and forest plantations of exotic species (Lara et al. 2012) in the central south zone of Chile began in 1974 and has resulted in a clear loss of biodiversity related to this landscape transformation (Echeverría et al. 2007, Alaniz et al. 2018). We have identified that several of the localities where the species was recorded in the past and it is no longer present, have GHFI values that correspond to disturbed landscapes. Similarly, several localities where *N. chilensis* could not be found are close to sites where the species has been previously recorded also have high values of GHFI. These data suggest that the effects of human-modified landscapes may be an important factor in the decline of *N. chilensis*.

The models projected to the period 2050 indicate that the suitability for N. chilensis will shift towards the north-east of these regions. This shift in habitat suitability leaves the two regions currently recognized in this study with high chances of finding N. chilensis over 700 km from the nearest currently suitable zone. Even though climate change does not seem to be the main cause for the decline of the species it will probably be in the case that there are still populations left. The niche breadth of a species impacts on its survival and adaptability during intervals of environmental change (Stigall 2015). In general terms, a generalist species with wide niche breadth is more adaptable and has higher chances of surviving a change in the environment than a specialist species with narrow niche breadth highly adapted to a narrow range of resources. Therefore, specialists are expected to have smaller populations and are more susceptible to extinction than are generalists (Rocha-Ortega et al. 2020). According to our results N. chilensis has a narrow niche breadth with low chances of resisting invasive species and, therefore, less likely to change their distribution to find proper conditions for survival. Hence, the introduction of an invasive predator such as V. germanica and changes in the climate would constitute a severe threat for the species.

Distribution of N. chilensis

One of the objectives of this study was to elucidate the distribution of *N. chilensis*. Nearly all known records from museums and the published literature are distributed in southern and central Chile and in southwestern Argentina but there were some intriguing references of records significantly isolated from the core distribution of the species.

A male type of Phryssopoda splendens, junior synonym of N. chilensis is labeled "Cobija, Gaudichaud 1836" (Dear 1979). Such data indicates it was collected by Charles Gaudichaud-Baupré, a collecting naturalist who was embarked from 1836 to 1837, aboard "La Bonite" (Papavero 1971). This ship landed in Cobija (Antofagasta, N of Chile) in June 1836, then a Bolivian port that is currently part of the territory of Chile, after the Pacific War. This seems the origin of all subsequent references of Bolivia as part of *N. chilensis* distribution. However, Gaudichaud-Baupré had previously studied animals from Valparaiso, and this location seems to be the most probable origin of the male type of *Phryssopoda* splandens.

Calliphora peruviana Macquart, 1851 falls into the synonymy of N. chilensis (Walker) (see details in Dear 1979, Whitworth 2012). In the original description, Macquart (1851) stated that the specimen was a female and cited other data as follows: "Pérou. Payta [Paita]. M. Eydoux. Muséum", housed in the MNHNP. Eydoux was a first-class surgeon and zoologist, who collected animals during the expedition of "La Bonite" together with Gaudichaud-Baupré in Valparaiso and Cobija. The location of Paita (Piura, NE of Peru) seems too far north for the species. The indication of "Eydoux" as collector seems an obvious mistake: we found no evidence that Eydoux ever visited the location. In addition, Papavero (1971) provides a synopsis of countries and localities associated to their respective zoological collectors, and this author has not associated samples of Eydoux to the Peruvian locality of Paita.

The fields belonging to the "La Oriental" farm, of 16,000 hectares, are within the Perito

Moreno National Park, on the shores of Lake Belgrano (Santa Cruz, Argentina). A single male was found in MLP labeled as "Estancia Nueva Oriental" determined by E. E Blanchard, presumably collected in this area. We could not find this name in maps or gazetteers, so we do not have a precise location for this specimen.

These three records were predicted in unsuitable areas by our ENM. The records from Cobija (Peru) and Paitá (Chile) are predicted in unsuitable areas far away from suitable areas so we conclude that these two specimens have been mislabeled. The record from "La Oriental", Santa Cruz (Argentina), remains doubtful as the exact location of the record could not be confirmed but is near suitable areas.

According to our results, the natural distribution of *N. chilensis* is restricted to Andean areas in temperate South America in Chile and Argentina. Future projections predict that proper climatic conditions for the survival of *N. chilensis* will shift towards the north-east. Therefore, the effect of climate change will have consequences in the distribution of the species as all the documented localities will become less suitable by 2050.

We currently know that *N. chilensis* is endemic to a restricted region in southern South America, that it is poorly studied and poorly represented in entomological collections, that it was collected for the last time in 1984 even though it has been exhaustively sought in areas predicted with high suitability and close to areas where it recorded in the past. Thus, new efforts to find *N. chilensis* are necessary to define if its status should be threatened or extinct. As a result of this study two regions were identified where the probabilities of finding the species are higher located through the Biobío and Maule Regions. Therefore, intensive collecting efforts should be focused on these regions. Considering all the information obtained in the present study ENMs have proved to be a useful tool to assess problems related to potentially threatened and endangered species. However, this information should be interpreted cautiously and validated with field studies and other evidence available.

CONCLUSIONS

There are many challenges to understand insect decline: a small fraction of the species has been monitored, millions of species remain unstudied, and most of the long-term population data come from human-dominated landscapes (Montgomery et al. 2020). Under this context ENMs are valuable tools to assess the study of species whose distribution is poorly known (Paiva Silva et al. 2014) and may be at risk of extinction. Previous findings indicate that species extinction risk is generally expected to increase under climate change scenarios as a consequence of range shift and decrease by cou-pling ecological niche modeling and climatic simulations (Sobral-Souza et al. 2015).

Few insect extinctions have been documented, currently in the IUCN database (https://www.iucnredlist.org/) only 70 species of insects are listed as critically endangered. Most studies agree that habitat loss and degradation combined with climate change are the leading stressors for insects and other groups (Didham et al. 2020). Moreover, invasions from ecologically dominant alien invasive insects reduce niche space by outcompeting and effectively replacing rare species (Cardoso et al. 2020). Innovative applications of old techniques, new technologies and increasing access to old and new data provide important information into how environmental conditions and human impact affects insect species, and into how conservation strategies should be designed.

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SUPPLEMENTARY MATERIAL

Table SI. Historical dataset (130 records) with information of number and sex of the specimens and locality. Records in red are the doubtful records.

 Table SII. ENM dataset (57 records). Occurrences closer

 to 18 km discarted.

Table SIII. Absences dataset (117 records) with suitabilities and Global Human Footprint Index (GHFI). Highlighted in grey are the 40 localities that are less than 15 km away from areas where the species has been recorded with their IDs.

Table SIV. Suitability's under future scenarios for the57 localities with presence records.

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