Environmental variables determining the presence of an avian parasite: the case of the *Philornis torquans* complex (Diptera: Muscidae) in South America

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Running title: *P. torquans* complex in South America

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Abstract

1. *Philornis* flies are exclusive of birds and their nests, being some of them of conservation concern. Despite many studies addressed different aspects of this problem, none have focused on the geographical distribution of these species.
2. In this study, besides providing a model map of environmental suitability of the *P. torquans* complex in South America, we also contributed with data on the constraints of its abiotic niche.
3. We provided baseline data (supplementary information) on sites where *P. torquans* complex is present in southern South America, valuable for future *Philornis* distribution modelling efforts.
4. According to our results, the *P. torquans* complex is potentially distributed across central-eastern Argentina, mostly restricted to the Pampean and Chaco (eastern Chaco district) biogeographical provinces.
5. The potential distribution of the *P. torquans* complex mainly relates to the "minimum temperature of the coldest month" and "mean temperature of warmest quarter". In addition, moisture/aridity seems to be exerting additional constraints.
6. Our work is the first one to identify macro-environmental variables driving the geographical distribution of a *Philornis* species by evaluating their contribution to its' environmental niche.
7. Besides the relevance of our model as a tool for bird's conservation, it integrates the most up-to-date methodological recommendations to predict a robust ecological niche; thus representing a methodological reference for future work on the distribution of this group of parasites.

Keywords: *Philornis torquans* complex; distribution model; southern South America; Maxent

Introduction

The infestation of live vertebrates with dipteran larvae which feed on the host's dead or living tissue and body fluids is known as myiasis (Zumpt, 1965). In birds, myiasis is mainly caused by species of the genera *Protocalliphora* [Hough, 1899 -Diptera: Calliphoridae], *Passeromyia* [Rodhain & Villeneuve, 1915 - Diptera: Muscidae] and *Philornis* [Meinert, 1890 - Diptera: Muscidae] (Little, 2008), *Carnus* [Nitzsch, 1818 - Diptera: Carnidae] (Petrescu & Adam, 2000), *Neottiophilum* [von Frauenfeld, 1868 - Diptera: Neottiophilidae] (Krivosheina *et al.*, 2017). Of these genera, the only one occurring in the Neotropics is *Philornis*, comprising about 50 described species (Couri, 1999; Dudaniec & Kleindorfer, 2006). *Philornis* adults are free living, while larvae are strictly associated with bird nestlings, establishing different types of associations: coprophagous, semi-haematophagous or subcutaneous (Dudaniec & Kleindorfer, 2006). Despite more than 250 bird species have been reported as *Philornis* hosts in South America (Couri, 1999; Dudaniec & Kleindorfer, 2006; Löwenberg-Neto, 2008; Antoniazzi *et al.*, 2011), there are enormous gaps of information on *Philornis* parasitism and its effect on host birds; especially concerning vulnerable and endangered bird species. Impact of *Philornis* spp. on hosts ranges from subtle (Kinsella & Winegarner, 1974; Oniki, 1983; Young, 1993; Fessl *et al.*, 2006) to strong and lethal (Dudaniec *et al.*, 2006, 2007; Quiroga & Reboreda, 2012), an depends on the outcome of the interaction between traits of both parasite and host (Bronstein, 1994; Manzoli *et al.*, 2018).

While in healthy populations effects of nest parasitism could sometimes be negligible; in geographically-restricted, fragmented and small-sized populations, the effects of *Philornis* parasitism could be exerting additional pressure (Bulgarella *et al.*, 2019); thus, pushing these populations to the edge of extinction. Evidence that this parasite can be a

serious threat to bird conservation is the severe impact caused by *Philornis downsi* [Dodge & Aitkens 1968] on Darwin's finches (i.e. Koop *et al.*, 2011) and by *P. pici* [Macquart, 1854] on Ridgway's hawks (*Buteo ridgwayi* - Hayes *et al.*, 2018). Indeed, it may cause up to 75% of nestlings mortality (Fessl *et al.*, 2006; Hayes *et al.*, 2018). Therefore, more research should be conducted on the occurrence and effects of these parasites. One aspect of particular interest and poorly known is the environmental dimensions determining the geographical distribution of *Philornis* spp. Such knowledge is essential for better understanding the ecology of the genus, and may be useful to identify *Philornis*-free areas that are prone to be colonized, to identify locations with high presence of these flies that might threaten populations of endangered bird species, or to locate habitats with low risk of *Philornis* occurrence for the re-introduction of bird species or reinforcement of their populations.

The present study is aimed to identify what macro-environmental variables drive the geographical distribution of *Philornis* species in South America by assessing their relative contribution to the environmental niche. We focus on *P. torquans* and *P. seguyi*, a relatively well-known species complex within *Philornis*, to start understanding the role of environmental dimensions on the geographic distribution of *Philornis*. As temperature and rainfall are presumed to be the most relevant abiotic parameters affecting *Philornis* spp. life cycle (Dudaniec *et al.*, 2007; Antoniazzi *et al.*, 2011; Manzoli *et al.*, 2013), we hypothesise that low temperatures and reduced precipitation will restrain the occurrence of these species.

Materials and Methods

Study species

Philornis torquans [Nielsen, 1913] and *P. seguyi* [Garcia, 1952] are the two subcutaneous *Philornis* species most commonly occurring in southern South America

(Couri *et al.*, 2009; Silvestri *et al.*, 2011), where eight *Philornis* species have been described but only half of them are recognized as valid by Couri *et al.* (2009) (namely, *P. torquans* , *P. seguyi* , *P. blanchardi* [Garcia, 1952] and *P. downsi*). Specimens identified morphologically as either *P. torquans* or *P. seguyi* are undistinguishable at the molecular level (Monje *et al.*, 2013). This is the reason why it was suggested that the subcutaneous *Philornis* morphs resembling *P. torquans* or *P. seguyi* in southern South America should be treated as *Philornis torquans* complex (Quiroga *et al.*, 2016). This complex of parasitic flies was selected because: i) its biology and ecoepidemiology have been studied for more than a decade (Antoniazzi *et al.*, 2011; Quiroga & Reboreda, 2012; Manzoli *et al.*, 2013, 2018; Saravia-Pietropaolo *et al.*, 2018); ii) this is the group of flies with the highest number of confirmed morphology-based records; and iii) it could be potentially affecting the endangered Yellow Cardinal (*Gubernatrix cristata* - BirdLife International, 2018), as this bird species hosts an unidentified *Philornis* species (Domínguez *et al.*, 2015; Beier & Fontana, 2019) in the vicinity of *P. torquans* complex records.

Species occurrence data

Occurrence data of *Philornis* species was obtained from field surveys conducted in Argentina and from existing literature. In every case, *Philornis* adults were obtained from larvae or pupae recovered from nestlings or nest remains, and were identified to species level following Couri (1999). Due to the absence of occurrence data of free-living adults, information obtained from immature *Philornis* stages represents a valid surrogate to assess the environmental suitability for the species. The specimens identified based on morphology as *P. torquans* or *P. seguyi* were considered as members of the *Philornis torquans* complex (see Quiroga *et al.*, 2016), which accounted for 80 occurrence records. After removing duplicate localities, the data was reduced to

34 occurrence sites (Table S1). Since spatial autocorrelation in environmental information and consequent non-independence of occurrence data could bias predictions (Kramer-Schadt *et al.*, 2013), we spatially filtered sites preserved for calibration with the package "spThin" in R Statistical Software 3.5.0 (Aiello-Lammens *et al.*, 2015; R Core Team, 2018). Spatial thinning of occurrence records provides an easy-to-implement and relatively straightforward method to alleviate the effects of sampling bias (Boria *et al.*, 2014; Aiello-Lammens *et al.*, 2015). To attain a uniform distribution of occurrences and to avoid excessive clustering within any particular region, we explored different filtering distances in sequential steps, visually inspecting results. Once a satisfactory distribution of occurrence data was obtained (i.e., when spatial clustering of records was no longer evident), we ended with 18 sites for the *P. torquans* complex (Fig. 1). We split the *P. torquans* complex locations randomly in equal quarts: one set of locations for calibration (75%) and another for evaluation during model calibration (25%).

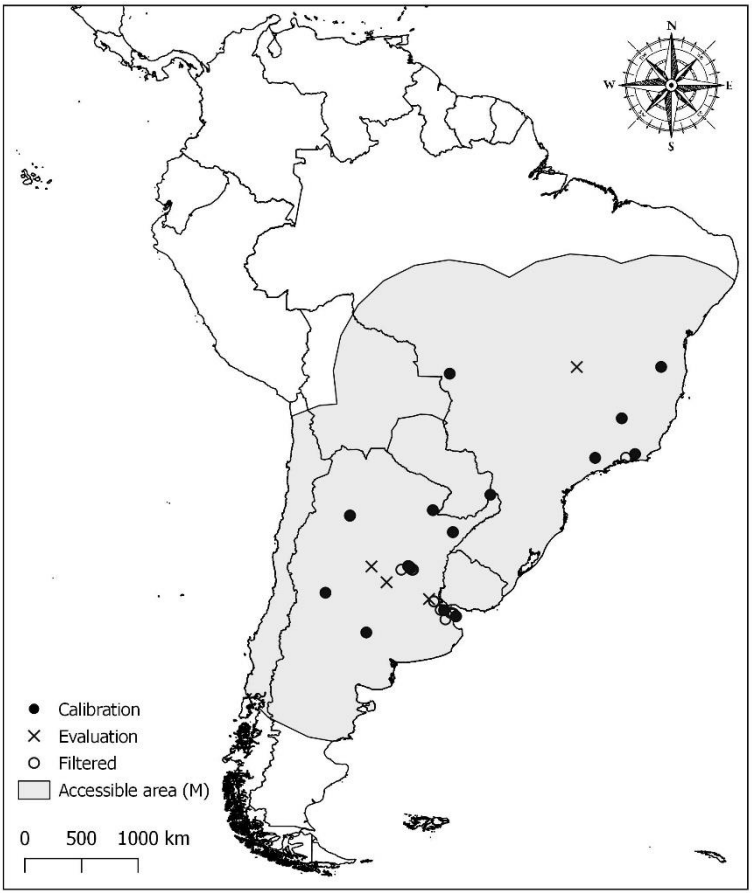

Figure 1. Geographic coordinates representing locations of *Philornis torquans* complex and accessible area (M) used in the construction of distribution models.

Environmental data and selection of variables

To characterize climatic conditions meaningful to biological species, we used the so-called "bioclimatic" variables based on WorldClim from the CHELSA database (www.chelsa-climate.org, Karger *et al.*, 2017). In addition, we included the climatic variables from the ENVIREM database, derived from and complementing the bioclimatic variables from WorldClim (www.envirem.github.io, Title & Bemmels, 2018). We excluded nine data layers (mean temperature of wettest quarter, mean temperature of driest quarter, precipitation of warmest quarter, precipitation of driest quarter, mean PET of coldest quarter, mean PET of warmest quarter, mean PET of driest quarter, mean PET of wettest quarter, and count of the number of months with

mean temperature greater than 10°C), as these variables include artefacts that create abrupt differences between neighbouring pixels (Escobar *et al.*, 2014; Raghavan *et al.*, 2019). We coarsed environmental data to 10' (~17 x ~17 km) spatial resolution, which approximately matches the uncertainty inherent in the occurrence data.

As a first step and in order to test our hypothesis, we selected a set of five variables based on current knowledge on the biology of *Philornis* spp.: i) mean temperature of warmest quarter (Bio10); ii) minimum temperature of coldest month (Bio06); iii) precipitation of driest month (Bio14); iv) precipitation of wettest quarter (Bio16) (the four of them from CHELSA); v) a climatic moisture index (CMI, a metric of relative wetness and aridity, from ENVIREM). The "mean temperature of warmest quarter" (Bio10) was selected because this variable is related to the sum of degree days available for development, a usual method used to predict the life stages of other dipteran species (e.g., Kasap & Alten, 2005; Nieto *et al.*, 2006; Gutierrez & Ponti, 2014; Harnden & Tomberlin, 2016; Yanmanee *et al.*, 2016). The "minimum temperature of the coldest month" (Bio06) was selected due to its negative effect on developmental times and survival of pupae and adults (Sinclair, 2015), therefore arguably limiting *Philornis* distribution. Furthermore, Manzoli *et al*. (2013) found that preceding increases in rainfall were highly correlated with the abundance of *Philornis torquans* parasitic stages. This aspect was considered by including the "precipitation of the driest month" (Bio14) and the "precipitation of the wettest quarter" (Bio16). A "climatic moisture index" (CMI) was included as an integrative marker of environmental conditions, strongly related to temperature and precipitation.

Additionally, we created six other sets of variables to be considered in the evaluation and calibration of models. The variables from the original set of data were grouped in three different sets: i) a dataset including only the 15 bioclimatic variables from

CHELSA (referred to hereafter as the *bioclim* dataset); ii) a dataset using the *bioclim* dataset plus the 11 climatic ENVIREM variables (hereafter referred to as the *climatic* dataset); and iii) a dataset using the *climatic* dataset plus the two topographic variables from ENVIREM (hereafter referred to as the *environmental* dataset). Then, we reduced model complexity and collinearity by selecting two simpler sets of variables from each of these three datasets, based on the calibration of preliminary Maxent models (details below). For the selection of these simpler sets of variables, we applied two procedures available in the R package "SDMtune" (Vignali *et al.*, 2019): removal of highly correlated variables ($R > 0.7$), and removal of variables with low importance for the model performance (percent contribution < 5%). Finally, for the calibration of models, we retained six sets of environmental variables: i) a set based on current knowledge on the biology of *Philornis* spp. (Set 1); ii) three sets of uncorrelated variables from the *bioclim*, *climatic* and *environmental* datasets (Sets 2a, 3a and 4); and iii) two sets of relevant variables selected from the *bioclim* and *climatic* datasets (Sets 2b and 3b) (the selection from the *climatic* and *environmental* datasets resulted in two equivalent sets of relevant variables) (Datasets in Table S2).

Niche modelling and assessment of variables importance

We used Maxent 3.4.1 for developing models (Phillips *et al.*, 2006). Maxent is a machine-learning method that estimates the species potential geographic distribution by finding the probability distribution of maximum entropy (closest to uniform), subject to the constraint of the expected values of the environmental predictors. Maxent was developed to use presence-only data by contrasting presences against background locations (Phillips *et al.*, 2006; Merow *et al.*, 2013), and has shown to outperform other algorithms, even when applied to small data sets like ours (Elith *et al.*, 2006; Hernandez *et al.*, 2006; van Proosdij *et al.*, 2016).

To minimize the impact of assumptions about absences from areas that are not accessible to the species (Barve *et al.*, 2011), we restricted model calibration to the area to which the species likely had access via dispersal. We defined the adequate accessible area (M) as a maximum area within 1000 km of any of the occurrences, based on the average geographic distance between a centroid point and all the occurrences (~730 km), the assisted dispersion of *Philornis downsi* to the Galapagos Islands (Kleindorfer & Dudaniec, 2016) and the dispersal capacity of other Muscidae species (Labud *et al.*, 2003; Showler & Osbrink, 2015).

The complexity of models built with Maxent can be adjusted with the inclusion of additional feature classes (i.e. transformations of the original predictor variables) that allow for increasingly complex models, as well as with a regularization multiplier that contributes to select those features and reduces overfitting (Merow *et al.*, 2013; Warren *et al.*, 2016). The preliminary models for each of the three data sets (the *bioclim*, *climatic* and *environmental* datasets), later used for variable selection, were calibrated using the "kuenm" R package (Cobos *et al.*, 2019). To determine the optimal model complexity, we explored all combinations of [a] 17 values of the regularization parameter (0.1–1.0 at intervals of 0.1, 2–6 at intervals of 1, and 8 and 10), and [b] nine sets of potential combinations of four feature classes: linear "l", quadratic "q", product "p", and hinge "h" ("l", "lq", "lp", "lqp", "h", "lh", "lqh", "lph", "lqph)".

After the selection of variables, we conducted a detailed model selection exercise, exploring all combinations of [a] the 17 values of the regularization parameter, [b] the nine sets of potential combinations of four feature classes, and [c] the six sets of bioclimatic variables (see above). As such, a total of 918 models were calibrated, and each model was evaluated for statistical significance (partial ROC tests), performance (omission rate), and the Akaike Information Criterion corrected for small sample sizes

(AICc). Final models were selected under the three criteria (first, statistical significance, then omission rate, followed by AICc) (Cobos *et al.*, 2019).

We used the best parameter settings chosen to create final models. For each final model, we ran 30 bootstrap replicates, with no clamping or extrapolation, and retaining a random partition of 25% of the points from each run. These final models, though only calibrated across M, were transferred to the extent of South America, particularly to southern South America, which is the focus of this contribution. We used the cloglog output format to assess median values across replicates as an estimate of the spatial distribution of suitable and unsuitable conditions for the *P. torquans* complex across South America. The uncertainty in model predictions was estimated using the range in the suitability values (i.e., maximum minus minimum) across the model replicates. To provide an additional assessment on the reliability of our model transfers, we calculated the mobility-oriented parity (MOP) metric (Owens *et al.*, 2013) to offer a view of the novelty of environmental values and combinations of values across the transfer area, with special attention paid to areas of strict extrapolation (i.e., transfer areas with values outside the range of climates in the calibration area).

We assessed the importance of each variable to determine the environmental suitability for the *P. torquans* complex with median estimates across replicates of percent contribution, permutation importance and Jackknife analysis. In order to determine the most limiting variables, we used the Maxent limiting factor mapping tool described in Elith *et al*. (2010), and implemented via the package “rmaxent” (Baumgartner *et al.*, 2017). The limiting factors are an interesting insight into the drivers of predictions, and provide a powerful basis for comparisons with physiological knowledge (Elith *et al.*, 2010).

Patterns of colours for figures were generated with the package "tanagR" (Cadena & Zapata, 2019), inspired by the plumage of passerine birds in the tanager family (Thraupidae). The package currently includes palettes based on 16 tanager species from Central and South America.

Results

We assessed 918 models for the final model calibration. Seven hundred and twenty-seven of them were statistically significant as compared with a null model of random prediction. Of such significant models, 137 (~19%) met the omission criterion of < 5%. Of the significant, low-omission models, only three met the AICc criterion of ΔAICc < 2. These three models were calibrated with the set of variables selected based on current knowledge (Set 1), and were variants of the regularization multiplier (Table 1). Models based on current knowledge selection of variables outperformed the ones calibrated with automated selected datasets, as the best of models calibrated with Set 1 presented a ΔAICc = 21.8 when compared with the best model calibrated with other set of variables.

Table 1. Performance metrics for parameter settings regarding regularization multiplier (RMs), feature classes (FCs), and sets of environmental predictors (Pred. sets), used for creating final models for the *P. torquans* complex. FCs are as follows: linear = l, quadratic = q, product = p, and hinge = h.

RMs	FCs	Pred. Sets	Partial ROC	Omission rate 5%	AICc	ΔAICc	Weight AICc	# of parameters
0.8	Lq	Set 1	0.00	0.00	362.95	0	0.21	4
0.9	Lq	Set 1	0.00	0.00	363.18	0.22	0.19	4
1	Lq	Set 1	0.00	0.00	363.41	0.46	0.17	4

The "minimum temperature of the coldest month" (Bio06) was the most influential variable, as evidenced by the percent contribution, permutation importance and Jackknife analysis (Table 2 and Fig. 2). Its response curve evidence a bell shape, with a central range optimal for prediction, while in both extremes its influence appeared to be detrimental (Fig. S1). The second most important variable was the "mean temperature of warmest quarter" (Bio10), followed by the "climatic moisture index" (CMI). The CMI response curve was similar to the one from Bio06, while the response curve from Bio10 evinced a sigmoidal shape with positive relation (Fig. S1). The "precipitation of the driest month" (Bio14) and the "precipitation of the wettest quarter" (Bio16) had nearly no influence on the distribution modelling of the *P. torquans* complex.

Table 2. Variable importance: percent contribution and permutation importance (median and sd). References: Bio10 = mean temperature of warmest quarter; Bio06 = minimum temperature of coldest month; Bio14 = precipitation of driest month; Bio16 = precipitation of wettest quarter; CMI = climatic moisture index.

Variable	Percent Contribution	Permutation Importance
Bio06	54.75 (5.67)	70.59 (8.09)
Bio10	25.10 (5.77)	18.71 (5.93)
Bio14	1.38 (3.29)	0.64 (4.27)
Bio16	0.19 (1.42)	0.88 (4.43)
CMI	12.89 (9.31)	6.44 (7.07)

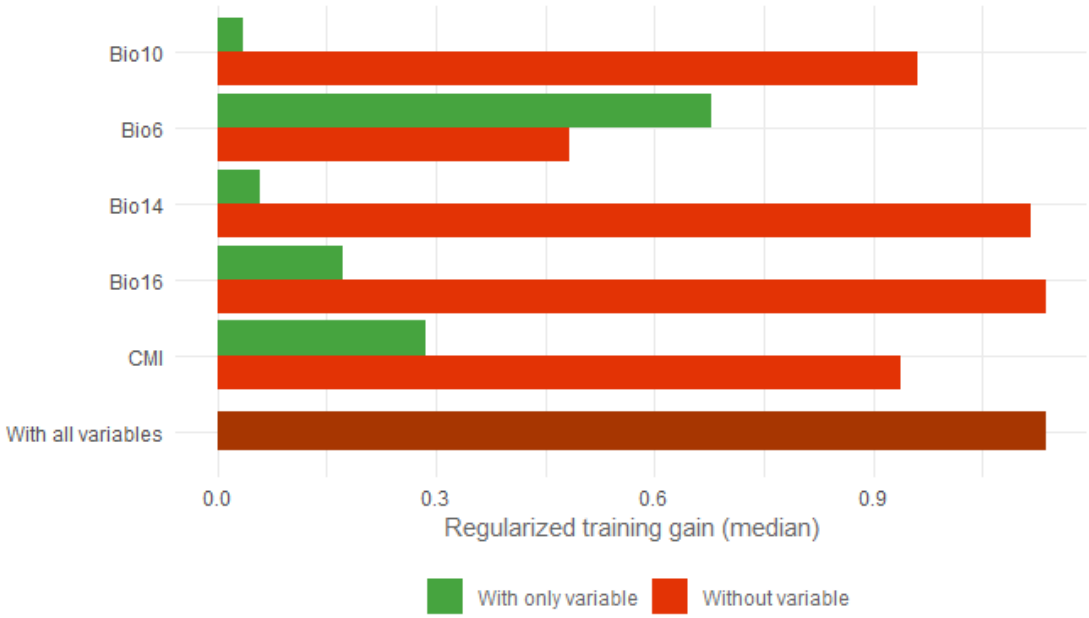

Figure 2. Results of the jackknife test of variable importance, when a variable is used in isolation or it is omitted from modelling. References: Bio10 = mean temperature of warmest quarter; Bio06 = minimum temperature of coldest month; Bio14 = precipitation of driest month; Bio16 = precipitation of wettest quarter; CMI = climatic moisture index. [Colours after the Green-Grass Tanager *Chlorornis riefferii*]

The minimum temperature of coldest month (Bio06) was the predictor associated with the largest decrease in habitat suitability in Brazil and northern South America (Fig. S2). For the majority of Argentina, the climatic moisture index (CMI) was the most limiting factor, while the mean temperature of warmest quarter (Bio10) limited suitability mostly along the Andean range (Fig. S2).

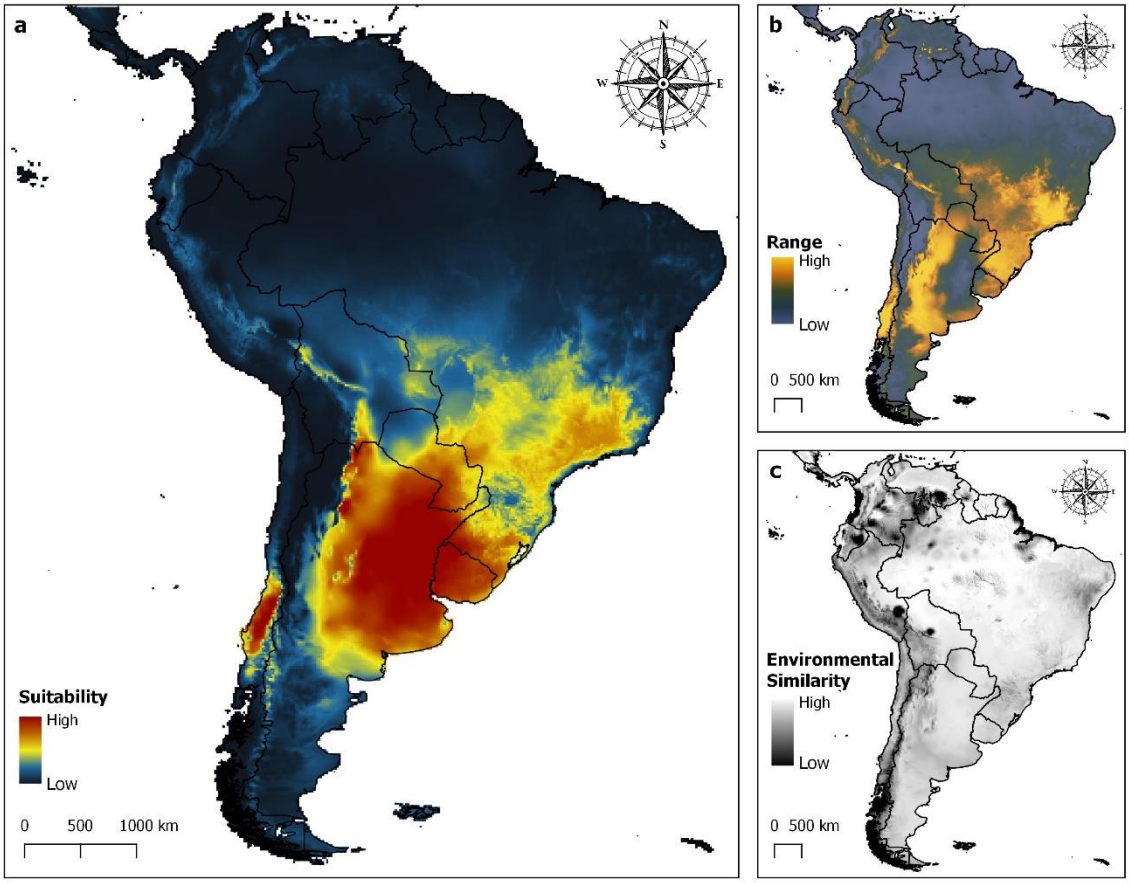

Figure 3. Climatologically suitable regions for the *Philornis torquans* complex distribution in South America. a) Median prediction. b) Uncertainty (range) associated with the median prediction of suitable regions for the *Philornis torquans* complex distribution in South America. c) Mobility-oriented parity analysis revealing areas in S. America for which the model predictions are based strictly on extrapolation. [Colours after Scarlet-Breasted Dacnis *Dacnis berlepschi* and Moss-backed Tanager *Bangsia edwardsi*]

As more than one best model was selected, we used the median and range of all replicates across parameters to consolidate results for the *P. torquans* complex. The median of the selected models (Fig 2A) identified areas with different levels of habitat suitability for the *P. torquans* complex across South America. Highly suitable areas were concentrated on the central-east of Argentina and Uruguay, comprising the

Pampean and Chaco (eastern Chaco district) biogeographical provinces (Fig. S3, see in Morrone, 2017). Suitability declined towards western Argentina, southern Brazil and Paraguay. A broad area in central Chile was identified as suitable, although it may not be accessible to the *P. torquans* complex by natural dispersion. The model showed moderate uncertainty areas mainly throughout central-western Argentina (the Monte biogeographical province), central Chile and the Andean range (Fig 2B and Fig. S3). The uncertainty observed was mainly due to the variability among replicates (~95%) (Fig. S3). The MOP analysis revealed that disparate areas in southern Chile and northern South America would present model extrapolation (Fig 2C).

Discussion

In this study, we provided a model map of environmental suitability for the *P. torquans* complex in South America and investigated what constrains its abiotic niche. Ecological niche modelling is a powerful tool to identify macro-environmental variables defining the environmental niche, and thus driving the geographical distribution of species. This study took into consideration many of the recent methodological recommendations to produce robust ecological niche models, as outlined by Feng *et al.* (2019): filtering and thinning occurrences (Boria *et al.*, 2014; Aiello-Lammens *et al.*, 2015); using an accessible area for model calibration (Barve *et al.*, 2011); testing a number of candidate sets of environmental variables and multiple combinations of model parameters (features, regularization multipliers, and sets of variables); using multiple statistical criteria (partial ROC, omission rates, and AICc) for model selection (Cobos *et al.*, 2019); replicating the model selected a number of times to determine that results are consistent (Morales *et al.*, 2017); and accounting for model uncertainty in geographical predictions (Owens *et al.*, 2013). As in any modelling approach, having a large sample size is a central issue in ecological niche modelling. As suggested by van Proosdij *et al.*

(2016), the final sample size in our study after spatial thinning seems appropriate to produce useful results. Moreover, selecting the best combination of parameters (features and regularization multiplier) further improves our ability to select the most appropriate model when dealing with a reduced number of occurrences (Morales *et al.*, 2017). Among a number of causes driving uncertainty in niche modelling, the nature of the used occurrence dataset might represent a concern to our modelling approach. As far as we know, there are no published records of free-living adults of any *Philornis* species trapped in the wild, with the sole exception of the introduced *P. downsi* in the Galapagos Islands (Causton *et al.*, 2019). Therefore, we modelled the ecological niche of the *P. torquans* complex from reported records of immature (parasitic) stages, as a proxy for the presence of adults. To date, no *Philornis* species is known to migrate, thus we assume that the adults are present year-round in the same area, as observed in *P. downsi* (Causton *et al.*, 2019). Despite modelling the niche of the adult *P. torquans* flies from its parasitic stage, we have no reason to suspect that the true geographical distribution might differ among life stages.

We hypothesised that low temperatures and reduced precipitation will restrain the occurrence of the *Philornis torquans* complex, as these abiotic parameters play a predominant role in establishing the distribution limits of organisms and have already been related with the intensity of parasitism by *Philornis* larvae (Dudaniec *et al.*, 2007; Antoniazzi *et al.*, 2011; Manzoli *et al.*, 2013). Since insects are ectothermic, their rate of development and survival can vary greatly in response to many biotic and abiotic factors (Adams, 1979; Couret *et al.*, 2014). Winters are critical period for insects at higher latitudes since overwintering conditions strongly affect their fitness (Irwin & Lee, 2000). Indeed, our model identified the minimum temperature of coldest month

(Bio06) as the most relevant variable (Table 2 and Fig. 2), revealing a detrimental effect in both sides of a suitable range of temperatures (Fig. S1).

Morphs suggested to belong to the *P. torquans* complex (Monje *et al.*, 2013) are considered to be originated in southern South America (somewhere near the border between Brazil and Uruguay - Löwenberg-Neto & De Carvalho, 2009). Representing the southernmost species of the genus, and unlike the majority of *Philornis* species, the *P. torquans* complex is adapted to colder, longer and drier winters; typical of temperate areas. The observed data across presence sites of the *P. torquans* complex indicates that minimum temperatures of the coldest month ranges between 3°C and 18°C. Therefore, it is highly likely that the *P. torquans* complex evolved to overwinter as adults or pupae, as known for other Diptera species (Protocalliphoridae, Culicidae, Muscidae) (Bellamy & Reeves, 1963; Stiner, 1969; Skidmore, 1985; Sabrosky *et al.*, 1989; Nasci *et al.*, 2001). Despite being unknown, we infer that the *P. torquans* complex may overwinter as adults, a well-known strategy for *Protocalliphora* blowflies (Sabrosky *et al.*, 1989) and recently reported for *P. downsi* in Galapagos (Causton *et al.*, 2019). The former is sustained in the fact that *Philornis* adults are known to survive over three months in captivity (Lincango & Causton, 2008; Saravia-Pietropaolo *et al.*, 2018) and had been trapped at the same territories all year round (Causton *et al.*, 2019).

On the other hand, insects adapted to cold winters may not perform well in mild winters (Irwin *et al.*, 2001). Our model suggests that warm winters (signalled by Bio06) may be limiting the northern distribution of the *P. torquans* complex (Fig. S2). Such scenario seems plausible, as warmer winter temperatures may increase energy consumption, (Tauber *et al.*, 1986; Harrington *et al.*, 2001; Irwin & Lee Jr, 2003; Sinclair, 2015). Therefore, these individuals may not be able to reach the next breeding season or may

leave them without enough energy reserves for early reproduction (Harrington *et al.*, 2001).

As aforementioned, the developmental rate of insects is related to environmental conditions, particularly as temperature impacts critical rate processes throughout development and adulthood (Kingsolver & Huey, 2008). The temperature dependence of ectotherms' developmental processes is commonly represented as the cumulative sum of degree-time products required for the development of key life stages, such as egg maturation or emergence from pupae (e.g., Kasap & Alten, 2005; Nieto *et al.*, 2006; Gutierrez & Ponti, 2014; Harnden & Tomberlin, 2016; Yanmanee *et al.*, 2016). In these regards, the mean temperature of the warmest quarter (Bio10) proved to be the second most important variable (Table 2 and Fig. 2), showing a positive relation with sigmoidal shape between predicted probability of presence and Bio10 (Fig. S1). This sigmoidal shape implies a threshold temperature (apparently around 10°C), above which the predicted probability of presence increases exponentially. The former makes sense when considering that the increase of Bio10 might favour the development of temperature-dependent non-parasitic stages, such as pupae maturation, which lately relates with the abundance of adults. Otherwise, temperatures below the apparent threshold seems to limit the distribution of the *P. torquans* complex, as evinced along the Andean range (Fig. S2).

The third most relevant variable, the climatic moisture index (CMI), resulted to be the most influential factor in most of Argentina, northern Chile and coastal Peru (Fig. S2). The CMI is an aggregate measure of potential water availability imposed solely by climate, ranging from –1 to +1, with wet climates showing positive values, dry climates negative (Vörösmarty *et al.*, 2005). The CMI values observed through the actual distribution of the *P. torquans* complex (mean -0.25, sd 0.19) indicate that the species

must endure mostly a dry environment when compared with most of South America. As reported for species laying eggs into a relatively dry environment (Grzywacz *et al.*, 2012), the eggs of the *P. torquans* morphs present a small portion of the egg surface that functions as a plastron (Patitucci *et al.*, 2017), a respiratory structure that facilitates oxygen income minimizing water loss (Hinton, 1960). The reduced size of the plastron of the *P. torquans* morph (Patitucci *et al.*, 2017) may have evolved as an adaptation allowing the radiation to the drier conditions typical of central Argentina (see Löwenberg-Neto & De Carvalho, 2009).

Opposed to our prediction, the ecological niche model suggests that precipitation has no direct influence on limiting the environmental suitability of the *P. torquans* complex. The precipitation of the driest month (Bio14) and the precipitation of the wettest quarter (Bio16) had a poor contribution to the model performance (Table 2), and showed a weak explanatory power in the jackknife analysis (Fig. 2). Despite it is clear that humidity and/or moisture are relevant environmental factors determining the *P. torquans* complex distribution, as reflected by CMI and supported by this model, the proximal influence of precipitation seems to be mainly related with the intensity of parasitism by *Philornis* species, as previously reported (Arendt, 1985, 2000; Dudaniec *et al.*, 2007; Antoniazzi *et al.*, 2011; Manzoli *et al.*, 2013).

The outcome of the geographical projection of the environmental niche model was a map of the potential distribution of the *P. torquans* complex in South America. According to our results, the *P. torquans* complex is potentially distributed across central-eastern Argentina, mostly restricted to the Pampean and Chaco biogeographical provinces, and declining with some uncertainty in the surrounding Monte biogeographical province (Fig. 3 and Fig. S3). The later makes sense due to the historical relationship among these three biogeographical provinces of the Chacoan

dominion (Morrone, 2017). Indeed, the Chacoan and the Monte provinces are closely related (revised in Morrone, 2017), and a sequence of biotic impoverishment from the Chaco province to the Pampean province, with the Monte province being intermediate between both, has been suggested (Cabrera, 1976; Morrone, 2017). Regarding the broad area predicted as suitable in central Chile, and despite its relative high uncertainty, the Andean range might represent a pronounced topographic barrier impeding the natural dispersion of the *P. torquans* complex to this area.

In conclusion, we present the first study to identify macro-environmental variables driving the geographical distribution of a *Philornis* species by evaluating their contribution to its' environmental niche. Our model is of relevance as a tool for bird conservation, and it integrates current methodological recommendations to produce a robust ecological niche prediction; thus representing a good reference for future work on the distribution of this parasite genus.

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Contribution of authors

PFC and MAQ participated in the design and coordination of the study, and drafted the manuscript; PFC performed the data analysis and modelling; AP carried out field

surveys and revised the existing literature; LM and PMB provided financial support and critically reviewed the manuscript. All authors revised the manuscript and gave final approval for publication.

Competing interests

We have no competing interests.

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