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The effects of climate change on the distribution of South American antbirds (*Thamnophilus punctatus* complex) as affected by niche divergences and contact zone interactions between species.

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Abstract

Several studies have shown that climatic change has been accelerating due to human activities, leading to dramatic effects on biodiversity. Modeling studies describe how species have reacted in the past to climatic change, and this information can help us to understand the degree of biotic susceptibility to current and future climatic change. This work aims to determine the effects of past, current and future climatic changes on the geographic distribution of the species complex *Thamnophilus punctatus*, a bird clade widely distributed across Neotropical dry forests. We also investigate if species that are phylogenetically similar have comparable climatic niches and, consequently, can be expected to respond similarly to climatic change. For this purpose, we calculated similarity, niche overlap, equivalence and genetic distance between all species, modeling their geographic distributions during the Last Glacial Maximum (LGM) as well as under current conditions and future (2050–2080) scenarios. Our results indicate that there are differences in responses to climatic changes from the LGM to the present among the five species of the *T. punctatus* complex and that the niches in the measured dimensions are not conserved among the studied species. We therefore suggest that the adequate environmental space of taxa of a widely distributed lineage can be shaped in distinct way, regardless of how closely related their species are or how much their niches overlap. Competitive exclusion in zones of contact is an important factor determining the geographical range of the species of the *Thamnophilus punctatus* complex, particularly for the very closely related species *T. sticturus*, *T. pelzelni* and *T. ambiguus*.

Key words: Birds, Climate change, Niche conservatism, South America.

INTRODUCTION

The ecological niche is the combined requirements of food, breeding sites, suitable climate parameters and other factors that individuals of a particular species need in order to survive and thrive. However, species are not static and may over time expand, contract, or shift niche. Closely related species may retain the niches of their ancestral species to some degree and tend to occupy similar if not identical niches (Warren et al. 2008). In other words, the abiotic factors and ecological requirements of lineages are frequently conserved, and the species maintain traces of their ancestral niche, a pattern known as niche conservatism (Medeiros et al. 2015; Warren et al. 2008; Wiens et al. 2010). Environmental niches change in space and time due to different climatic conditions (and the resulting change in selection pressure) faced by organisms over time (Broennimann et al. 2012). These climatic conditions can be driven by various geological events and thus these events can shape the various distribution patterns and influence the process of species diversification.

The biomes that make up the Neotropical region have undergone several cycles of expansion and contraction of forests (Arruda et al. 2018), driven by climatic fluctuations with periods of warming and cooling. These cycles have had significant impacts onr the distribution, migration, speciation, geographic isolation and extinction of organisms (Antonelli et al. 2018; Arruda et al. 2008; Costa et al. 2017; Hoorn et al. 2010; Ledru et al. 2009; Zachos et al. 2001). Some biomes in this region have remained more stable over time than others, one such biome being the Amazonian Rainforest (Arruda et al. 2018).

Recently, rainforests and South American savannahs have been experiencing significant and increasing human interference that has altered the landscape of several biomes and changed their climate. For example, deforestation and agricultural expansion have threatened the climatic and ecological stabiliy of Amazonia and Cerrado, which may become even more threatened in the future (Nobre et al. 2007; Fernandes 2013). In the Atlantic Forest (but increasingly so also in Amazonia), the main problem currently is the loss of forest area due to biome fragmentation, because this biome coincides with the primary urban development area in Brazil where human exploitation is extensive (Collevatti et al. 2011). Forest fragmentation has also affected the mechanism of transferring moist air from the ocean, reducing rainfall (Makarieva and Gorshkov 2007). Low-level air moves from areas with weak evaporation to areas with more intense evaporation, such as Amazonia, and this mechanism plays an important role in the maintenance of optimal moisture stores in the soil, compensating the gravitational water runoff. In the Brazilian semi-arid region, the main problem is desertification attributed to the historical and unsustainable use of the Caatinga, including the clear-cutting of vegetation and the removal of other resources. In expected climate change scenarios, these areas will have an even drier climate, with reduced rainfall and increasing water shortages as a result of the expected increase in air temperature, increasing the aridity across Caatinga environments (Marengo et al. 2011). According to Marengo et al. (2009), different South American regions may experience different responses to future climate change scenarios: regions such as northeastern Brazil and central-eastern Amazonia may experience further rainfall deficits, whereas warming may lead to excessive rainfall along the northwest coast of Peru–Ecuador.

In a scenario of climatic changes triggered by human activity, the ability of many organisms to adapt and survive is reduced and the species that are unable to rapidly adapt or move can suffer drastic population losses or even extinction (Bickford et al. 2010). Within this scenario, some authors suggest that phylogenetically similar species would tend to have similar ecological responses to climatic change, since they will tend to retain some degree of their ancestral niche (e.g. Peterson et al. 1999). Other authors suggest that environmental niche overlap is closely tied to geographic overlap, but not to phylogenetic distances (e.g. Warren et al. 2008) and, consequently, responses to climatic change are independent of the phylogenetic distance between species. Additionally, widely distributed species are more likely to vary their niches and have a wider range of environmental tolerance, both in the known cases of past climatic change and the expected changes in the future (Marengo et al. 2009; Hoorn et al. 2010; Collevatti et al. 2011; Marengo et al. 2011; IPCC 2014).

We focus on three general hypotheses related to niche conservatism and niche shifting caused by climatic change: H0 – There is niche conservatism among bird species (i.e., the niches are phylogenetically constrained). An outcome of this is that climatic change will have the same effect on the distribution of closely related species. H1 – A rejection of H0 means that the niches are not conserved (not phylogenetically constrained) and might imply that birds with a large niche overlap will be affected in the same way by climatic changes, independently of their phylogenetic relationships. H2 – A rejection of H0 and H1 means that climatic changes might influence the niche of taxa of a widely distributed lineage, regardless of the phylogenetic relationships or the niche overlap between the species considered.

We tested the three hypotheses described above using the *Thamnophilus punctatus* species complex (Thamnophilidae), which has a wide distribution in the Neotropical region. Species belonging to this clade have vocal, morphological and molecular differences with respect to more distant relatives in the genus (Isler et al. 1997; Peters 1951; Zimmer and Isler 2003). This species complex is a suitable model for inferring changes in geographic distributions because it has a wide distribution across the Neotropical region (Fig. 1). Its constituent species occur in various distinct biomes and environments, such as deciduous, semi-deciduous and gallery forests in open biomes, border zones, secondary forests, semi-deciduous forests of the Atlantic Forest domain, and campinas and campinaranas (sandy soil vegetation) of the Amazonian Forest (Isler et al. 1997; Peters 1951; Zimmer and Isler 2003). Thus, the geographic distribution pattern of this bird clade makes it possible to compare species responses to climatic change in the different biomes in which it occurs.

The overall aim of this study is to model the past, present and future potential distribution of the *Thamnophilus punctatus* species complex and test the three hypotheses mentioned above in order to identify species-specific responses to climatic change in different South American biomes.

MATERIALS AND METHODS

Environmental variables

We used a total of 19 variables composed of temperature and precipitation in various combinations, with maximum and minimum extremes, seasonality, annual variation, and daily and monthly averages with a pixel resolution of 30’’, about 0.9 km² per pixel. The selection of environmental variables used in the models was determined using the Jackknife test (Phillips and Dudik 2008) to estimate the level of significance of an environmental variable individually in the analysis of species distribution and to select the variables with the highest model gain (Phillips et al. 2006; Phillips and Dudik 2008). The variables used in this study are available through Worldclim (Hijmans et al. 2005) and each one consists of a bioclimatic map (Global Climate Models-GCMs, MIROC).

A correlation matrix was generated independently for three scenarios: Last Glacial Maximum (LGM; approximately 20,000 years ago), present (1960–1990), and future (2050–2080), all of them in South America. From this matrix, we excluded highly correlated variables, taking into account values greater than 0.8, resulting in the predictive variables that were used for modeling. Uncorrelated variables were selected in order to generate distribution models via the Maxent algorithm (Phillips et al. 2006). A total of 11 variables were selected: altitude; mean diurnal range, mean of monthly (max temp - min temp); min temperature of coldest month; mean temperature of driest quarter; mean temperature of coldest quarter, precipitation of wettest month; precipitation of driest month; precipitation of driest quarter; precipitation of warmest quarter and precipitation of coldest quarter. For the data treatment, we used the Qgis Program 2.18 and R Studio, and the results were then treated in the Qgis Program 2.18 for further analysis.

The occurrence data of the five species of the *T. punctatus* complex were obtained from the Emílio Goeldi Museum (MPEG) of Pará-Brasil, Species Link and the Global Biodiversity Information Facilit (GBIF) (Fig. 1). The software Qgis 2.18 was used to clean and validate the georeferencing data, eliminating repetitions, points outside the distribution of each species, and coordinates in the same grid cell. The occurrence points of each species were combined with data from the environmental databases to generate potential distribution models through Maxent (Phillips et al. 2006).

Similarity, equivalence and niche overlap

Niche overlap is a metric that evaluates whether two environmental niches are superimposed and ranges from 0 (no overlap) to 1 (full overlap). The niche equivalency test assesses if the overlap between niches of two species is less than would be expected if niches were identical. The niche similarity test differs from the equivalency test by addressing whether the environmental niche occupied in one range is more similar to the one occupied in the other range than would be expected by chance (Warren et al. 2008; Broennimam et al. 2012).

We compared the performance of the niche variables of different species using univariate analyses of each of the 11 remaining bioclimatic variables in our models, grouped by species pairs. For this we used the Kruskall-Wallis test (Hollander and Wolfe 1973) and subsequently the Dunn test (Dunn 1964) where density graphs are generated through the 5.4 sm package (Bowman and Azzalini 2014).

Multivariate comparisons between the disjunct populations of the two species were also performed. In these comparisons, niche overlap was quantified using Principal Component Analysis (PCA), following the approach proposed by Broennimann et al. (2012), using ecospat functions (Broennimann et al. 2016) in R. We used the first two axes of the PCA calibrated for the entire climatic space of the study area, which includes all occurrences of disjunct populations (Broennimann et al. 2012).

The climatic space delimited by the axes was defined for 100 x 100 cells, with the overlap estimated using Schoener's D metric (1970) as revised by Warren et al. (2008).

Subsequently, we performed the niche equivalence test, which determines if the niche overlap is constant when randomly relocated in the distribution of disjunct populations. Lastly, we evaluated niche similarity, which addresses whether the environmental niche occupied by a population at one interval is more similar to the other than would be found at random. This test was based on 100 replicates, where, if the observed overlap includes up to 95% of the simulated values, the taxon is considered to occupy similar niches in both of the analyzed distributions. In order words, the niches of the two compared species are more similar than would be expected at random (Warren et al. 2008; Broennimann et al. 2012).

Geographic distribution modeling

There are a number of methods available that can be used to model species distributions. Among these, the Maxent algorithm in the R platform has been shown to be a reliable methodology for predicting distribution scenarios (Phillips et al. 2006; Phillips 2008; Anderson and Raza 2010; Guisan et al. 2017) and was the one we chose to use.

A total of 15 climate suitability maps were used, one model for each of the five species of the *T. punctatus* complex in past, present and future conditions. We took into account three different climatic scenarios, and generated five models with the bioclimatic variables from the Last Glacial Maximum (approximately 20,000 years ago), five models using values of baseline (current) bioclimatic variables (WorldClim 1960–1990) and five models with the bioclimatic variables from the estimated future conditions (2050–2080) available in Worldclim (Hijmans et al., 2005). As each map was made from a total of 10 replicates, each model reflects the mean value of replicates for each species.

We calculated the variation of climatically suitable areas between the climatic scenarios for each species using binary maps with and without the climatic suitability obtained by Maxent (values of minimum probability of representing an adequate habitat). As such, six different values for prediction thresholds from the present day distribution model were compared with the known current distribution: 1- Minimum training presence logistic threshold, 10 percentile training presence logistic threshold, 2- Equal training sensitivity and specificity logistic threshold, 3- Equal test sensitivity and specificity logistic threshold, 4- Balance training omission, 5- Predicted area and threshold value logistic threshold, and finally 6- Equate entropy of threshold and original distributions logistic threshold. The threshold that matched best with the known current distribution was then used to produce binary species distribution maps under each chronological scenario.

DNA extraction, amplification and sequencing

We sampled 41 individuals covering almost the entire distribution of the *T. punctatus* species complex. All tissues sequenced were derived from voucher specimens deposited in the ornithological collections of the Museu Paraense Emílio Goeldi (MPEG) in Brazil and the Louisiana Museum of Natural History (LSU) in the USA. The following taxa were sampled: *Thamnophilus punctatus*, *Thamnophilus* *stictocephalus, Thamnophilus pelzelni, Thamnophilus sticturus* and *Thamnophilus ambiguus* (Supplementary material S1).

DNA was extracted and sequenced at the Department of Biological and Environmental Sciences, University of Gothenburg, Sweden. We used the DNeasy kit (Qiagen Inc.) following the manufacturer's protocol and published DNA primers (Sorenson et al. 1999) to amplify and sequence one mitochondrial gene (NADAH subunit 2 [ND2]) following standard PCR protocols.

Genetic distances (P- distance) between all pairs of species in the complex were estimated using the MEGA6 software package (Table 2). We used Mantel test to investigate the relationships among the matrices of genetic distance, niche overlapping and differences among the variations within the given scenarios (LGM/present, and present/future). This test was performed with the vegan package in R (Oksanen et al. 2019).

RESULTS

Geographic distribution modeling

Fifteen climate suitability maps were generated with AUC (Area Under the Curve) training values > 0.9, under each of the past, current and future climate scenarios, with a standard deviation of 0.003. These results indicate that the models had a clearly improved performance over that of a random prediction. Therefore, they reflect a biologically more realistic scenario of climatic suitability for each species, with higher precision and better discrimination of suitability. The primary output of most models is a raster representing the probability of species occurrence. For most applications, it is often necessary to select a threshold of probability to classify each pixel into two categories, ‘suitable’ or ‘present’, and unsuitable’ or ‘absent’ (Bean et. al 2012). All generated distribution models were adjusted to minimum probability of occurrence, generating 15 binary maps with both absence and presence of climatic suitability for each studied species in the three scenarios. The Equate entropy threshold and original distributions logistic threshold allowed a distribution scenario similar to the known current distribution of each species, with only a few areas that extend beyond this distribution. These additions could be climatically suitable areas that the species do not currently occupy, not necessarily errors in the model (Fig. 2).

Comparisons between the modeled distributions suggest that *T. ambiguus* and *T. stictocephalus* underwent a contraction of their distribution from the LGM to that of the present day but may expand this in the future. *Thamnophilus punctatus* has expanded its distribution through time, but this is expected to shrink in the future. The distribution of *T. pelzelni* retracts and that of *T. sticturus* expands from the past through the current into the estimated future climate scenarios (Fig. 2).

Overlap, equivalence, niche similarity and genetic divergence.

The multivariate analysis based on the climatic niche indicated that the PCA explains 77.3% of the total variation, when combining the PC1 (49.1%) and PC2 (28.2%) axes (Fig. 3). When overlapping the correlation circle with climatic projections of ecological niche, the bioclimatic variables that best explain the density of occurrence of each species are: *T. ambiguus*: alt, bio17, bio18, bio13 and bio14 (variables of precipitation); *T. pelzelni*: bio2, bio13, bio11, bio9 and bio6; *T. punctatus*: bio6, bio11, bio13, bio9 and bio18; *T. stictocephalus*: bio6, bio13, bio9, bio11 and bio6 and *T. sticturus*: bio2, bio18 e bio13 (Fig. 3) It is mostly precipitation driving the distributions of *T. ambiguus*, *T. punctatus* and *T.sticturus*, and temperature driving the distributions of *T. pelzelni* and *T. stictocephalus*.

The species of the *Thamnophilus punctatus* complex presented, in general, low values for climatic niche overlap, and the hypothesis of niche equivalence between all species was rejected. Niche similarity values varied between approximately 12% and 76%, with the highest values observed between *T. ambiguus* and *T. stictocephalus* and between *T. ambiguus* and *T. pelzelni,* with 76% and 65% similarity respectively.

Genetic analyses indicated a high degree of genetic distance (p-distance) between species of the *T. punctatus* complex, but within expectations for closely related species (Table 2). The Mantel test indicated that there were not significative correlations between: 1) SchoenerD x Genetic Distance (p-distance) $r = -0.5826$, $p > 0.05$; 2) Schoener D x LGM/Present $r = 0.5531$, $p > 0.05$; 3) Schoener D x Present/Future $r = 0.1729$, $p > 0.05$; 4) Genetic distance x LGM/Present $r = -0.322$, $p > 0.05$; 5) and Genetic Distance (p-distance) x Present/Future $r = 0.2654$, $p > 0.05$.

DISCUSSION

Our study indicates that niche conservatism is unlikely to be a factor in the response to climatic change as the most closely related species did not have identical climatic niches and these species pairs did not respond identically in the modeled climate change scenarios. H0 was therefore rejected as a viable hypothesis. Furthermore, species with a large climatic niche overlap did not respond to the climatic change scenarios in the same way either, which meant that the first alternative hypothesis (H1) was also rejected. Instead, our analysis suggests that climatic changes determine variations in climatic suitability where each species occurs, due to each species being dependent on several region-specific variables, regardless of genetic proximity or degree of niche overlap.

Our results are qualitatively similar to those of McCormack et al. (2009), who examined whether allopatrically distributed species of *Aphelocoma* jays can occupy similar climatic niches. They found that these species show a low correlation with climatic variables, such as temperature and precipitation, and show a stronger correlation with vegetation type instead. The expansion and retraction dynamics of modeled distributions for *Aphelocoma* jays follow historical events of biome landscape changes over time, as influenced by climatic changes rather than phylogenetic proximity or niche equivalence. Thus, other ecological and evolutionary processes should also be taken into account as determinants of species distributions, such as speciation, extinction, dispersal and vegetation (Kozak and Wiens 2010; McCormack et al. 2009).

An alternative explanation for the rejection of our hypotheses related to niche conservatism and niche shifting caused by climatic change is that the species of the *T. punctatus* complex are all quite closely related and replace each other geographically, probably reflecting speciation by geographical vicariance during the course of the Pleistocene and competitive exclusion in zones of contact. This is particularly relevant for the very closely related *T. sticturus*, *T. pelzelni* and *T. ambiguus* (Brumfield and Edwards 2007), which may have been split by climatic change effects during Pleistocene oscillations and kept their current distribution by exclusion in zones of contact. This species-rich family initially diversified in tropical rainforest biomes, but the Thamnophilini tribe shifted to more open savannah habitats along the periphery of the Amazon Basin, beginning in southern Brazil (Bravo 2012; Belmonte-Lopes 2013). This would probably have required some flexibility in its thermal tolerance, as inhabitants of this region would have had to endure periods of cold weather caused by southern polar winter winds, notably in the Pleistocene epoch (Servant et al. 1993). There is a good deal of empirical evidence to suggest that species differ greatly in their ability to tolerate cold: most species prefer hotter temperatures but differ greatly in their abilities to tolerate cold, which may be a specialized condition that allows some groups to take advantage of uncontested food resources that exist (at least for part of the year) at high latitudes (Araujo et al. 2013). This may also be relevant for *Thamnophilus* species, given their biogeographic history. Cold-tolerant species can fairly easily settle or return to warmer climates, but the opposite movement may impose strong selection pressure on populations and is therefore rare (Khaliq et al. 2015). Our interpretation is that this group of *Thamnophilus* antshrikes is thermally flexible (Smith et al. 2012, Araújo et al. 2013; Khaliq et al. 2015; Stager et al. 2015), but the distributions of the individual species are constrained by the biogeographic history, with isolation of populations in different parts of a broad ancestral range. These patterns may presently be maintained by competitive interactions (exclusion) in places where these closely related species coincide or by geographic barriers such as rivers.

Geographic distribution modeling

The models we generated under each climate scenario indicate that there have been differences in responses to climatic changes from the LGM to the present among the five species of the *T. punctatus* complex. These results could potentially be generalized for the avifauna that occurs in similar environments, and, if so, they may indicate ecosystem responses to climate change. Thus, further studies could focus on other species complexes that are widely distributed in open areas, in order to determine if climatic changes have had similar effects on species occurring in the same environments and regions and may also do so under ongoing and future climatic changes. Below we discuss the changes modelled for each species individually, highlighting the peculiarities and similarities among them, taking into account the results from previous studies.

Thamnophilus punctatus

The models generated for *T. punctatus* indicate suitable areas for their occurrence both in the northern and southern regions of Amazonia, which does not corroborate their known current distribution. One hypothesis to explain this mismatch with the current geographical distribution of *T. punctatus* is the presence of an ecological substitute (*T. stictocephalus*) that may compete with *T. punctatus* (Urbina-Cardona and Loyola 2008). The large Amazonian rivers could isolate these two species, preventing them from exploring new environments. This, in essence, is a possible case of historical contingency affecting the distribution, rather than a current limit due entirely to lack of suitable habitat.

Considering that *T. punctatus* is currently found in more open areas of dry forests such as the whitesand “campinas” and boundary forests of Amazonia (Peters 1951; Zimmer and Isler 2003), expansion and contraction would be expected in the LGM and the present, respectively, due to the climatic variations of these periods (Ab'Saber 1977; Prado and Gibbs 1993; Hoorn et al. 2010). However, our models indicated a stability of the size of the climatically suitable areas for this species. For the future, these areas are expected to be somewhat reduced, but overall stability will remain. According to Arruda et al. (2018), with the contraction of the Amazon forest in the past, substitution for other types of vegetation occurred in preserved areas. This means that even with no loss of forest area, more sandy environments of the Amazon river beds were colonized by tree species specialized in occupying these types of arid environments. Such evidence indicates that the Amazon maintained climatically adequate areas for *T. punctatus* between the two scenarios, past and present.

Thamnophilus stictocephalus

The models for *T. stictocephalus* predict a significant reduction in the size of climatically adequate areas from the past to the present. The expansion of savannahs during cool periods in the past (Arruda et al. 2018; Häggi et al. 2017) may have been an important factor in *T. stictocephalus* having broader suitability areas in southern regions of the Amazon. The model for the current scenario predicts suitable areas where the species is not known to occur, and a growing suitability area in future scenarios.

The current distribution of *T. stictocephalus* (Fig. 1) suggests past climatic changes where savannah areas expanded into southern Amazonia. Although this would indicate a favorable scenario for its future expansion under natural conditions, current forest fragmentation due to the advance of the agricultural frontier in southern Amazonia, especially in the Brazilian states of Pará and Rondônia (Fernandes 2013), may limit their actual spread into environmentally suitable areas.

Thamnophilus sticturus

The expansion and contraction of biome vegetation has historically been concentrated in areas of vegetation transition, in addition to the expansion of the Atlantic Forest through the southeastern Brazilian route (Arruda et al. 2018; Costa et al. 1997). The distribution of *T. stictrurus* may be restricted to its current distribution as a result of this. The existence of areas predicted by the model to be climatically suitable for this species that occur outside the current distribution of this species (i.e. where no records of occurrence exist), might be explained by competitive exclusion or the effect of unmeasured eco-environmental variables that do constitute part of the species' niche but were not accounted for in this study (Raxworthy et al. 2003; Sobreron and Peterson 2005; Pearson et al. 2007; Urbinas-Cardona and Loyola 2008; Warren et al. 2008). They may also relate to factors that limit dispersal, such as geographical barriers, as in the example of the Paraguay River that may explain the separation between *T. Pelzelni* and *T. sticturus* (Grohnert and Piacentini 2018). Climate models predict intense climatic changes in the distribution region of *T. sticturus*, with extreme rainy and dry periods, combined with intense ongoing exploitation of the Pantanal as well as the southern and eastern Amazonian regions for agriculture and energy generation (Marengo et al. 2006). Even so, our simulations indicate an increase in areas with a suitable climate for this species.

Thamnophilus pelzelni

The distribution modeling for *T. pelzelni* shows a small decrease in areas of climatic suitability, indicating stability between the LGM and the present. According to Arruda et al. (2018), the Caatinga is a stable climatic domain in South America when the climatic change between the LGM and the present is considered. The expansion and contraction dynamics in this area have been restricted to its transition zones, although this still deserves more detailed studies. Since the distribution of *T. pelzelni* is associated with a potentially stable area in this period, distribution stability would be predicted for the species. As the climate changes, *T. pelzelni* will have a significant reduction in potentially appropriate areas of occurrence, but the species will not be further threatened, because it will be able to occupy some new areas in the future, counterbalancing the loss in other areas (Fig. 2, Table 2). In this scenario, future extinctions at regional levels may occur (Grant and Bowen 1998), impacting the genetic diversity of the species.

Thamnophilus ambiguous

Climatic variation between the LGM and the present did not identify climatically favorable areas for the expansion of the distribution of *T. ambiguus*. Several studies point to a decrease in the size of the Atlantic Forest (where *T. ambiguus* maintains populations) between the LGM and the present, especially along the coast due to the inland advance of the ocean front, followed by the replacement of the forest by the underwater vegetation present today (Carnaval et al. 2009; Costa et al. 2017; Jaramillo and Cárdenas 2013). However, in future scenarios expansion is expected (Fig. 2, Table 2). This expansion may be brought on by Atlantic Forest fragmentation due to increasing temperatures and changes of other variables, as well as by anthropic action in this region (Collevatti et al. 2011), which could result in the expansion of the bordering forest areas and secondary forests that are the preferred habitat for this species.

Niche overlap

The niche overlap analyses presented here suggest that divergence of populations separated by past dispersal barriers (such as the lower Amazon river or past climatic change), later reinforced by competitive exclusion where expanding populations come into contact, might be an important factor in the diversification of the species in the *Thamnophilus punctatus* complex. Similar results have been previously suggested for other species using primarily climatic variables (Warren et al. 2008). This further supports the importance of climate change, potentially during Pleistocene oscillations, and competitive exclusion in zones of contact in determining current geographical range, particularly for the very closely related species *T. sticturus*, *T. pelzelni* and *T. ambiguus*.

The highest degree of niche overlap found was between *T. pelzelni* and *T. sticturus*, with approximately 33% overlap. These two species are associated with savannah and dry forest environments. *T. sticturus* is however distributed across a larger range of habitats, such as transition areas between Cerrado, Chaco, Amazonian Forest and Pantanal (Isler et al. 1997; Peters 1951; Zimmer and Isler 2003).

When comparing the genetic analyses, the niche overlap and the area variations between the scenarios, we found no correlation between the different variables. Although these species share a small portion of their niches, they are also subject to different climatic conditions due to differences in their geographic distributions (Warren et al. 2008; Broennimann et al. 2012).

T. pelzelni and *T. sticturus* presented a decrease and an increase respectively in the area of their climatic suitability among the modeled scenarios. These divergences were also observed for other species of the complex, for example, *T. punctatus* and *T. stictocephalus*. Therefore, in a global warming scenario, phylogenetically close species may have different distribution responses, especially in the event that they are widely distributed across a wide range of environmental conditions (Broennimann et al. 2012).

Conclusions

In summary, our results suggest that climate niche divergence was important for isolation and speciation within the *T. punctatus* complex, potentially during Pleistocene oscillations. The exclusive niches and geographical distributions determine variations in the climatic suitability for species occurrence, due to each species being dependent on several region-specific conditions. The current distributions of sister species can also be associated with competitive exclusion in zones of contact and rivers creating barriers in the Amazon. However, the fragmentation of the Amazon Forest due to the advancing of agriculture in southern Amazonia in the Brazilian states of Pará and Rondônia (Fearnside 2018) and the advance and development of cities along the coast of Brazil (Urbina-Cardona and Loyola 2008) may limit the spread of species to areas suitable for occupation.

According to Häggi et al. (2017), one of the factors that contributed to Amazonian biodiversity is that it had stable climatic conditions. Therefore, many species become highly threatened in a climate change scenario driven by the fragmentation of large forest areas (Bickford et al. 2010; Fernandes 2013; IPCC, 2014; Marengo et al. 2009). This should be most evident for species occupying environments of intense anthropogenic exploration, such as *T. ambiguus* in the Atlantic Forest. Although the distribution of *T. pelzelni* is associated with a potentially stable area during climatic change, the dry forest habitats have also become highly threatened due to intense and historical human explorations. Therefore, the predictions presented here show which species are most susceptible to climatic variations but point to the need for associations with environments and historical biogeography. Additional work should be undertaken to test the effects of climatic changes on other species, in order to provide a more complete picture of the effects on different biomes and species. Taken together, this line of research will provide crucial information to better identify environments that deserve immediate attention for conservation.

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589 FIGURES AND CAPTIONS

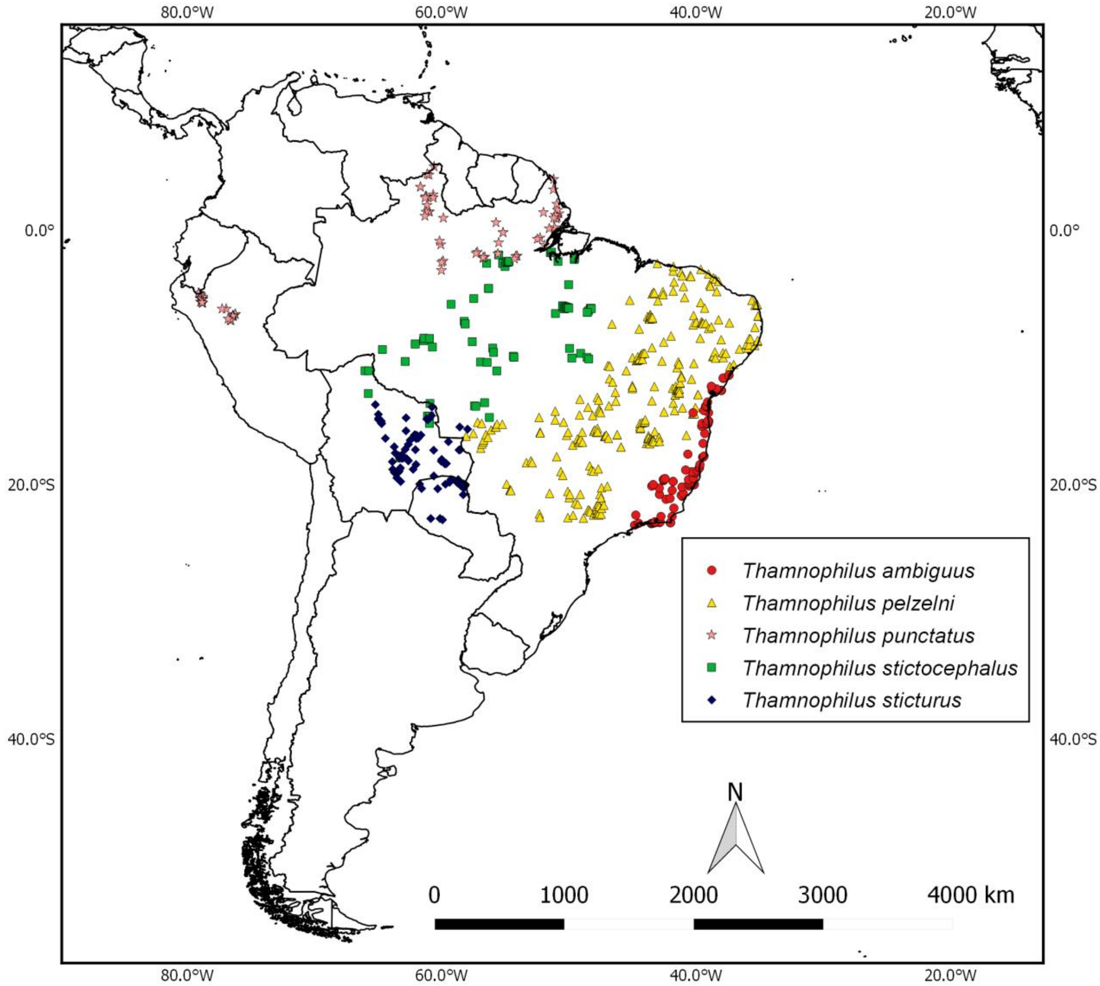

Figure 1: Species occurrence records of the five species of the *Thamnophilus punctatus* complex.

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Figure 2: Predicted distribution maps for the past, current and future distributions of the *Thamnophilus punctatus* complex. (a)- *T. ambiguus*, (b)-*T. pelzelni*, (c)- *T. punctatus*, (d)- *T. stictocephalus*, (e)- *T. sticturus*. LGM, Last Glacial Maximum. Parts of the modelled range that correspond to the actual range are illustrated in red.

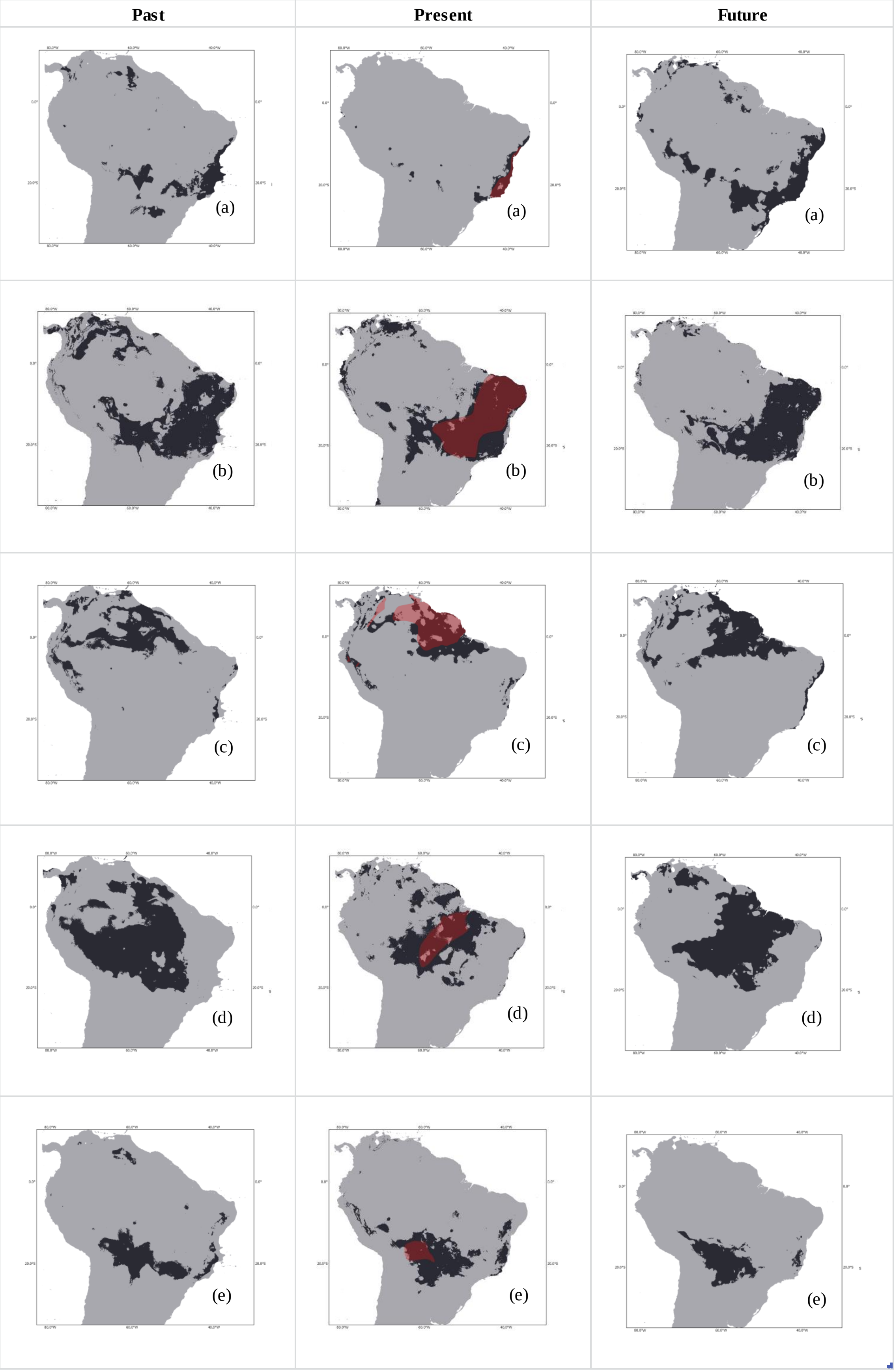

Figure 3: Environmental variables correlated to the ecological niche of the *Thamnophilus punctatus* complex at the limits of PCA. Shading represents the occurrence density of each species, analyzed separately. The solid and dotted contour lines show 100% and 50%, respectively, of the available environmental space. (a)- *T. ambiguus*; (b)- *T. pelzelni*; (c)- *T. punctatus*; (d)- *T. stictocephalus*; (e)- *T. sticturus*; (f)- Correlation circle.

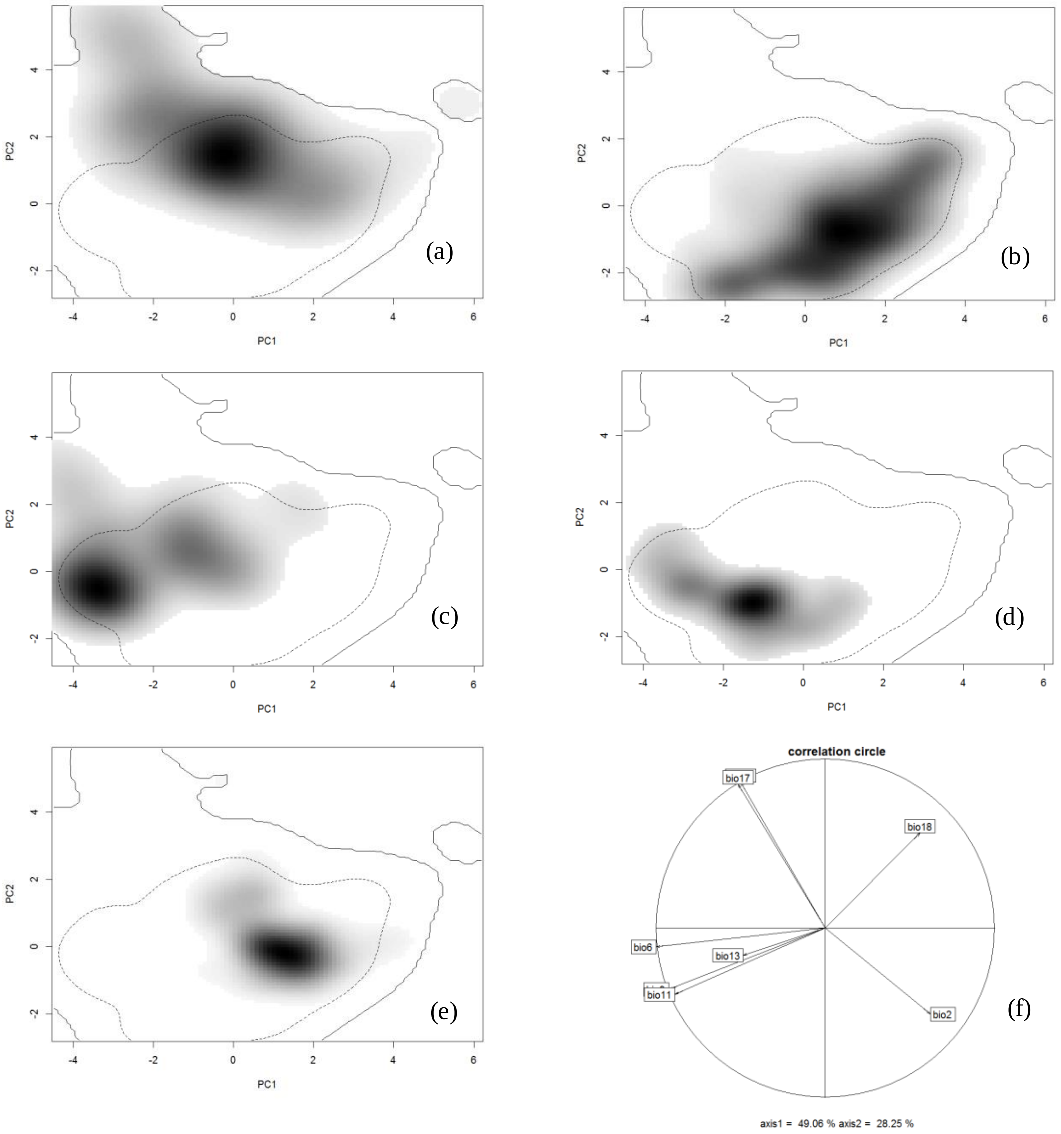

Table 1: Fragmentation of area between the Last Glacial Maximum (LGM), present and future from the potential distribution maps of the *Thamnophilus punctatus* complex based on the distribution models.

Species	Area of LGM (km^2)	Present Area (km^2)	Future Area (Km^2)	LGM/Present Variation (km^2)	Present/Future Variation (Km^2)	LGM/Present Fragmentation (% Variation)	Present/future Fragmentation (% Variation)
Thamnophilus ambiguus	598,341	288,215	1,247,199	-310,126	+958,984	51.83	332.73
Thamnophilus pelzelni	2,363,950	2,131,183	1,157,940	-232,767	-973,243	9.84	45.66
Thamnophilus punctatus	1,000,194	1,067,250	972,664	+67,056	-94,586	6.28	8.86
Thamnophilus stictocephalus	3,038,385	1,325,835	2,152,030	-1,988,382	+826,195	65.44	62.31
Thamnophilus sticturus	682,879	1,050,003	1,207,384	+367,124	+157,381	34.96	14.99

Table 2: Overlap values (SchoenerD), equivalence, niche similarity and genetic distance among the five species of the *Thamnophilus punctatus* complex. The niche overlap measures intersection levels between ranges of the environmental space occupied by the two populations or species; niche equivalence indicates whether niche overlap is constant by randomly relocating the occurrence of both populations between their two ranges; and niche similarity measures to what extent the niche of one population or species can predict the occurrence of the other. Genetic distance measures the degree of genetic divergence between one species and another.

Combination	Schoener D	Niche Equivalence	Niche Similarity	Genetic Distance
T. ambiguus Vs. *T. pelzelni*	0.131817	1	0.653465347	0.0379
T. ambiguus Vs. *T. punctatus*	0.224464	1	0.405940594	0.0698
T. ambiguus Vs. *T. stictocephalus*	0.012273	1	0.762376238	0.0651
T. ambiguus Vs. *T. sticturus*	0.149502	1	0.376237624	0.0430
T. pelzelni Vs. *T. punctatus*	0.142882	1	0.475247525	0.0568
T. pelzelni Vs. *T. stictocephalus*	0.247345	1	0.207920792	0.0594
T. pelzelni Vs. *T. sticturus*	0.333783	1	0.138613861	0.0232
T. punctatus Vs. *T. stictocephalus*	0.310135	1	0.128712871	0.0324
T. punctatus Vs. *T. sticturus*	0.090668	1	0.544554455	0.0585
T. stictocephalus Vs. *T. sticturus*	0.054553	1	0.534653465	0.0589

The effects of climate change on the distribution of South American antbirds (*Thamnophilus punctatus* complex) as affected by niche divergences and contact zone interactions between species.

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Table S1 Collection locality, voucher number, institutions of origin, and GenBank accession numbers for *Thamnophilus punctatus* species complex samples used in this study. Institution acronyms: Museu Paraense Emílio Goeldi (MPEG) and Louisiana Museum of Natural History (LSUMZ).

Taxon	**Institution**	**Voucher**	**Locality**	**GenBank**
Thamnophilus stictocephalus	MPEG	57616	BR, AM, Manicoré, Rodovia do Estanho, Fazenda Copeares	
Thamnophilus stictocephalus	MPEG	57617	BR, AM, Manicoré, Rodovia do Estanho, Fazenda Copeares	
Thamnophilus punctatus	MPEG	56530	BR, RR, Mun. Alto Alegre - Faz. Paraense	
Thamnophilus punctatus	MPEG	56355	BR, RR, Caracaraí, PARNA Viruá - Posto Aliança - Marg. E. Rio Branco	
Thamnophilus punctatus	MPEG	56531	BR, RR, Alto Alegre - Faz. Paraense	
Thamnophilus punctatus	MPEG	55711	BR, PA, Rio Xingu, Senador José Porfírio	
Thamnophilus punctatus	MPEG	61013	BR, PA, Monte Alegre, Parque Estadual Monte Alegre, Ilha Grande	
Thamnophilus stictocephalus	MPEG	61834	BR, PA, Portel, Flona do Caxiuanã	
Thamnophilus punctatus	MPEG	64678	BR, PA, Flota de Faro, ca 70 km NW de Faro	
Thamnophilus punctatus	MPEG	65136	BR, PA, Itaituba, Flona Amanã, Pista de Pouso Maranhão	
Thamnophilus punctatus	MPEG	65411	BR, PA, Alenquer, ESEC Grão-Pará	
Thamnophilus stictocephalus	MPEG	61833	BR, PA, Portel, Flona do Caxiuanã, Plot PPBIO	
Thamnophilus punctatus	MPEG	66658	BR, PA, Óbidos, ESEC Grão-Pará	
Thamnophilus pelzelni	MPEG	68035	BR, MA, São João dos Patos- Jatobá dos Noletos- Mancha Verde	
Thamnophilus pelzelni	MPEG	68044	BR, PI, José de Freitas- Eco Resort Nazareth	
Thamnophilus pelzelni	MPEG	68039	BR, PI, Piracuruca- Parque Nacional de Sete Cidades	
Thamnophilus pelzelni	MPEG	68032	BR, PI, Castelo do Piauí- Faz. Bonito	
Thamnophilus pelzelni	MPEG	68026	BR, PI, Guadalupe- Faz. Maharish- Cerrado dos Indianos	
Thamnophilus pelzelni	MPEG	68018	BR, PI, Uruçuí- Vale do Rio Pratinha	
Thamnophilus stictocephalus	MPEG	67142	BR, PA, Ourilandia do Norte, Serra da Onça	
Thamnophilus stictocephalus	MPEG	67141	BR, PA, Ourilandia do Norte, Serra da Onça	
Thamnophilus punctatus	MPEG	69942	BR, PA, Faro, Vila Maracanã, Rio Xingu	
Thamnophilus stictocephalus	MPEG	71075	BR, RO, Machadinho D'Oeste, margem esquerda Rio Jiparaná	
Thamnophilus pelzelni	MPEG	70725	BR, BA, Ilhéus, Ecoparque de UMA	
Thamnophilus pelzelni	MPEG	L_170	BR, MT, Fazenda Invernada, Chapada dos Guimarães	
Thamnophilus	MPEG	L_487	BR, MT, Fazenda Baía de Pedra, Cáceres	

sticturus

Taxon	Institution	Voucher	Locality	GenBank
Thamnophilus sticturus	MPEG	L_514	BR, MT, Fazenda Baía de Pedra, Cáceres	
Thamnophilus pelzelni	MPEG	L_540	BR, MT, Sítio Marimbondo, Chapada dos Guimarães	
Thamnophilus pelzelni	MPEG	L_552	BR, MT, Estrada para Água Fria, Chapada dos Guimarães	
Thamnophilus stictocephalus	MPEG	74151	BR, PA, Santarém, RESEX Tapajós/Arapiuns, Capixauã	
Thamnophilus stictocephalus	MPEG	74205	BR, PA, Santarém, RESEX Tapajós/Arapiuns, Capixauã	
Thamnophilus stictocephalus	MPEG	74206	BR, PA, Santarém, RESEX Tapajós/Arapiuns, Capixauã	
Thamnophilus punctatus	LSUMZ	32638	PE, Cajamarca Department, Las Juntas, junction of Rios Tabaconas and Chinchipe	
Thamnophilus punctatus	LSUMZ	32916	PE, Cajamarca Department, Las Juntas, junction of Rios Tabaconas and Chinchipe	
Thamnophilus punctatus	LSUMZ	48289	Guyana	
Thamnophilus punctatus	LSUMZ	44235	PE, San MartÌn Department	
Thamnophilus punctatus	LSUMZ	44566	PE, San MartÌn Department	
Thamnophilus punctatus	LSUMZ	44567	PE, San MartÌn Department	
Thamnophilus stictocephalus	LSUMZ	14412	BO, Santa Cruz Department	
Thamnophilus stictocephalus	LSUMZ	14416	BO, Santa Cruz Department	
Thamnophilus punctatus	LSUMZ	65765	SR, Sipaliwini District	