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First Brazilian record of *Chiroxiphia napensis* (Aves: Pipridae) and revision of the distribution of the *C. pareola* complex in the Amazon

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ABSTRACT

We present the first Brazilian record of *Chiroxiphia napensis*, documented by an adult male specimen collected on the right bank of the upper Japurá River. We also compiled verifiable records of all Amazonian taxa in the *C. pareola* complex to update their range maps. New records extended considerably the ranges of all taxa. By assuming river-delimited distributions to infer areas from point records, we generated a predictive distributional map that suggests testable hypotheses about occurrence in unstudied areas and that pinpoints topics for future research. We interpret *C. napensis* as endemic to the Amazon-Japurá interfluve, its range extending narrowly beyond this area in the foothills of the Andes. We suggest that the unusual distribution pattern of *C. regina* could be the result of river avulsion. We also detected a region of possible contact between *C. regina* and *C. pareola*, and a large area in northern Amazonia from which the complex appears to be absent.

KEYWORDS: Amazonas, blue-backed manakin, endemism, predictive mapping, river barriers

Primeiro registro brasileiro de *Chiroxiphia napensis* (Aves: Pipridae) e revisão da distribuição do complexo *C. pareola* na Amazônia

RESUMO

Apresentamos o primeiro registro brasileiro de *Chiroxiphia napensis*, documentado por um exemplar macho adulto coletado na margem direita do alto Rio Japurá. Também compilamos registros verificáveis de todos os táxons amazônicos do complexo *C. pareola* para atualizar o mapa de suas distribuições. Novos registros estenderam consideravelmente as distribuições de todos os táxons. Assumindo a premissa de delimitação geográfica por rios para propor áreas a partir de registros pontuais, produzimos um mapa preditivo de distribuições que sugere hipóteses testáveis sobre ocorrência em áreas ainda sem estudos e que aponta tópicos para futuras pesquisas. Interpretamos *C. napensis* como espécie endêmica do interflúvio Japurá-Solimões, sua distribuição estendendo estreitamente além dessa área no sopé dos Andes. Sugerimos que o padrão incomum de distribuição de *C. regina* seja resultado de avulsão fluvial. Detectamos uma zona de possível contato entre *C. regina* e *C. pareola*, e também uma área grande no norte da Amazônia onde o complexo parece não ocorrer.

PALAVRAS-CHAVE: Amazonas, endemismo, mapeamento preditivo, rios como barreira, tangará-príncipe

INTRODUCTION

Although range maps are publicly available for every known bird species (BirdLife International 2023), accurate mapping of Amazonian birds still suffers from large gaps in field documentation and from rapidly changing taxonomy (Lees et al. 2020). Mapping subspecies, in particular, represents an important challenge, in part because subspecies can be hard to identify and because they are inherently less interesting to most users of range maps, for whom “species” is usually the relevant unit (Rising 2007). Thus, Amazonian bird subspecies are rarely mapped carefully (but see Rego [2022] for what should soon represent an immense improvement).

There is also a recent trend of raising subspecies to species status based on new information, especially behavior, vocalizations, and molecular genetics (e.g., Isler and Whitney 2011; Carneiro et al. 2018; Azuaje-Rodríguez et al. 2020). So, taxonomic revisions regularly result in treating as full species former subspecies whose individual ranges have not been carefully documented. This creates an unfortunate trade-off between improved taxonomic treatment and reduced distributional accuracy.

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Another challenge when mapping the distribution of any species is deciding how to extrapolate from known point records to an area of presumed occurrence (Graham and Hijmans 2006). Just because there may be large unsampled expanses between detection points in the relatively understudied Amazon, for example, that does not mean individual records should be treated as truly isolated and so representative of disjunct distributions. How much to "fill in" between documented points and how far to "fill out" away from these points are important decisions in the mapping process. Thus, if a goal of range maps is to predict reasonably where the species should be expected to occur (Gaston and Fuller 2009; Merow et al. 2017), it is important to make explicit the assumptions used for extrapolation from points to areas (Graham and Hijmans 2006). In the Amazon, delimitation of bird species ranges by rivers is so common (Haffer 1974, 1978, 1997a; Naka and Brumfield 2018) that assuming a species occurs continuously up to the nearest large river may be a reasonable supposition.

The blue-backed manakin, *Chiroxiphia pareola* (Linnaeus 1766), is a complex of four subspecies (Dickinson and Christidis 2014; Clements et al. 2022; Gill et al. 2023; Remsen et al. 2023), recently the subject of detailed molecular phylogenetic analyses (Silva et al. 2018; Nascimento et al. 2021). Those studies offer molecular support for recognizing three diagnosable phenotypes, which Silva et al. (2018) recommend treating as distinct species: *C. pareola*, *C. regina* Sclater 1856, and *C. napensis* Miller 1908. This full-species taxonomic treatment was adopted formally in Brazil (Pacheco et al. 2021) and is followed by us here. The phenotypic characters, however, used to distinguish species in the complex are found only in adult males; females and immature males (hereafter "green individuals") appear to be indistinguishable (Snow 2020). Because these taxa can be hard to identify (see Material and Methods) and because they have most often been treated as subspecies (Hellmayr 1910, 1929), a precise notion of their geographic distributions is still lacking. Until recently, only Haffer (1987) had mapped individually the Amazonian forms of the complex.

During a recent, in-depth survey of all avian taxa known from the Brazilian state of Amazonas, one of us (AMG) identified a museum specimen of *C. (pareola) napensis* that considerably extends its known range. Here, we present the details of that specimen, which appears to be the first record of the taxon for Brazil. We then used this and other recent records of all members of the complex to revise the distribution maps of all three taxa in the Amazon. We compare our revised map to the previously available one (Haffer 1987), discuss the pros and cons of the river-delimitation assumption we applied (see Material and Methods), and suggest locations for future research based on uncertainties revealed by mapping.

MATERIAL AND METHODS

We identified most specimens and photographs of adult male members of the *Chiroxiphia pareola* complex by a combination of crown and back color (Miller 1908). Yellow-crowned *C. regina* differs conspicuously from the other two, which have red crowns (Figure 1). *Chiroxiphia napensis* and *C. pareola*, in turn, differ basically in the shade of blue of their backs (Figure 1). This is subtle and, without direct comparison of specimens, we suspect visual identification may not always be possible (see Discussion).

To update the previously proposed distributions by including more recent information, we plotted records identified to subspecies from the Global Biodiversity

Figure 1. Dorsal view of adult male specimens of Amazonian *Chiroxiphia* species (from left to right): *C. pareola* (INPA 7106), *C. napensis* (INPA 6572), and *C. regina* (INPA 4263). Note the slightly darker blue back of *C. napensis*, compared to *C. pareola*, considered a diagnostic feature (Miller 1908).

Information Facility (GBIF; gbif.org) and specimens from the collection at our home institution, the Instituto Nacional de Pesquisas da Amazônia (INPA), where expeditions to remote Amazonian localities have been frequent over the last two decades. In addition to these, we searched recent literature and perused openly accessible online platforms (eBird, ebird.org; WikiAves, www.wikiaves.com.br) for identifiable photographs that extend or clarify range limits. We excluded records based on subspecies designations attributed to green individuals, which we believe to be unidentifiable by appearance, and to cases of either red-crowned taxon (*C. pareola* or *C. napensis*) purportedly encountered within or near the established range (as presented by Haffer 1987) of the other, assuming these to be either errors of identification or use of outdated taxonomy.

To infer species distributions from locality point data we assumed that distributional limits coincide with rivers (but not that every river must necessarily mark the limit of a species' distribution) and that multiple members of the complex are not sympatric unless identifiable point records show them to be. Thus, we inferred that an interfluve is fully occupied by a species, even if only one occurrence is known within it, as long as no other taxon in the complex is also known to occur there. Interfluves with no known records were assumed not to contain any member of the complex. The only exceptions to this approach were in headwaters or upper reaches of rivers, for example, at the base of the Andes, where it is also common for distributions to extend across these much narrower rivers (Haffer 1978, 1992, 1997a; Weir et al. 2015). Thus, at the periphery of the Amazon we relaxed our river-delimited rule where locality data strongly suggested localized range continuations across rivers (see Discussion).

RESULTS

Among the specimens of the *C. pareola* complex in the INPA collection, there are five from the upper Japurá River near the Colombian border with Brazil, a region from which no member of the complex had been previously documented. Three of these (INPA 6573, 6574, 6575) are from the left (north) bank of that river, and two (INPA 6572, 6576) are from the right (south) bank. Unfortunately, four are green individuals. The one adult male identifiable to species is INPA specimen number 6572 (Figure 1, center)—locality "colocação Arapanã", right bank Rio Japurá, *ca*. 65 km southeast of Vila Bittencourt, Amazonas, Brazil (1º51'S, 69º02'W); collected in mistnet on 10 September 2014 by Marco Aurélio-Silva; prepared by Cristiane Dreves and Gisiane R. Lima; tissue sample A-18271.

This specimen is clearly identifiable as *C. napensis* by its bright red crown, eliminating *C. regina*, and by the somewhat darker blue back relative to *C. pareola* (Figure 1). The distinction between a scarlet-red crown described for *C. napensis* versus crimson in *C. pareola* (Miller 1908; Hellmayr 1910, 1929) was not apparent to us in the specimens examined (see Discussion). This and numerous other records of *C. napensis* (blue symbols in Figure 2) found in northeastern Amazonian Peru and southeastern Colombia extended the distribution of the species considerably eastward of what was previously known (dashed blue outline in Figure 2).

Similarly, the distributions of *C. regina* and *C. pareola* also proved to be more extensive than previously known. Numerous records extended the distribution of *C. pareola* westward at the northern and southern extremes of the Amazon and also eastward to the limits of southeastern Amazonia (Figure 2). Likewise, recent records extended the distribution of *C. regina* (shown in yellow in Figure 2) to the east, west, and south, bringing it into close proximity to the other species in several areas (see Discussion). On the other hand, we found no evidence of the occurrence of *C. regina* anywhere between the Amazon and Japurá rivers, where *C. napensis* was found.

DISCUSSION

Based on our data, the specimen of *C. napensis* from the right bank of the upper Japurá River documents for the first time the presence of this taxon in Brazil. It also represents the easternmost record to date, some 250 km northeast of the nearest record in extreme southeastern Colombia (Leon 2020). Because *C. napensis* had not been considered part of the Brazilian avifauna (Pacheco et al. 2021), it has no common name in Portuguese. We propose "*tangará-do-oeste*" in reference to its distribution, the westernmost of all Brazilian *Chiroxiphia* (generically known in Brazil as "*tangarás*"). We also note that Hellmayr (1929), despite treating this taxon as a subspecies, referred to it with the English common name of "Napo manakin".

Although genetic analyses leave no doubt about the distinctiveness of *C. napensis* and *C. pareola* (Silva et al. 2018; Nascimento et al. 2021), we found the plumage features that distinguish adult males of each to be subtle at best. Indeed, the first red-crowned specimens found in Ecuador were treated for decades as *C. pareola* (Sclater 1888; Allen 1889) before Miller (1908) described *C. napensis*. As we reported above, the shade of red in the crown may not be distinguishable and even the blue of the back appears to require good light and close comparison of specimens in the hand to distinguish (Figure 1). The diagnosability of these plumage traits should ideally be evaluated in larger series of genetically identified specimens.

However, even recognizing the more extensive distributions revealed here, *C. napensis* and *C. pareola* continue to be separated by well over 1000 kilometers between their nearest points of occurrence. Thus, in the absence of genetic analyses (which should be completely diagnostic), we recommend using geographic criteria for identifying red-crowned members of this complex. Occasional specimens in the databases we

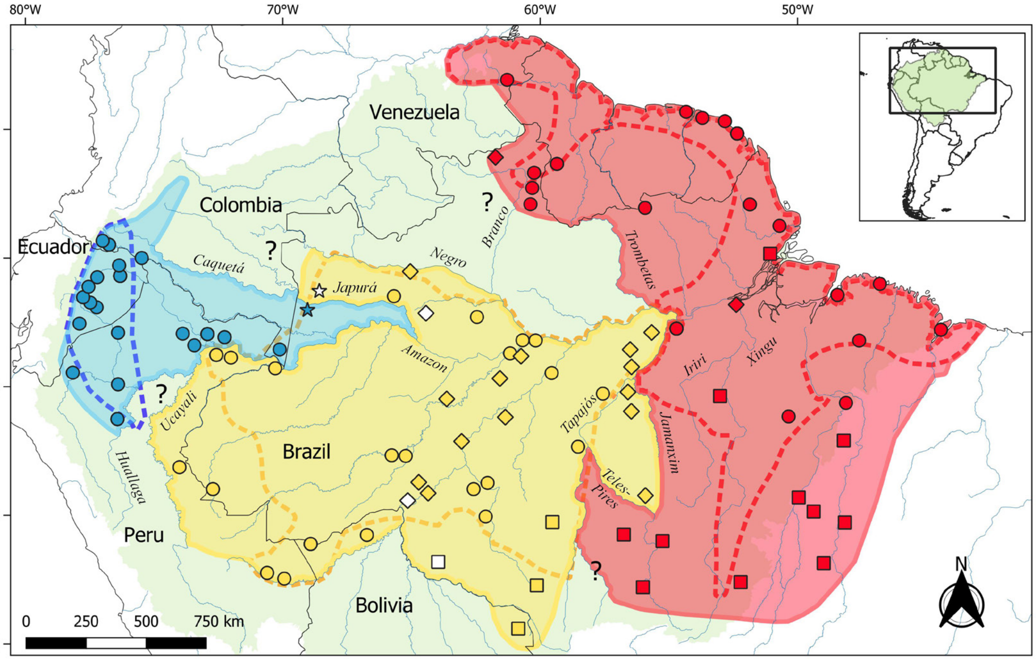

Figure 2. Distributions of lowland species of the genus *Chiroxiphia* in the Amazon (light green): *C. pareola* (red), *C. regina* (yellow), *C. napensis* (blue). Point localities are records identified to subspecies from GBIF (circles), the INPA Bird Collection (diamonds), and citizen science platforms and selected literature (squares); they do not represent a complete review of all known specimens or records (see Material and Methods). Stars indicate localities of those INPA specimens recently collected on opposite banks of the upper Japurá River (see Results), including the first Brazilian specimen of *C. napensis* (blue star). White-filled symbols indicate localities of unidentified *Chiroxiphia* specimens (females or immature males) that, when identified, could help clarify range limits. Colored areas are our extrapolations based on these points (see Material and Methods), except parts of Colombian and Venezuelan ranges, from Hilty and Brown (1986) and Hilty (2003), respectively. Dashed outlines delimit the distribution of each taxon as presented by Haffer (1987), based on many fewer specimen records available at the time. Question marks indicate areas where further research is especially necessary to confirm absence or co-occurrence. Country boundaries are represented by thin black lines and major rivers by thin blue lines. Names in italics indicate those rivers mentioned in the text.

examined, apparently identified as the "wrong" taxon for the region (and so excluded from our analyses, see Material and Methods), should be reevaluated with molecular data.

Distribution patterns

Perhaps not surprisingly, adding some 35 years of observations since Haffer's (1987) map led to the recognition of larger ranges for all taxa and to a clearer picture of how they relate to one another spatially. We found no evidence of sympatry among the members of the complex, but did find that they approach one another closely in many parts of their ranges. The lack of obvious barriers between *C. regina* and *C. pareola* in southern Amazonia (Figure 2) suggests a possible contact zone between them in that region (see below). On the other hand, records of *C. napensis* and *C. regina* can be found near one another, but only on opposite banks of the upper Amazon River in eastern Peru and Colombia and also on opposite sides of the Japurá River in Brazil. This strongly suggests that these rivers delimit parts of the ranges of these species.

We interpret these records as supporting a distribution for *C. napensis* primarily within the Amazon-Japurá interfluve (Figure 2). Although the Japurá and its largest Colombian tributary, the Caquetá, are not usually listed among the major rivers delimiting avian areas of endemism (Haffer 1978; Cracraft 1985; but see Borges and Silva 2012), a number of other taxa appear to be limited by them or to replace one another on their opposite banks. Examples include *Mymoborus myotherinus* (Spix 1825) subspp., *Rhegmatorhina* Ridgway 1888 spp., and *Terenotriccus erythrurus* (Cabanis 1847) subspp. (Gomes 2023). This suggests not only that *C. napensis* is more widespread in southern Amazonian Colombia than current records indicate, but also that *C. regina* should be expected to occur in eastern Colombia.

Another regularly observed pattern reflected here is the relaxation of river limits in the narrower, upper reaches of these same rivers (Haffer 1978, 1992, 1997a; Weir et al. 2015). It is common for species otherwise limited to northwestern or southwestern Amazonian interfluves (e.g., *Pteroglossus pluricinctus* Gould 1835, *Cercomacroides serva* [Sclater 1858], *Hypocnemis peruviana* Taczanowski 1884) to extend narrowly further north or south along the base of the Andes in Peru and Colombia, much as we observed in *C. napensis* (see maps in BirdLife International 2023). Similar situations seem to occur with *C. pareola* in the upper Rio Branco (Naka 2011) and on tributaries of the upper Tapajós (see below).

The limitation of *C. regina* in northern Amazonia to the Japurá-Negro interfluve, on the other hand, creates a peculiar pattern not previously described. As cited above, the Japurá is a known, albeit perhaps under-heralded, distributional barrier in birds. However, limitation to this interfluve in the north combined with a widespread distribution in southern Amazonia, i.e., a "leapfrog" pattern (Remsen 1984) of spatial alternation of *C. regina* with *C. napensis*, is unusual. One conceivable explanation for this pattern is that *C. regina* colonized the north bank of the Amazon River only relatively recently and only between the Negro and Japurá rivers. River dynamics, in which a portion of *terra firme* once occurring on one side of a river is effectively transferred to the other side when a stretch of the river changes course (avulsion), have been documented near Coari on the middle Amazon (Ruokolainen et al. 2019) and could be responsible for passively dispersing a population of *C. regina* across the river in one particular area. This phenomenon has been mentioned before in the context of Amazonian bird distributions (Haffer 1997b, Haffer 2008) and can now be detected using molecular population genetic techniques (Musher et al. 2022).

Although Haffer (1987) did not state specifically how he extrapolated from points to areas, it is fairly clear that he did not assume river delimitations unless specimens actually were found near a major river (such as *C. regina* and *C. pareola* on opposite banks of the lower Tapajós River; see dashed outlines in Figure 2). Thus, his maps may be seen as conservative and seemingly not based on any particular rules or premises other than the expectation that a given taxon have a continuous distribution between known points and that inferred distributions should not be extended far beyond documented localities.

Because we used a specific premise of river-delimitation to infer distributions, we extrapolated the range of *C. pareola* to all of northeastern Amazonia east of the Trombetas River, but left the entire area between the Negro and Trombetas rivers blank, because no member of the complex has yet been found anywhere there. Similarly, we extended the distribution of *C. pareola* south and west throughout part of the Tapajós-Xingu interfluve, including across the upper Teles-Pires River, but north of this only as far west as the right bank of the Jamanxim River, because *C. regina* was recorded in the Jamanxim - Teles-Pires interfluve. Further south still it becomes increasingly difficult to identify barriers between the two species, and future research will be necessary to determine if indeed there are any barriers, or if the species come into direct contact.

All range maps involve subjective decisions about where to predict presence. By assuming the prevalence of rivers as range delimiters, we hope to challenge the reader to test these assumptions with future investigations. Nevertheless, our approach has also been subjective. What rivers do we consider large enough to limit ranges? How far up the headwaters or how narrow must a river be to stop being a barrier? How important as barriers are other landscape features, such as phytophysiognomy, i.e., bird habitat, or topography? How detailed should a map at this scale be? See Vale et al. (2017) for an example of the relevance of scale and habitat.

Future directions

In our map (Figure 2), we indicate with white symbols the localities where sequencing DNA of existing specimens is necessary for identification purposes, and we mark with question marks regions where further field surveys should be most helpful in clarifying *Chiroxiphia* distribution patterns. Sampling within the predicted occurrence areas will allow testing the assumptions used for mapping. Detection of any errors in our predictions, such as the possible existence of contact or hybrid zones, should help identify the processes underlying these species' distributions.

Although this study elucidates only a single case, we believe it is representative of many more as yet to gain attention. Just as Hellmayr (1910, 1929) began the century-long convention of treating members of the *C. pareola* complex as subspecies, without any explicit justification, likewise many dozens of other species were inexplicably "lumped" during the last century (e.g., Amadon et al. 1979; see Pratt 2010). Whether by switching the burden of proof to the lumpers, as very reasonably proposed by Gill (2014), or by invoking ever-more detailed molecular studies, the trend of raising current bird subspecies to species is likely to continue in the Amazon. With that will come increasing awareness of the inadequacy of current distributional information. Using the same assumptions we applied here, we predict the presence in Brazil of several more taxa as yet undocumented, such as *Brachygalba lugubris caquetae* Chapman 1917*, Herpsilochmus dugandi* Meyer de Schauensee 1945, *Grallaria dignissima* Sclater and Salvin 1880*, Pseudopipra pipra discolor* (Zimmer 1936), and *Cyphorhinus (arada) salvini* Sharpe 1882.

CONCLUSIONS

We conclude that *Chiroxiphia napensis* occurs in Brazil, probably throughout the area between the Japurá and upper Amazon rivers in *terra firme* forest habitat. The species was probably overlooked because it is difficult to identify, occurs in a very under-studied part of the Amazon, and was treated as a subspecies for over a century. Based on a premise of primarily river-delimited distributions, we predict that *C. napensis* should also be considerably more widespread in the Colombian Amazon than the few current records might suggest. We also present new information on the distributions of the other Amazonian species within the same complex, *C. pareola* and *C. regina*, expanding considerably their known ranges. Our proposed distribution map provides clear and testable hypotheses of species presence and absence, an advance over previous representations, and a stimulus for further investigation.

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