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BRIEF COMMUNICATION

Fine-scale endemism of Amazonian birds in a threatened landscape

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Abstract The region recognized as the Rondônia area of endemism is one of the most threatened in the Brazilian Amazon. In addition to rampant deforestation that took place during the 1980s and 1990s, it is now the locus of infrastructure development and economic expansion. However, the patterns of species distribution and diversity in this region are much more complex than previously recognized. Patterns of distribution of birds, primates, and butterflies strongly suggest that the Rondônia area of endemism is not biogeographically homogenous. On opposite banks of the Madeira tributaries, in particular the Aripuanã and Jiparaná rivers, there are genetically, morphologically, and vocally distinct bird populations with restricted distributions and geographic substitution. These areas are relatively small and already highly threatened by deforestation and economic development. Up to 70 % of the Jiparaná basin has been deprived of its original forest cover. Thus, their unique populations deserve to be recognized as conservation priorities and urgently included in conservation planning blueprints. Many restricted taxa, including many yet to be described, may already be highly endangered or locally extinct. Conservation planning in the Brazilian Amazon directed at specifying areas to be protected has focused on the larger proposed areas of endemism. If fine-scale endemism in threatened areas does exist in other Amazonian regions, then conservation policies that do not recognize these patterns will not adequately protect regional diversity.

Keywords Amazonia · Areas of endemism · Conservation · Deforestation · Cryptic endemism · Phylogeography

Introduction

The Neotropical region supports the world's richest avifauna, being responsible for nearly a third of all living species (Ridgely and Tudor 1989, 1994). As in other regions,

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biodiversity is not evenly distributed throughout the Neotropics. For instance, Cracraft (1985) proposed 33 areas of avian endemism for South America, identifying a significant biogeographical substitution pattern for birds across the region. Within the Neotropics, Amazonia has the highest avian diversity (da Silva et al. 2005), with the majority of species being endemic (Stotz et al. 1996). The distribution of species within Amazonia is also highly non-random. Lowland Amazonia is a mosaic of areas of endemism that match the major interfluvia (Fig. 1). Different species or subspecies of birds and other taxa, such as primates, occur on opposite banks of large rivers—a phenomenon which has been uniquely described for Amazonia. These areas of endemism, in turn, have become the units of planning for biodiversity conservation action in Brazil (Dinerstein et al. 1995; da Silva et al. 2005). Therefore, the validity of the proposed areas of endemism will underpin the effectiveness of conservation planning in the region, in particular the placement of protected areas.

The areas of endemism recognized today were based on studies of the geographic distribution of morphologically distinct taxa, without considering their evolutionary relationship (Aleixo and Rossetti 2007). Moreover, the proposed areas of endemism were defined at a time when species distribution data was much more scant than is the case today, in addition to being highly heterogeneous. Recent molecular data are challenging the notion that previously proposed areas of endemism reflect common historical relationships among co-distributed species (Fernandes et al. 2013). Other studies have shown that more restricted endemism seems to exist within some of the larger areas of endemism (Cohn-Haft et al. 2007; Naka 2011; Borges and da Silva 2012). Here, I review the patterns of diversification in one of the most threatened region of Amazonia, the proposed area of endemism of Rondônia, located between the Madeira and Tapajós rivers (Fig. 1).

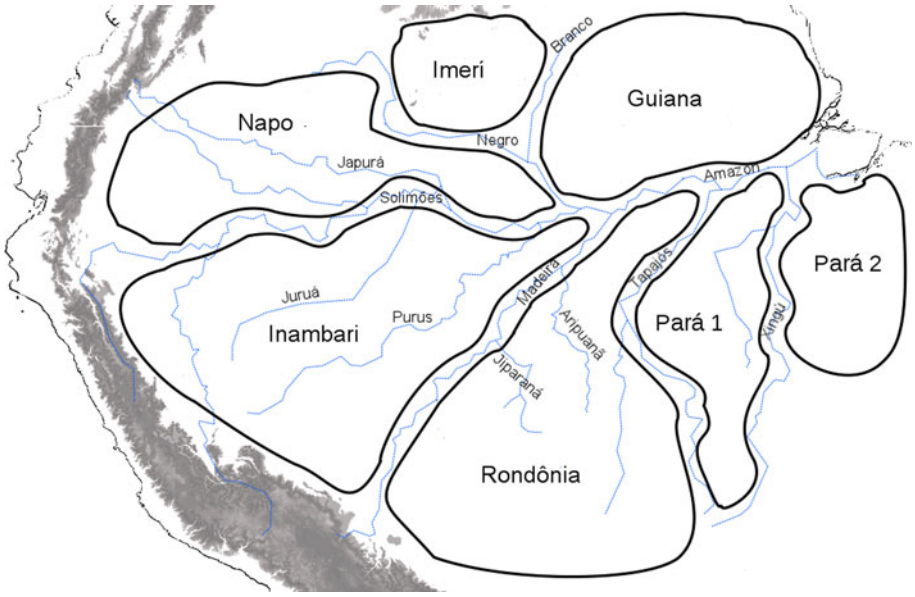

Fig. 1 Generalized localizations of Amazonian areas of avian endemism based on Cracraft (1985) and da Silva et al. (2005). The major rivers are shown by *dotted blue lines* and their names are indicated. (Color figure online)

Internal biogeographical incongruence of the area between the rivers Madeira and Tapajós

The Madeira and Tapajós are amongst the largest southern tributaries of the Amazon River. Studies focusing on birds and primates that occur between these two rivers have revealed a complex biogeographic pattern. The tributaries of the Madeira River in the Rondônia area of endemism (Fig. 1) appear to also constitute a barrier to the distribution of birds (Hellmayr 1910), primates (van Roosmalen et al. 1998, 2000), and such invertebrates as butterflies (Hall and Harvey 2002).

Hellmayr (1910) was the first to suggest that the Madeira–Tapajós (M–T) interfluvium has a distinct avifauna with some endemic taxa. He also highlighted that differences in species composition apparently exist between the middle (Aripuanã basin) and upper course of the Madeira (Jiparaná basin). Willis (1969) corroborated the complexity of bird distribution patterns in this area, including the parapatric occurrence of *Rhegmatorhina berlepschi* and *R. hoffmannsi* (Thamnophilidae) within the M–T interfluvium. On this basis, Willis (1969) suggested that the Tapajós River has occasionally changed course, resulting in the isolation of previously continuous populations, followed by evolutionary differentiation. Another similar case of geographic replacement of species within the M–T area was reported by Haffer (1997) while documenting the occurrence of two species of barbets in this interfluvium: *Capito brunneipectus* inhabiting the northern portion, while *Capito dayi* is found to the south. van Roosmalen et al. (1998, 2000) described geographic substitution of primate species of the genera *Mico* and *Calicebus* on opposite banks of rivers within this interfluvium, while also describing a new species of marmoset (*Mico humilis*) that only occurs on the western bank of the Aripuanã River, which is a right bank tributary to the Madeira River. This study highlighted the importance of small rivers in delimiting primate distributions and gave impetus to field work by Cohn-Haft et al. (2007) focusing on birds. They found numerous cases of species with restricted distributions in this region, several opposite river bank replacements, and vocal variation in birds delimited by small rivers. The pattern was so clear that they referred to this phenomenon as "mini-interfluvia". For example, *Picumnus aurifrons* (Picidae) shows distinct plumage coloration on opposite banks of the Aripuanã River. *Hypocnemis cantator* species complex (Thamnophilidae) (Isler et al. 2007), in turn, has vocally and morphologically distinct populations with restricted ranges, delimited by the Madeira, and two of its right tributaries, the Jiparaná and Aripuanã rivers. Five new bird species restricted to certain parts of the M–T interfluvium were recently described: *Hypocnemis rondoni* (Thamnophilidae), *Herpsilochmus stotzi* (Thamnophilidae), *Epinecrophylla dentei* (Thamnophilidae), *Zimmerius chicomendesi* (Tyrannidae) (Jiparaná-Aripuanã mini-interfluvium); and *Tolmonyias sucunduri* (Tyrannidae) (Sucunduri-Tapajós mini-interfluvium) (Whitney et al. 2013a, b, c, d, e).

Sardelli (2005) found genetic differentiation (cytochrome b) among morphologically indistinguishable populations of *Hemitriccus minor* (Tyrannidae) apparently delimited by the Jiparaná and Aripuanã rivers. This study raised the possibility of the existence of cryptic endemism in mini-interfluvia, which so far has not been considered in widespread conservation strategies. Subsequent and more detailed studies using deep sampling of three Amazonian understory birds (*Glyphorynchus spirurus*, *Hylophylax naevius*, *Myrmeciza hemimelaena*; Fernandes 2012; Fernandes et al. 2012, 2013) found genetic differentiation among populations within Rondônia and in other proposed areas of endemism, such as Napo and Inambari. *Glyphorynchus spirurus*, a small woodcreeper of the forest understory, has a very complex biogeographic pattern, with deep molecular divergence but no clear morphological variation between lineages from the M–T interfluvium, thereby confirming

the existence of cryptic endemism associated to the mini-interfluvia occurring between the Madeira and Tapajós rivers. Specimens of *H. naevius* and *M. hemimelaena*, a pair of two small understory antbirds, deposited at the Instituto Nacional de Pesquisas da Amazonia (INPA), Museu Paraense Emílio Goedi (MPEG), and the ornithological collection of the University of São Paulo (MZUSP) are suggestive of new morphological forms. Populations of the new form of *H. naevius* are delimited by the Madeira and the Jiparaná rivers (Fernandes 2012), while the new form of *M. hemimelaena* seems to be endemic of the mini-interfluvium of the Aripuanã-Jiparaná rivers (Fernandes et al. 2012). Genetic differentiation of mitochondrial genes corroborated the geographic distribution of these differentiated morphological forms (Fernandes 2012). Similar geographic patterns, with different races being separated by small Amazonian rivers in the Rondônia region, have also been found for riodinid butterflies (*Charis cleonus* species complex, Hall and Harvey 2002). The distribution of *C. humaita* and *C. maues*, matches that of *Mico* and *Calicebus* species and the birds mentioned above, whose small ranges can be attributed primarily to geographical isolation promoted by several smaller tributaries (Hall and Harvey 2002).

Collectively, these results highlight important issues. First and foremost, they strongly challenge the proposal that the area of endemism of Rondônia delineates a biogeographically homogenous region. Furthermore, similar hydrological and geomorphological dynamics of the Rondônia area prevail throughout other areas of the Amazon basin, suggesting that fine-scale endemism developed in response to "mini-interfluvia" might exist in other Amazonian regions (see also Naka 2011; Borges and da Silva 2012 for fine-scale endemism in the Napo region).

Historical biogeography and cryptic diversification in the Rondônia area

It is thus increasingly clear that many of the proposed areas of endemism in Amazonia are often composed of non-monophyletic populations (Aleixo and Rossetti 2007). For instance, the diversification patterns described in the M–T interfluvium reveal non-monophyletic populations and incongruences suggesting a complex history (Sardelli 2005; Fernandes et al. 2012, 2013; Fernandes 2012; Ferreira 2013; Sousa-Neves et al. 2013). *H. naevius* (Thamnophilidae), *G. spirurus* (Furnariidae), *Malacoptila rufa* (Bucconidae) *and Xiphorhynchus ocellatus* (Dendrocolaptidae) show non-monophyletic populations inhabiting the proposed area of endemism of Rondônia (Fig. 3, see also Ferreira 2013; Sousa-Neves et al. 2013). Each of these species has a unique area cladogram between the M–T interfluvium (Rondônia region).

The first split in *H. minor* corresponds to the course of the lower Jiparaná River, followed by the division of the current course of the Aripuanã River (Sardelli 2005). On the other hand, for *G. spirurus* the first split corresponds to the course of the Aripuanã and divides Rondônia 1 and 2 from Rondônia 3 and 4 as show in Fig. 3. The topology of *H. naevius* phylogeny shows a surprising pattern of diversification between the Madeira and Tapajós rivers. The molecular phylogeny of *H. naevius* indicates that the Jiparaná River (Fig. 1) has greater importance as a geographical barrier than the larger Madeira river itself. The division which corresponds to the course of the lower Jiparaná River has a more basal position in the phylogeny than the split across the mid-course of the Madeira (Fig. 2). A similar pattern was found in *Malacoptila rufa* (Ferreira 2013) where the division corresponding to the Aripuanã River is older than the division corresponding to the course of the Madeira. There are at least two possible explanations for this phenomenon. The documentation of two separate active large mega-fans from the Late Pleistocene,

involving each the Jiparaná and the Aripuanã drainages (Latrubesse 2002) would suggest much wider and complex paleo-drainages in this interfluvium than those found today, thus possibly explaining the complex diversification patterns in this region. The second related explanation was first addressed by Willis (1969) who suggested that the complex pattern of geographic distribution of *Rhegmatorhina* spp. (an ant-following antbird) in the M–T interfluvium could be attributed to changes in the course of the Tapajós River. Tectonically mediated mega-drainage capture was shown for the Rio Negro (Almeida-Filho and Miranda 2007). This may be applied to other regions in Amazonia as in the Rondônia area of endemism. The Jiparaná or Aripuanã may once have captured a significant part of the Madeira or even the neighboring Tapajós drainages, or both, but later became mere tributaries, following the major continental-wide drainage reorganization of the Amazon basin during the Late Pliocene (see also Fernandes et al. 2012, 2013). This can be further corroborated by the pattern of *G. spirurus* in the upper Tapajós basin where the population structure seems to be unrelated with rivers or any other geographic barrier (Fig. 2, see also Fernandes et al. 2013). The same pattern is described for Barbets (*Capito bruneipectus* and *C. dayi*, Haffer 1997). One could speculate that shifts in the course of the Tapajós River may once have caused allopatry in birds.

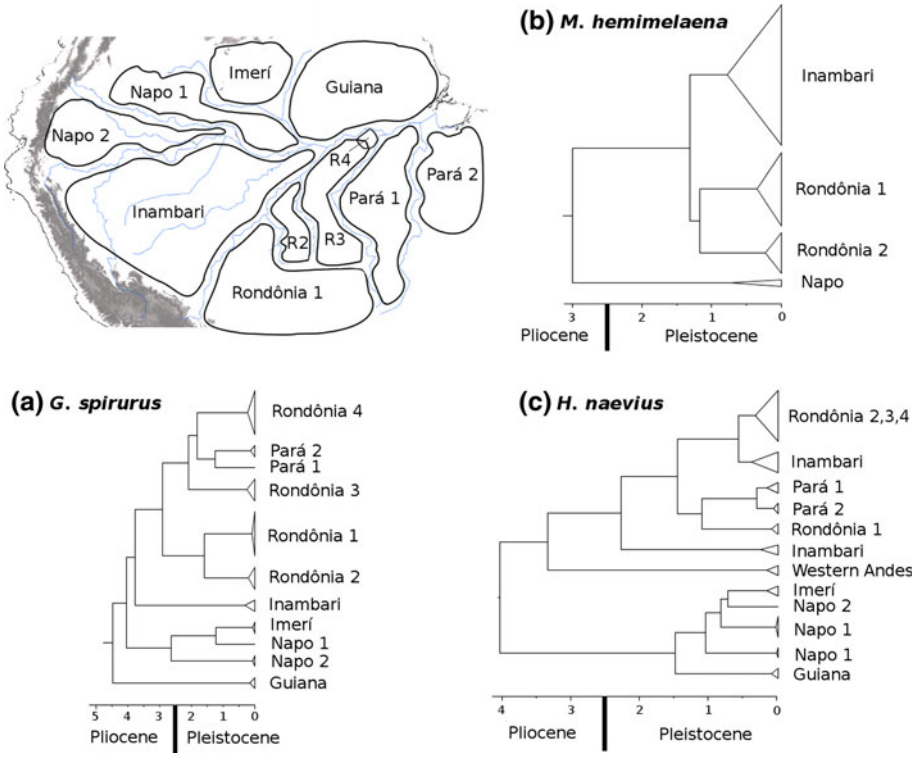

Fig. 2 Area cladograms based on molecular dating analyses (modified from Fernandes et al. 2012, 2013; Fernandes 2012). Map depicts major divisions of Amazonia following Cracraft (1985). Note the subdivisons of the Rondônia region delimited by the Jiparaná (J) and Aripuanã (A) rivers. R2 = Rondônia 2, R3 = Rondônia 3, R4 = Rondônia 4

These differences in the patterns of diversification found in the area of endemism of Rondônia reflects the complexity of the history of the Amazon Basin which were revealed by molecular analyses. Knowing the evolutionary relationships among lineages allows one to predict potential regions where new species could have been originated. In addition, cryptic endemism can be revealed by investigating relationships among taxa using molecular data. For example, only half of the 16 lineages of *G. spirurus* described by Fernandes et al. (2013) are morphologically distinguishable, indicating a very high degree of cryptic diversity and only few of these are monophyletic. Four of these lineages inhabit the M–T interfluvium and are similar in morphology, replacing each other on opposite banks of the Jiparaná and Aripuanã rivers indicating fine-scale endemism.

As first noticed by Capparella (1988, 1991) the high degree of ancient structure among bird populations showing little phenotypic differentiation appears to be a common and predominantly Amazonian pattern. High degree of genetic divergence among populations of Amazonian birds in relative absence of morphological differentiation has been reported in several studies conducted in lowland Amazonia (Antonelli et al. 2010). This could be due to the high incidence of species complexes in this region. These complexes commonly feature absence or only slight variation in morphological and behavioral characters, masking the occurrence of different species that can be uncovered by genetic analyses. Particularly for its uniqueness, this phenomenon seems to represent an unprecedented diversification process and therefore must be preserved and better understood. If cryptic endemism is prevalent in Amazonia, then it affects a huge proportion of global biodiversity. Thus it is important to conduct intensive and extensive surveys to detect more cases of cryptic speciation and to understand on which scale it works (Cohn-Haft 2000; Aleixo 2009).

The vanishing Brazilian Amazon forest in the state of Rondônia

The southern part of the M–T interfluvium is located within the so-called "arc of deforestation", which is a longitudinal band along the eastern and southern edges of the Amazonian forest (Fearnside 2005). Deforestation in this area has been directly linked with the advancement of the agricultural frontier and with cattle ranching migrating northwards from Central Brazil. The state of Rondônia, whose 243,044 km^2 area approximates that of Portugal, is located in the heart of the "arc of deforestation". Thus, it is the most endangered area in the M–T interfluvium and one of the most deforested Amazonian states in Brazil, directly following Pará and Mato Grosso (INPE, Instituto Nacional de Pesquisas Espaciais).

The first settlements in Rondônia occurred during the rubber boom, late in the 19th century, all with a minor impact (Pedlowski et al. 2005). The first major intrusion of people was in the late 1960s caused by the abandonment of colonization projects along the Transamazon Highway and a series of settlement programs for small farmers assigned to 100-ha lots sponsored by the Brazilian government (Fearnside and Ferreira 1985; Pedlowski et al. 2005). Government land in many parts of the state outside of settlement areas were sold to large landholders. Pasture became the most common replacement for forest, both by small and large farmers, thus aggravating the impact of human populations on the forest (Fearnside and Ferreira 1985). Ilegal settlers in large and small areas used the deforestation as the primary means of securing land tenure claims (Fearnside and Ferreira 1985). The rapidly expanding network of roads facilitated the entry of loggers and land grabbers to previously untouched areas or even conservation units (Fearnside and Ferreira

1985). The paving of the Marechal Rondon Highway (Cuiabá-Porto Velho, or BR-364), and a vast expansion of the associated network of smaller roads, as part of a regional development program called POLONOROESTE (Fearnside and Ferreira 1985), was a key point leading up to the "fishbone" deforestation patterns as obvious by satellite imagery as seen today (Fig. 3). Roads are clearly related to deforestation caused by settlements, and in the state of Rondônia have been responsible for the destruction of over 60,696 km^2 of forest by 2001, which corresponds to 10 % of the total area deforested in the Amazon (Ferraz et al. 2005).

Deforestation rates in the Brazilian Amazon have been declining since 2005, reaching the lowest figures in 2012, which also applies to Rondônia. In 2004, 3858 km^2 of forest were cleared but the rate declined to 773 km^2 in 2012. Nevertheless, by 2012 around 85,000 km^2 of the entire surface area of the state of Rondônia has been deforested (Fig. 3) (see "PRODES", Satellite Monitoring of the Brazilian Amazon, INPE—http://www.obt.inpe.br/prodes/index.php). This deforestation in the state of Rondônia is quite recent. In the 1950s, the entire state was still covered by natural vegetation. Twenty-three percent of the deforested areas is now covered by pasture, while more than half of this (63 %) are degraded pastures (Instituto Nacional de Pesquisas Espaciais, INPE). The potential of the forest still needs to be explored and appreciated in its full ecologically pristine state.

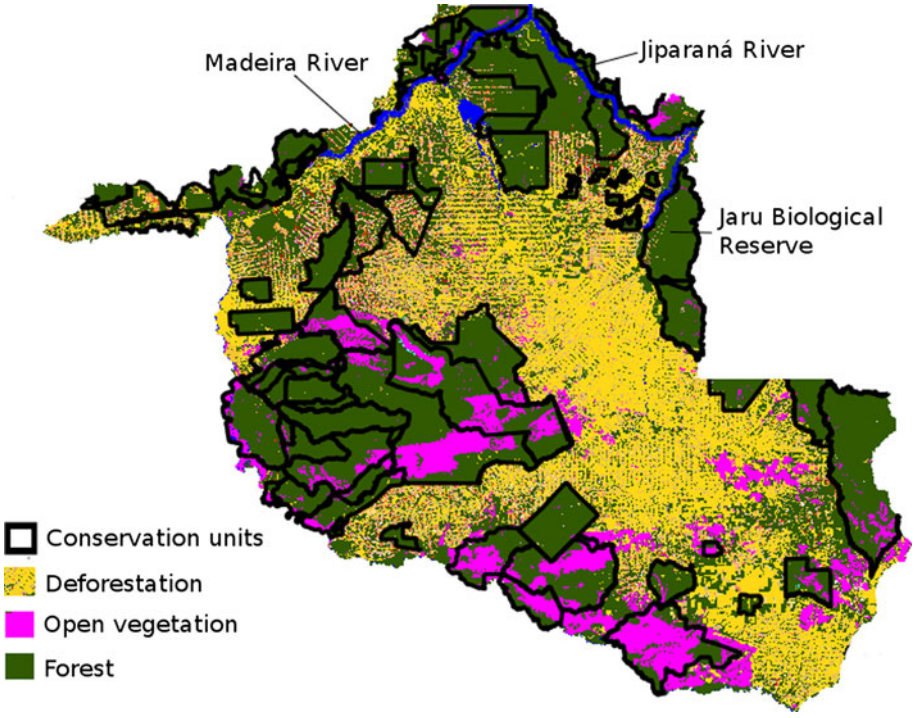

Fig. 3 Deforestation (*yellow*) and Conservation Units (*black*) in the state of Rondônia in 2012 (basic map data downloaded from "PRODES", Satellite Monitoring of the Brazilian Amazon, INPE at http://www.obt.inpe.br/prodes/index.php). *Hypocnemis ochrogyna* and a new species of the *Hylophylax naevius* species complex as well as other birds, are endemic to the region between the rivers indicated in the figure and, as clearly indicated by the figure, are under serious risk of imminent extinction. (Color figure online)

The relevance of "Mini-Interfluvia" for conservation planning

A standard method to delineate priority sites for conservation is the selection of biogeographically homogenous units, followed by the establishment of a system of protected areas that is representative and captures biodiversity patterns across the larger ecosystem. A commonly used blueprint is the classification of ecoregions (Dinerstein et al. 1995; Olson et al. 2001) where the entire interfluvium is commonly equated with an area of endemism, or at least a common biogeographical history is implied. Ecoregions have served in the past as the basis for planning of new protected areas in the context of the very ambitious ARPA (Áreas Protegidas da Amazônia) project, while areas of endemism have been the basis for other proposals to increase representation of protected areas in the Brazilian Amazon (da Silva et al. 2005).

However, this paper calls attention to the hidden biogeographical complexity characterizing the distribution of several taxa within proposed ecoregions and areas of endemism. These patterns are arguably associated with the role played by smaller rivers in triggering genetic and morphological differentiation. This, in turn, has important conservation planning implications, particularly for regions undergoing rapid and extensive deforestation.

If fine-scale endemism is indeed a common phenomenon across the Amazon basin, it becomes paramount to introduce such consideration in systematic conservation planning efforts for the region. Large-scale conservation planning initiatives, such as ecoregions (Olson et al. 2001), biodiversity hotspots (Myers et al. 2000), and endemic bird areas (Cracraft 1985) do not identify target regions for fine-scale conservation action (Eken et al. 2004). The existence and location of many already or imminently threatened taxa with small ranges in the vast Amazon lowlands is only beginning to be recognized and applied in conservation planning (Vale et al. 2008). The latter authors have identified smaller regions of endemism in the Amazon that are likely to be heavily deforested in the near future (2020) by ongoing or proposed infrastructure development, jeopardizing many taxa (whether cryptic or not) that are endemic to those areas; specifically, those studies revealed that many floodplains and the southern portion of the Rondônia area of endemism are likely to be heavily deforested in the near future. Two endemic species, *Clytoctantes atrogularis* and *Rhegmatorhina berlepschi*, are likely to soon face critical habitat loss due to ongoing heavy deforestation in the Rondônia area of endemism. These studies (Vale et al. 2008; Bird et al. 2012), have served as the basis for a review of the Brazilian Red List of threatened birds in the Amazon, reinforced by the conservation arguments of this paper.

Capparella (1991) has recommended that the inter-riverine areas of the Amazon should also be the subject of special conservation attention. Mesquita et al. (2007) also mentioned the importance of recognizing "mini-interfluvia" in the placement of new protected areas in the Amazon. As a result, several protected areas were established between the Madeira and Tapajós rivers since 2004 (protected areas in the Madeira basin now cover 26 % of its catchment area; Castello et al. 2013). But this is clearly not enough. For example, the Jaru Biological Reserve located in the Jiparaná- Aripuanã interfluvium, originally decreed as a forest reserve with 1,085,000 ha in 1961, has been greatly reduced in size (Fearnside and Ferreira 1985). Much of the reserve was incorporated in an area where 500-ha estates were sold through sealed tenders (licitação) for development of cocoa plantations, which left the reserve with an official area of only 353,163 ha (Fearnside and Ferreira 1985). Smaller neighboring sites have been found to contain significant diversity, with more than 400 species per site being recorded there (Oren and Parker 1997; Stotz et al. 1997; Aleixo and Poletto 2007; Cohn-Haft et al. 2007; Fernandes and Lima 2009; Whittaker 2009).

Hypocnemis rondoni, *Herpsilochmus stotzi, Epinecrophylla dentei, Hypocnemis* sp Nov, *Myrmeciza* sp Nov, known to be endemic to the Jiparaná-Aripuanã interfluvium, were documented within the Jaru Reserve. Some of these too have corresponding ecological replacements on the western bank of the Jiparaná River, outside of Jaru (Fernandes and Lima 2009). The western bank of the Jiparaná River, in turn, is undergoing rapid deforestation (Fig. 3). Therefore, the new morphological and genetic form of the *Hylophylax naevius* complex mentioned above, as well as *Hypocnemis ochrogyna* (Isler et al. 2007) and other birds which are apparently restricted to a small area on the western Jiparaná River, are under serious risk of imminent extinction. Also, forests around the Jaru Reserve, especially those on the western Jiparaná River, are not well protected. Reserves in Rondônia face increasing pressure from the incursion of illegal loggers and are susceptible to illegal deforestation (Pedlowski et al. 2005, see also Fig. 3). Accordingly, these reserves, especially in the state of Rondônia, urgently need to be protected, while the limits of the reserves, such as the Rebio Jaru, should be expanded to include both banks of the rivers. In essence, the relatively small and increasingly fragmented forests that remain in the Jiparaná basin—no more than 30 % of the original forest cover—still contain large numbers of restricted endemics under high probability of extinction in the absence of focused conservation action on the ground.

Patterns of geographic distribution that focus on morphology alone will continue to serve as the basis for setting site-based conservation policies, given that few molecular phylogenies exist for most Amazonian birds and other vertebrates. Therefore, more efforts need to be directed at the survey of areas that are biogeographical gaps across the region, and to additional molecular work. There is already a good knowledge base regarding the sampling effort spread throughout the Amazon basin on birds. Representative collections of birds already exist in Brazilian institutions, particularly at the Instituto Nacional de Pesquisas da Amazônia (INPA) and the Museu Paresense Emílio Goeldi (MPEG). However, spatial sampling bias still remains a problematic issue in the Amazon and is incongruent among different taxa, interferring with research attempt of elucidating possible geographical patterns of diversity (Vale and Jenkins 2012). Thus, a concerted effort should be to establish extensive taxon-specific inventories from previously poorly surveyed regions and to make these available in open access databases such as Specieslink (http://www.splink.org.br). Along with genetic sequencing programs of all the relevant material present in existing ornithological collections of Amazonia this may help to unveil geographic patterns of diversity. This new body of evidence could then serve to generate new fine-grained priorities for site-based protection while there is still time to act proactively in preventing the extinction of restricted-range endemics.

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