Molecular Phylogenetics and Evolution 55 (2010) 178–184

Contents lists available at ScienceDirect

Molecular Phylogenetics and Evolution

journal homepage: www.elsevier.com/locate/ympev

Are lowland rainforests really evolutionary museums? Phylogeography of the green hylia (*Hylia prasina*) in the Afrotropics

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ARTICLE INFO

Article history:
Received 30 June 2009
Revised 15 October 2009
Accepted 20 October 2009
Available online 10 November 2009

Keywords:
Hylia prasina
Africa
Guineo-Congolian
Lowland
Rainforest
Diversification
Phylogeography

ABSTRACT

A recent trend in the literature highlights the special role that tropical montane regions and habitat transitions peripheral to large blocks of lowland rainforest play in the diversification process. The emerging view is one of lowland rainforests as evolutionary 'museums'; where biotic diversity is maintained over evolutionary time, and additional diversity is accrued from peripheral areas, but where there has been little recent diversification. This leads to the prediction of genetic diversity without geographic structure in widespread taxa. Here, I assess the notion of the lowland rainforest 'museum' with a phylogeographic study of the green hylia (Aves: Sylviidae: *Hylia prasina*) using 1132 bp of mtDNA sequence data. The distribution of genetic diversity within the mainland subspecies of *Hylia* reveals five highly divergent haplotype groups distributed in accordance with broad-scale areas of endemism in the Afrotropics. This pattern of genetic diversity within a currently described subspecies refutes the characterization of lowland forests as evolutionary museums. If the pattern of geographic variation in *Hylia* occurs broadly in widespread rainforest species, conservation policy makers may need to rethink their priorities for conservation in the Afrotropics.

1. Introduction

From its inception, students of biogeography have relied on the species distribution as the fundamental unit of analysis. Analyses of the distributional patterns of African rainforest birds have played an especially important role in the formulation of biogeographical theory and models of species diversification (Chapin, 1923, 1932; Moreau, 1954, 1966; Diamond and Hamilton, 1980; Fjeldså and Lovett, 1997). For example, the coincidences of distributional patterns among the Afrotropical lowland rainforest avifauna have been used to delineate areas of endemism (shaded areas in Fig. 1; Diamond and Hamilton, 1980; Mayr and O'Hara, 1986; Prigogine, 1988). The existence of these regions of high endemism in the absence of obvious contemporary physical barriers to dispersal led to early iterations of the Refuge Hypothesis (Moreau, 1954) of biotic diversification. The Refuge hypothesis posits that contemporary areas of endemism remained environmentally stable through evolutionary time; their forested habitats were impervious to the spatiotemporal variation in the distribution of rainforest brought about by past climatic fluctuations (Diamond and Hamilton, 1980; Crowe and Crowe, 1982; Mayr and O'Hara, 1986). The environmental stability in these refuges provided a safe-haven in a changing environment and promoted allopatric diversification in forest-restricted taxa.

In arguing for the Refuge Hypothesis as a model of diversification in the Afrotropics, Diamond and Hamilton (1980), Crowe and Crowe (1982), and Mayr and O'Hara (1986) examined mainly species with restricted distributions, taxa that do not occur throughout the lowland rainforest. Such species fit the refuge model well by having endemic taxa in one or more area of endemism. However, the remaining lowland forest inhabitants are broadly distributed across the Guineo-Congolian forest. These widespread species are assumed to lack substantial geographic variation (Mayr and O'Hara, 1986; Roy, 1997; Roy et al., 2001; Fjeldså et al., 2005, 2007) and as such, their distributions do not seem to fit the lowland rainforest refugial model. The prevalence of widespread Guineo-Congolian species led to an alternative hypothesis of biotic diversification: the Montane Speciation Hypothesis (Roy, 1997; Fjeldså and Lovett, 1997; Roy et al., 2001; Fjeldså et al., 2005, 2007; Fjeldså and Bowie, 2008). The Montane Speciation Hypothesis takes the tenets of the Refuge Hypothesis (allopatric diversification driven by climate induced range expansion and contraction) but shifts the focus away from diversification in the lowland rainforests and instead contends that montane regions were the main centers of recent (i.e., late Tertiary through the present) diversification for Afrotropical birds. A stated corollary to this hypothesis is that the Guineo-Congolian lowland rainforest, rather than acting as a center of recent diversification as the Refuge hypothesis posits, represents an evolutionary 'museum' where "species could have persisted since the Miocene

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doi:10.1016/j.ympev.2009.10.027

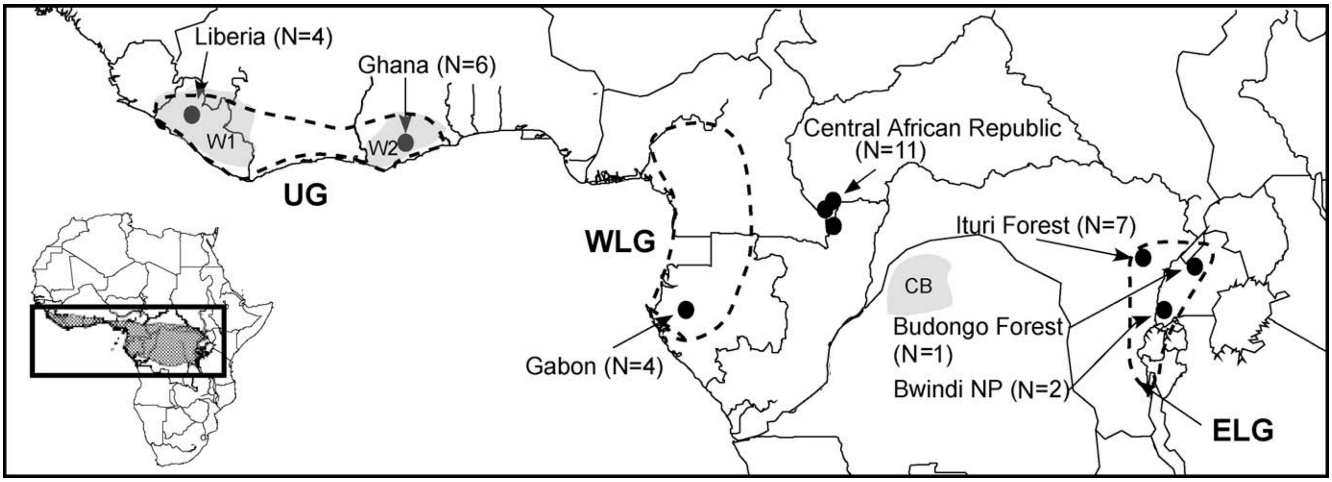

Fig. 1. Sampling localities for *Hylia prasina* samples used in this study. Five major lowland rainforest areas of endemism modeled after Mayr and O'Hara (1986, hashed outlines) and Prigogine (1988, gray filled). Shaded area in inset map approximates the distribution of the Guineo-Congolian rainforest. UG, Upper Guinea; W1, West African refugium 1; W2, West African refugium 2; WLG, Western Lower Guinea; ELG, Eastern Lower Guinea; CB, Congo Basin.

climatic optimum, but where there has been little subsequent diversification." (Fjeldså and Bowie, 2008, p. 244)

An important consideration is that the distributional patterns used to support the characterization of the Guineo-Congolian rainforest as an evolutionary 'museum' (i.e., the prevalence of widespread, undifferentiated taxa) may be based on poorly understood distributional limits. Phylogeographic studies have demonstrated that widespread lowland rainforest species that appear outwardly uniform actually comprise a remarkable degree of geographically structured genetic diversity (e.g., Beresford and Cracraft, 1999; Schmidt et al., 2008; Nguembock et al., 2009 in Africa; Zou et al., 2007 in Southeast Asia; Marks et al., 2002; Cheviron et al., 2005 in South America; Miura and Edwards, 2001 in Australia).

Critical to this discussion is an understanding of how genetic diversity is distributed in widespread taxa throughout the Guineo-Congolian forest. If lowland rainforests have acted as evolutionary 'museums' and conserved ancient diversity rather than fostered diversification, one would predict a high degree of standing genetic diversity, but limited geographic structure in widespread taxa (Fjeldså et al., 2007). Alternatively, geographic variation coincident with purported refugia (areas of endemism) would suggest *in situ* diversification in the lowlands, consistent with the tenets of the Refuge Hypothesis, i.e., that repeated episodes of climate-induced isolation in lowland rainforest refuges played a role in shaping Guineo-Congolian rainforest biodiversity.

Here, I examine the phylogeography of the green hylia (Aves: Sylviidae, *Hylia prasina*). This species represents a monotypic genus and occurs primarily in the understory and mid-stratum of primary and mature secondary Guineo-Congolian rainforest. Two subspecies are described (Dickinson, 2003). The first, *Hylia prasina poensis*, is found only on islands in the Gulf of Guinea and is defined by the relative whiteness of its throat (Alexander, 1903). The second, *Hylia prasina prasina*, is widely distributed across the Guineo-Congolian forest from western Gambia through central Angola to western Kenya. The broad distribution of the mainland subspecies of *Hylia* makes it an ideal candidate to assess the notion of lowland rainforests as the evolutionary slow lane.

2. Materials and methods

2.1. Molecular data

Two mitochondrial genes (complete ND3 and a portion of ND2) were sequenced for 35 individuals of *H. prasina* (Table 1 and Fig. 1) from localities scattered throughout the African lowland rainforest. Based on the phylogenetic hypotheses of Sefc et al. (2003), Barker et al. (2004), and Johansson et al. (2008), I selected two relatively close outgroup taxa and obtained their DNA sequences from GenBank: the Eurasian Reed Warbler (*Acrocephalus scirpaceus*, GenBank No. AM889139), and the Tit-Hylia (*Pholidornis rushiae*, GenBank No. AY136586). DNA was amplified and sequenced using the primer sets L10755 and H11151 for ND3 (Chesser, 1999), and L5215 (Hackett, 1996) and H6113 (Slikas et al., 2000) for ND2. Total genomic DNA was extracted from muscle using the reagents and protocols provided with the QIAamp Tissue Kit (QIAGEN). PCR amplification followed protocols detailed in Marks et al. (2007) and sequencing reactions followed the manufacturer's protocols (ABI Big Dye 3.1). Sequences were analyzed on an ABI 377 automated DNA sequencer. DNA was sequenced in both directions and verified and aligned using Sequencher 3.1.1 (Gene Codes, Ann Arbor, MI).

2.2. Phylogeographic analysis

An appropriate maximum likelihood (ML) model was identified using Modeltest 3.06 (Posada and Crandall, 1998) under the Akaike Information Criterion (GTR + I with the proportion of invariable sites set to 0.589). Maximum likelihood tree searches were conducted using PAUP* (Swofford, 2002) with 10 random addition sequence replicates. Support for nodes was assessed by ML bootstrap analyses with 100 replicates and Bayesian analysis using MrBayes 3.1 (Ronquist and Huelsenbeck, 2003) and the same model as the ML analysis. Two independent runs with four chains each were conducted for 2,000,000 generations and sampled every 1000 generations. The first 500 trees from each run were discarded as a burn-in to insure that sampling was from the stationary portion of the distribution of parameters, and the remaining 3000 trees were used to construct a majority-rule consensus tree. A haplotype network was constructed using Network v4.5 (fluxus-engineering.com). An initial median joining network was calculated and screened using the MP option (Polzin and Daneschmand, 2003) to delete superfluous median vectors and links that are not contained in the shortest trees in the networks. Finally, several measures of genetic diversity were calculated, including uncorrected proportional genetic distances, the total and average number of polymorphic sites per population, the number of haplotypes in a population, and nucleotide diversity (π).

Table 1
Sampling localities for *Hylia prasina* samples used in this study.

Voucher No.	Source	Country	Locality	Haplotype group
429609	FMNH	Central African Republic	Parc National de Dzanga-Ndoki, Mabea Bai	CAR
429610	FMNH	Central African Republic	Parc National de Dzanga-Ndoki, Mabea Bai	CAR
429612	FMNH	Central African Republic	Parc National de Dzanga-Ndoki, Mabea Bai	CAR
429613	FMNH	Central African Republic	Res Spec Foret Dense de Dzanga-Sangha, 12.7 km NW Bayanga	CAR
429615	FMNH	Central African Republic	Parc National de Dzanga-Ndoki, 38.6 km S Lidjombo	CAR
429690	FMNH	Central African Republic	Parc National de Dzanga-Ndoki, 38.6 km S Lidjombo	CAR
429691	FMNH	Central African Republic	Parc National de Dzanga-Ndoki, 38.6 km S Lidjombo	CAR
DOT 2110	AMNH	Central African Republic	Sangha-Mbare Prefecture, Bayanga	CAR
DOT 10579	AMNH	Central African Republic	Sangha-Mbare Prefecture, Bayanga	CAR
DOT 10605	AMNH	Central African Republic	Sangha-Mbare Prefecture, Bayanga	CAR
DOT 12480	AMNH	Central African Republic	Sangha-Mbare Prefecture, Bayanga	CAR
357295	FMNH	Democratic Republic Congo	Ituri Forest, Mambasa, Epulu	ELG
357296	FMNH	Democratic Republic Congo	Ituri Forest, Mambasa, Epulu	ELG
357297	FMNH	Democratic Republic Congo	Ituri Forest, Mambasa, Epulu	ELG
357299	FMNH	Democratic Republic Congo	Ituri Forest, Mambasa, Epulu	ELG
357300	FMNH	Democratic Republic Congo	Ituri Forest, Mambasa, Epulu	ELG
357301	FMNH	Democratic Republic Congo	Ituri Forest, Mambasa, Epulu	ELG
357302	FMNH	Democratic Republic Congo	Ituri Forest, Mambasa, Epulu	ELG
389401	FMNH	Gabon	Minvoul, 31 km ESE, along IOBT trail	Gabon
N15070	NMNH	Gabon	Ogooue Maritime Prov., Rabi Oil Field	Gabon
N16073	NMNH	Gabon	Ogooue Maritime Prov., Moukalaba-Doudou National Park	Gabon
N10061	NMNH	Gabon	Ogooue Maritime Prov., Rabi Oil Field	Gabon
396661	FMNH	Ghana	Assin Foso, ca. 30 km S	Ghana
396662	FMNH	Ghana	Assin Foso, ca. 30 km S	Ghana
396663	FMNH	Ghana	Assin Foso, ca. 30 km S	Ghana
396664	FMNH	Ghana	Assin Foso, ca. 30 km S	Ghana
396665	FMNH	Ghana	Assin Foso, ca. 30 km S	Ghana
396666	FMNH	Ghana	Assin Foso, ca. 30 km S	Ghana
DOT 2003	AMNH	Liberia	Lofa County, 1 km E, 10 1/2 km N of Ziggida, 540 M	Liberia
DOT 2035	AMNH	Liberia	Lofa County, 1 km E, 10 1/2 km N of Ziggida, 540 M	Liberia
DOT 2547	AMNH	Liberia	Lofa County, 1 km E, 10 1/2 km N of Ziggida, 540 M	Liberia
DOT 2564	AMNH	Liberia	Lofa County, 1 km E, 10 1/2 km N of Ziggida, 540 M	Liberia
385170	FMNH	Uganda	Bwindi National Park, Ngoto Swamp	ELG
385171	FMNH	Uganda	Bwindi National Park, Ngoto Swamp	ELG
391775	FMNH	Uganda	Budongo Forest, Nyabyeya Forestry College	ELG

Note: FMNH, Field Museum of Natural History; AMNH, American Museum of Natural History; NMNH, National Museum of Natural History.

3. Results

3.1. Phylogeographic analysis

A total of 1132 nucleotides of mtDNA was sequenced, consisting of 781 bp of ND2 (GenBank accession Nos. GU122784–GU122818) and 351 bp of ND3 (GenBank accession Nos. GU122819–GU122853) from 35 individuals of *H. prasina* (Table 1). These sequences encompassed 32 mtDNA haplotypes. Excluding outgroups, 750 (66.3%) sites were constant, 205 (18.1%) were variable but parsimony uninformative, and 177 (15.6%) were parsimony informative. Aligned mtDNA sequences appeared to be of mitochondrial rather than nuclear origin. Sequences contained no stop codons, overlapping fragments contained no conflicts, and codon positions contained the expected relative levels of polymorphism.

Maximum likelihood and Bayesian analyses recovered the same overall topology. There was a general lack of support for relationships among five highly supported clades (Fig. 2). The one exception was high bootstrap and posterior probability support for a sister relationship between Gabon and CAR haplogroups. The MP haplotype network recovered the same five haplotype clusters (Fig. 3). Differences among analytical methods were only evident in minor rearrangements among terminal taxa. A strong geographical component was evident among the five haplogroups. The first one was comprised of individuals from Liberia, the second individuals from Ghana, the third individuals from Gabon, the fourth individuals from the sampling localities of CAR, and the fifth with individuals from the three sampling localities of Eastern Lower Guinea (DRC and Uganda).

3.2. Genetic diversity indices

Overall haplotype diversity was high with only two shared haplotypes (Table 2). One shared haplotype was present in three of the four individuals sampled from Liberia. Another haplotype was shared between two individuals in Eastern Lower Guinea; one each from Ituri Forest and Bwindi National Park. Genetic diversity within localities, as assessed by the average number of polymorphic sites and nucleotide diversity (π), was low and values for each locality were similar (Table 2). The average number of polymorphic sites within a locality ranged from 3.8 (0.3%) in Ghana to 5.9 (0.5%) in Ituri Forest. In contrast to the low genetic diversity within localities, genetic divergence among localities ranged from 1.7% to 5.1% (Table 3).

4. Discussion

A recent review of diversification in African forest birds characterized the Guineo-Congolian lowland rainforest as a biological museum (Fjeldså and Bowie, 2008). As such, the entire lowland rainforest is viewed as evolutionarily static where “species could have persisted since the Miocene climatic optimum, but where there has been little subsequent diversification.” (Fjeldså and Bowie, 2008, p. 244) If that were the case, one would predict a high degree of standing genetic variation without geographic structure or, perhaps, clinal variation in a species over wide geographic distances (Fjeldså et al., 2007). However, such a pattern does not occur in *Hylia*. The observed genetic homogeneity within highly divergent, geographically structured haplotype groups present in *Hylia* refutes the lowland-forest-as-museum characterization

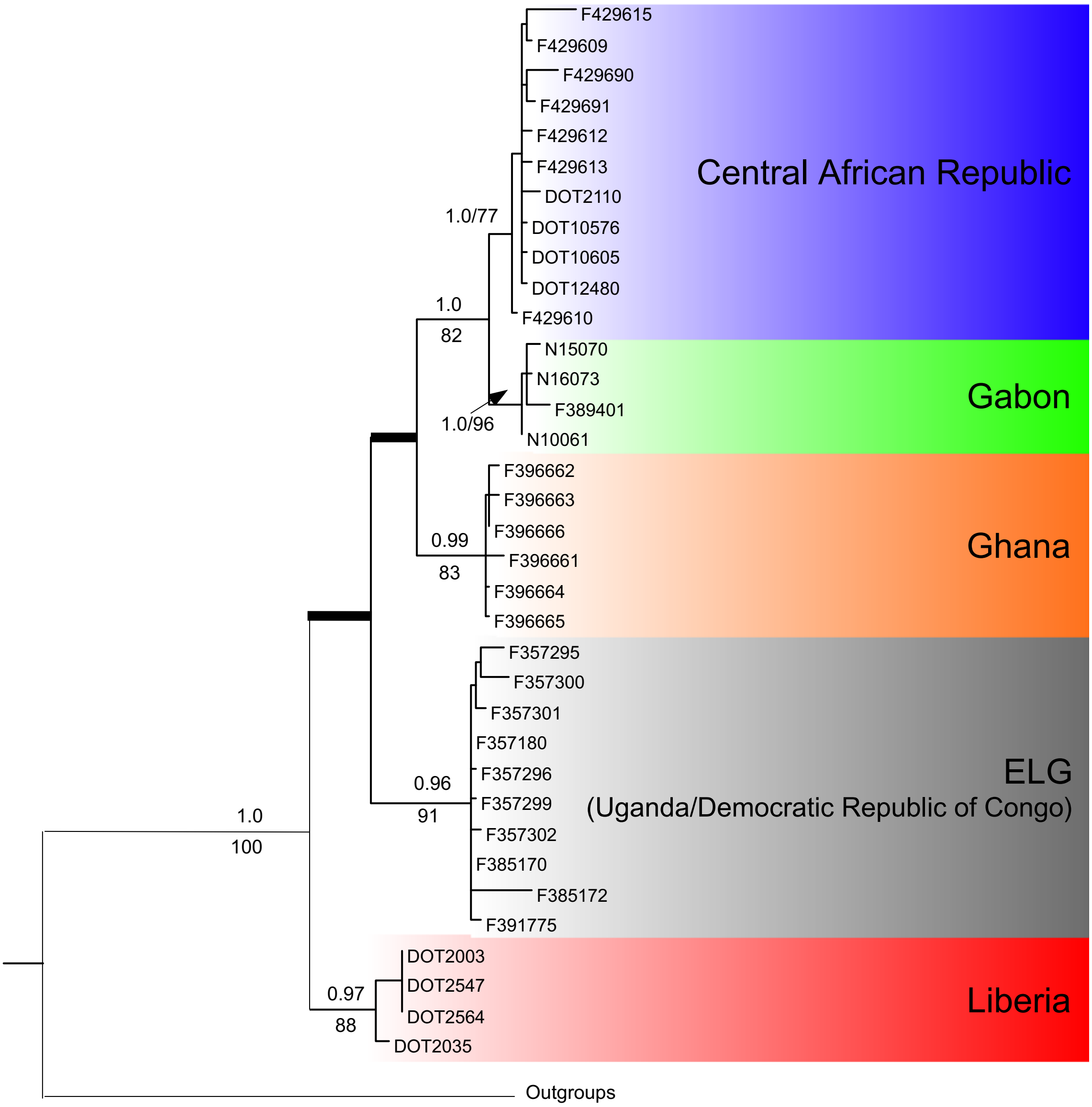

Fig. 2. Maximum likelihood tree of *Hylia prasina* haplotypes. Numbers above branches are Bayesian posterior probabilities. Numbers below branches are maximum likelihood bootstrap proportions. Thickened branches received <0.95 posterior probabilities or <75% bootstrap support.

(Fjeldså and Lovett, 1997; Fjeldså et al., 2005, 2007). In discussing widespread lowland rainforest taxa Fjeldså et al., (2007, p. S360) remarked, "The morphological variation is subtle in most cases and apparently clinal, with no indication of breaks to gene flow." The data presented here demonstrate that within a single described subspecies, genetic diversity can be substantial and, more importantly, exhibit significant geographic structure. Instead of the panmictic widespread taxon that is suggested by current taxonomy, these data suggest at least five reciprocally monophyletic clades with geographically restricted distributions centered in Liberia, Ghana, Gabon, Central African Republic, and eastern DRC and Uganda. Finer-scale geographic sampling is needed to examine the integrity of haplotype networks between sampled core areas (i.e., presence and locations of contact zones). Nevertheless, the geographic structure suggests geographical limits for each of the haplogroups.

The mtDNA data reveal a pattern of diversification within the Guineo-Congolian lowland rainforest that is not reflected in the current taxonomy of *Hylia*. It merits noting that the pattern of mtDNA geographic variation in *Hylia* is nearly identical to that described for two other widespread Afrotropical birds that have been examined in detail. For example, recent work with the forest robin (Genus: *Stiphrornis*) by Beresford and Cracraft (1999) and Schmidt et al. (2008) shows that *Hylia* and *Stiphrornis* share a pattern of geographic variation with genetically diagnosable populations in the Upper Guinean forests of West Africa, and the Lower Guinean forests of Gabon, Central African Republic, Democratic Republic of Congo, and Uganda. A second example comes from the brown illadopsis (*Illadopsis fulvescens*). Nguembock et al. (2009) demonstrate considerable genetic structure across the distribution of this widespread forest bird again with unique haplotype groups in Liberia, and Central African Republic and with additional haplotypes from regions not sampled in this study (i.e., Angola and Tanzania). The recent work with *Stiphrornis* has led to the description of two new species from the formerly widespread taxon (Beresford and Cracraft, 1998; *Stiphrornis sanghensis* from Central African Republic, Schmidt et al., 2008; *Stiphrornis pyrrholaemus* from Gabon). Specific taxonomic recommendations for *Hylia* await additional data from molecular markers and studies of morphology and vocalizations.

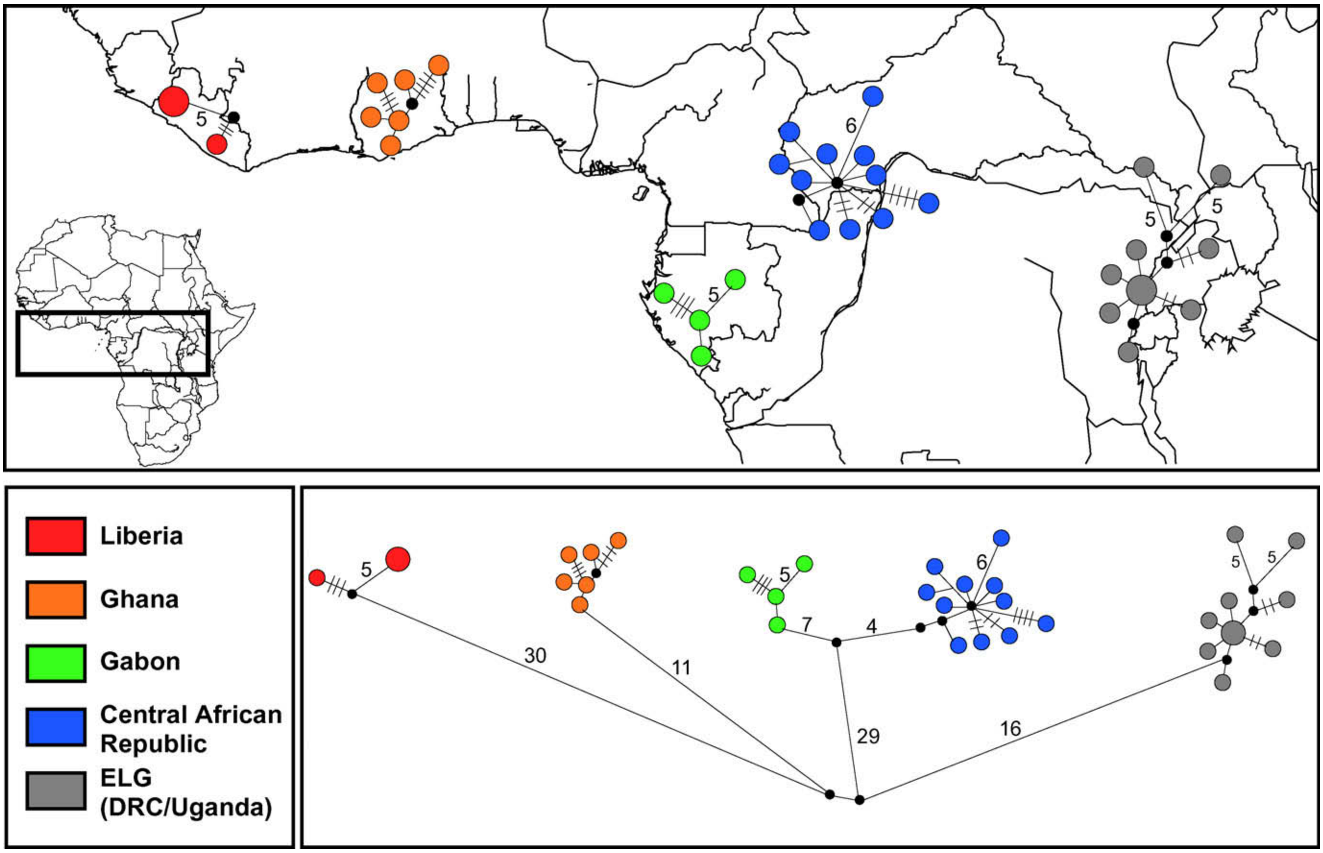

Fig. 3. Map with generalized locations of sampling localities and maximum parsimony network estimated for sampled haplotypes. Each ellipse represents a unique haplotype, with its size corresponding to frequency of occurrence. Each line connecting two haplotypes represents a single mutational step; cross hatches represent additional steps. Numbers along lines indicate five or more steps separating haplotypes. Filled black circles represent missing (unsampled) haplotypes.

Table 2
Genetic diversity indices for sampled localities of *Hylia prasina*.

Locality	*N*	No. of haplotypes	No. of polymorphic sites Total (avg.)	Nucleotide diversity (n)
Upper Guinea				
Liberia	4	2	9 (4.5)	0.004 ± 0.003
Ghana	6	6	10 (3.8)	0.003 ± 0.002
Western Lower Guinea				
Gabon	4	4	10 (5)	0.004 ± 0.003
Central African Republic	11	11	28 (5.3)	0.005 ± 0.003
Eastern Lower Guinea	10	9	26 (5.6)	0.005 ± 0.003
Ituri Forest	7	7	19 (5.9)	0.005 ± 0.003
Budongo	1	1	N/A	N/A
Bwindi	2	2	7 (4.6)	0.004 ± 0.003

However, not every species investigated to date shows this same pattern of genetic diversity across the Guineo-Congolian rainforest. For example, the olive sunbird (*Nectarinia olivacea*) is a common inhabitant of the lowland rainforest understory as well as other habitats throughout its range. Bowie et al. (2004) investigated patterns of genetic diversity across the geographic distribution of this taxon and revealed very limited genetic structure among Guineo-Congolian lowland rainforest populations sampled and none of the unique lowland rainforest haplotype groups observed in *Hylia* or the other taxa mentioned above. To discover whether the cryptic geographic variation evident in *H. prasina* occurs more generally in Afrotropical birds will require phylogeographic studies of widespread co-distributed and syntopic species. If the pattern of genetic diversity in *H. prasina*, *Stiphrornis*, and *I. fulvescens* is the rule for widespread lowland forest taxa, rather than the exception, conservation policy makers may need to rethink their priorities for species and habitat preservation in the Afrotropics.

4.1. Conservation priorities in the Afrotropics

The cryptic genetic variation and geographic structure in widespread taxa such as *Hylia*, *I. fulvescens* (Nguembock et al., 2008), and *Stiphrornis* (Beresford and Cracraft, 1998; Schmidt et al., 2008) highlights an issue of substantial conservation importance for African rainforests. It suggests that a great deal more diversity exists than is currently expressed in taxonomy, even in a group as well studied as birds. Currently recognized species and subspecies that are considered well protected from extinction by virtue of their broad distributions may in fact encompass several evolutionary units that are vulnerable to extinction through habitat loss. The

Table 3
Average pairwise sequence divergence between the the five haplotype groups.

		1	2	3	4	5
1	ELG	-				
2	Gabon	0.051	-			
3	CAR	0.051	0.017	-		
4	Ghana	0.043	0.038	0.036	-	
5	Liberia	0.047	0.051	0.050	0.045	-

potential loss of biodiversity caused by local extirpation through habitat destruction could be even greater than already expected for African rainforests.

A database of African bird distributions (available online at: http://www.zmuc.dk/commonweb/research/biodata.htm, Hansen et al., 2007) is widely used in macroecology studies (Jetz and Rahbek, 2001, 2002; Jetz et al., 2004). Such studies use the distributional information in range maps as the fundamental unit of analysis. Macroecological analyses are increasingly being used to inform decisions about areas in need of conservation prioritization (Hurlbert and Jetz, 2007). It follows, then, that the notion of African lowland forest as evolutionary museums rather than centers of diversification is being perpetuated and incorporated into conservation prioritization. In a synthesis of current approaches to conservation prioritization, Brooks et al. (2006) characterized the entire Congo Basin (as well as lowland Amazonia and New Guinea) as an area with low vulnerability, but high irreplaceability. The implication being that habitat loss in part of the Congo Basin would not result in a major loss of biodiversity because most species are widespread and suitable habitat exists in other parts of the extensive forest. Moreover, Brooks et al. (2006) specifically mention habitats peripheral to the lowland rainforest (ecotonal and montane areas) as regions of special conservation interest because they represent areas of "evolutionary process." Although there is ample evidence that these regions are important evolutionary staging grounds (Smith et al., 1997, 2005; Fjeldså and Lovett, 1997; Bowie et al., 2006; Fjeldså and Bowie, 2008), the data presented here suggest that they need not be considered more important to the diversification process than lowland forests.

Acknowledgments

I thank F.H. Sheldon, J.V. Remsen, M. Hellberg, R.G. Moyle, G.A. Voelker and J.D. Weckstein, and an anonymous reviewer for helpful comments on this manuscript. Museums that contributed specimens to this project include: Field Museum, American Museum of Natural History, and the National Museum of Natural History. I appreciate the valuable help of Drs. Bashwira Sanvura Augustine and Charles Kahindo M. Ngabo, Robert Kizungu Byamana, and all of my colleagues at CRSN Lwiro, DRC, Mike Adu'ncia and colleagues at the Ghana Wildlife Authority, NCRC in Accra, Ghana, Drs. Kityo, and Dranzoa at Makerere University, and the Uganda Wildlife Authority.

For funding, I thank the LSUMNS graduate student fund, the Field Museum of Natural History, the Chapman Memorial Fund of the AMNH, NSF ATOL Grant to FHS (DEB-0228688), T. Vinton Holmes, the Biological Sciences Graduate Students Organization (BioGrads), and all of the supporters of the LSUMNS Birdathon.

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