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Historical biogeography and speciation in the Neotropical highlands: Molecular phylogenetics of the jay genus *Cyanolyca*

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ABSTRACT

Phylogenetic relationships were studied in the genus *Cyanolyca*, an assemblage of jays distributed from Mexico south to Bolivia. Given its fragmented distribution along the humid forests of the Neotropics, the genus *Cyanolyca* is a model group for exploring hypotheses on biogeography and speciation. Phylogenetic analyses were based on two mitochondrial and three nuclear loci; taxon sampling includes all species in the genus and most subspecies. Maximum parsimony, maximum likelihood, and Bayesian analyses produced trees that were congruent and highly robust at both terminal and deep nodes of the phylogeny. *Cyanolyca* comprises two major clades: one contains the Mesoamerican "dwarf" jays, and the other consists of two main groups—*C. cucullata* + *C. pulchra* and the "core" South American species. Prior hypotheses of relationships were explored statistically using Maximum Likelihood and Bayesian approaches. Dispersal-Vicariance analysis revealed the importance of the Northern Andes as a major center for biological diversification, and the effects of dispersal across the Panamanian Land Bridge in the composition of South American and Mesoamerican avifaunas. Phylogenetic patterns are highly congruent with an allopatric mode of speciation. Implications of these results are discussed in the context of the biogeography of Neotropical montane forests.

1. Introduction

Neotropical montane regions hold the world's highest diversity of birds, as well as that of many other organisms (Churchill et al., 1995; Stattersfield et al., 1998). These mountain chains stretch from Mexico south to Argentina and Chile, in a fragmented, complex mosaic of topographic units belonging to diverse geologic formations (Simpson, 1975; Ferrusquía-Villafranca, 1993; Coates and Obando, 1996; Gregory-Wodzicki, 2000). Regardless of its origins, the region sustains extensive tropical montane forests and numerous lineages that overlap broadly in areas with similar environmental conditions (Chapman, 1926; Hernández-Baños et al., 1995; Peterson et al., 1999).

Early distributional studies and recent empirical work suggest that Neotropical montane avifaunas are derived, at least partially, from lineages that have moved from lower to higher montane elevations (Chapman, 1926; Gerwin and Zink, 1989; Bates and Zink, 1994; García-Moreno et al., 1999a; Pérez-Emán, 2005; Brumfield and Edwards, 2007) and from lineages that have expanded their distributions via the Panama Land Bridge (Chapman, 1917; Haffer, 1974). Moreover, the complex topography and fragmented nature of Neotropical montane forests suggest that diversification in situ after initial biological interchange might play a decisive role in shaping distributions of largely overlapping lineages (Chapman, 1926; Remsen, 1984; Cracraft, 1985; Hernández-Baños et al., 1995; García-Moreno and Fjeldså, 2000).

Most models that attempt to explain geographic variation and speciation in situ depend on the following: effects of deep river valleys as barriers to gene flow and consequent evolution of distinctive geographic forms (Chapman, 1926; Vuilleumier, 1969; Remsen, 1984; Cracraft, 1985; García-Moreno and Fjeldså, 2000); the linearity of the Andes, which results in elongate geographical ranges and reduces potential contact and gene flow among parapatric forms (Remsen, 1984; Graves, 1985, 1988) and the effects of Pleistocene glaciations on the cyclic fragmentation, isolation, and reconnection of montane forests (Hooghiemstra et al., 2000) and their avifaunas (Vuilleumier, 1969; Haffer, 1974; Hackett, 1995). Clearly, these propositions are not mutually exclusive, and could operate across various temporal, spatial, and taxonomic scales.

Cyanolyca jays are model organisms for testing hypotheses of diversification across the Neotropical montane forests. Being a relatively small assemblage that represents one of the two New World jay (NWJ) lineages that reached South America, these jays are sedentary and inhabit humid montane forests from Mexico south to Bolivia (Fig. 1). Most are allopatric, and their ranges are highly subdivided, creating (putatively) isolated and morphologically distinct populations (Hellmayr, 1934). Current taxonomic

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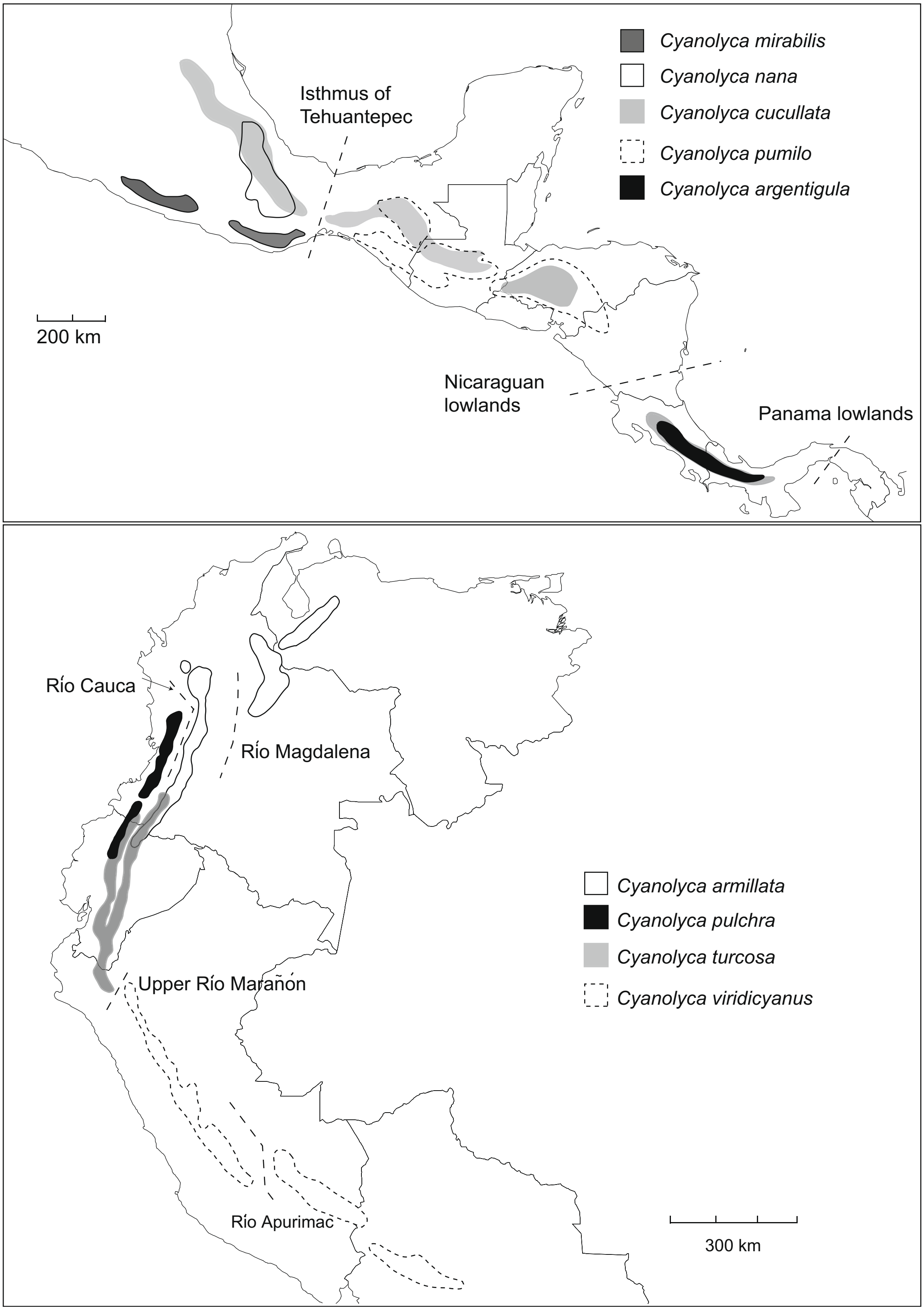

Fig. 1. Maps of Mesoamerica and northern South America showing the distribution of the nine species of *Cyanolyca*.

treatments (e.g., Sibley and Monroe, 1990; Madge and Burn, 1994; Dickinson, 2003) recognize nine species: *Cyanolyca mirabilis*, *C. nana*, *C. pumilo*, *C. argentigula*, *C. pulchra*, *C. cucullata*, *C. armillata*, *C. turcosa*, and *C. viridicyanus*. The first four species, the so-called “dwarf jays,” are allopatric and have been recognized as full species since early revisions (e.g., Hellmayr, 1934; Blake and Vaurie,