Crossing or bypassing the Andes: a commentary on recent range extensions of cis-Andean birds to the West of the Andes of Colombia

Cruzando o desviando los Andes: un comentario sobre extensiones de distribución recientes de aves cis-Andinas al oeste de los Andes de Colombia

Cruzando ou desviando os Andes: um comentário sobre extensões de distrubuição recentes de aves cis-Andinas ao oeste dos Andes da Colômbia.

Jorge E. Avendaño[1,2], José O. Cortés-Herrera[3], Elkin R. Briceño-Lara[4], Diego A. Rincón-Guarín[5]

[1] Museo de Historia Natural "Jorge Ignacio Hernández Camacho", Instituto Alexander von Humboldt, Claustro San Agustín, Villa de Leyva, Colombia.
[2] Present address: Programa de Biología y Museo de Historia Natural, Universidad de los Llanos, Villavicencio-Meta, Colombia.
[3] Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá, Colombia.
[4] Corporación Autónoma Regional de Santander, San Gil, Colombia.
[5] Smithsonian Tropical Research Institute, Apartado 0843-03092, Balboa, Ancón, Panamá.
Email: jorgeavec@gmail.com

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Resumen

Varias especies de aves cis-Andinas (i.e. Orinoco-Amazonas) han sido reportadas recientemente en la vertiente occidental de la Cordillera Oriental y el valle medio del Magdalena de Colombia (i.e. trans-Andes). En este artículo presentamos los registros adicionales para tres de estas especies. El Colibrí Llanero (*Polytmus guainumbi*), la Mirla Caripelada (*Turdus nudigenis*) y el Chango Llanero (*Quiscalus lugubris*). Reportamos por primera vez el Moriche Blanco (*Cissopis leverianus*) en la región trans-Andina. También discutimos algunas hipótesis que explicarían estos registros trans-Andinos con base en la ecología de estas especies y las características del paisaje. Dada la acelerada tasa de pérdida de hábitat y fragmentación a lo largo de las laderas Andinas y tierras bajas circundantes, en conjunto con el efecto del calentamiento global sobre los rangos de las especies, sugerimos que las expansiones a través y alrededor de los Andes podrían ser más comunes durante las próximas décadas. Las especies generalistas podrían liderar las expansiones, mientras que las especies especialistas podrían enfrentar reducciones poblacionales debido a sus limitadas habilidades de dispersión. Estos registros evidencian la necesidad de monitorear la transformación del paisaje, la colonización y viabilidad de las poblaciones de aves, así como la necesidad de continuar el trabajo de campo, incluso en regiones consideradas relativamente bien muestreadas en el país.

Palabras clave: Dispersión, extensión de distribución, levantamiento de los Andes, pasos de montaña, trans-Andino, transformación del paisaje

Abstract

Several cis-Andean (i.e. Orinoco-Amazon) bird species have been recently recorded on the west slope of the Cordillera Oriental and the middle Magdalena valley, in Colombia (i.e. trans-Andes). Here, we provide addi-

tional records for three of these species. White-tailed Goldenthroat (*Polytmus guainumbi*), Spectacled Thrush (*Turdus nudigenis*) and Carib Grackle (*Quiscalus lugubris*). We report Magpie Tanager (*Cissopis leverianus*) for the first time in the trans-Andean region. We also discuss some hypotheses explaining these trans-Andean records based on the ecology of these species and landscape characteristics. Given the accelerated rate of habitat loss and fragmentation along the Andean slopes and adjacent lowlands, coupled with the effect of global warming on species' ranges, we suggest that cross- and bypass-Andean expansions could become more common in the next decades. Generalist species could lead those expansions, whereas specialist species could face population reductions due to their limited dispersal abilities. These records show the necessity of monitoring the dynamics between landscape transformation, colonization and population viability of birds, and continuing fieldwork, even in areas considered relatively well sampled in the country.

Key words: Andean uplift, dispersal, landscape transformation, mountain passes, range extension, trans-Andean

Resumo

Várias espécies de aves cis-Andinas (ex. Orinoco-Amazonas) têm sido reportadas recentemente na vertente ocidental da cordilheira Oriental e o vale Meio do Magdalena, em Colômbia (ex. trans-Andes). Nesse artigo apresentamos registros adicionais para três dessas espécies. Beija-flor-de-bico-curvo (*Polytmus guainumbi*), Caraxué (*Turdus nudigenis*) e Iraúna-do-norte (*Quiscalus lugubris*).Reportamos pela primeira vez a Tietinga (*Cissopis leverianus*) na região trans-Andina. Também discutimos algumas hipóteses que explicariam esses registros trans-Andinos com base na ecologia dessas espécies e características da paisagem. Devido à acelerada taxa de perda de habitat e fragmentação ao longo das encostas Andinas e terras baixas ao redor, em conjunto como efeito do aquecimento global sobre o território das espécies, sugerimos que as expansões através e ao redor dos Andes poderiam ser mais comuns durante as próximas décadas; As espécies generalistas liderar as expansões, enquanto que as espécies especialistas poderiam enfrentar reduções populacionais por causa de suas limitadas habilidades de dispersão. Esses registros mostram a necessidade de monitorar a transformação da paisagem, a colonização e a viabilidade das populações de aves, assim como continuar o trabalho de campo, incluso nas regiões consideradas relativamente bem amostradas no país.

Palavras chaves: Dispersão, extensão de distribuição, levantamento dos Andes, passagem de montanha, trans-Andino, transformação da paisagem

Introduction

The Eastern Cordillera (Cordillera Oriental) of Colombia have played a significant role in the biogeography of northwestern South America, by separating tropical lowland forests of the Amazonian basin from those of west of the Andes in Colombia and Central America (Chapman 1917; Haffer, 1967; Brumfield and Caparella 1996). However, of 1410 tropical lowland evergreen forest species, only about 10% (146) occur in both east and west of the Andes (Stotz *et al.,* 1996). The occurrence of species with predominantly Amazonian distributions in the west of the Andes is often explained by four additive mechanisms operating at different time scales: (i) species could have been widely distributed in the whole northwestern South America before the final uplift of the Andes (Chapman 1917); (ii) dispersal over low passes in the northern Andes (Chapman, 1917); (iii) dispersal via corridors of tropical wet forest or grasslands around the northern tip of the Colombian Andes during the Quaternary (Haffer, 1967); and (iv) recent range extensions caused by deforestation, which facilitates expansion of non-forest dwelling species (i.e. grassland and/or open country species).

In recent decades, many studies have improved our knowledge about distribution of Colombian birds. However, most of them have focused on forested and remote areas in the Andes, while less attention has been devoted to the distribution of open country species, which could be favored by current forest fragmentation (e.g. Stiles *et al.,* 1999; ABO, 2000; De las Casas *et al.,* 2004; Estela and López-Victoria, 2005; Estela *et al.,* 2005; Echeverry-Galvis and Morales-Rozo, 2007; Johnston-Gonzáles *et al.,* 2006; Cuervo *et al.,* 2007; Donegan *et al.,* 2007; Avendaño 2012; Donegan 2012). Recently, some predominantly Amazonian species (cis-Andes) have been recorded in the west of the Andes of Colombia (trans-Andes) (Freeman *et al.,* 2012). However, little discussion has been developed about the ecological and biogeographical implications of these range ex-

tensions. Here, we give new data for three predominantly Amazonian species that have been recently recorded in the Caribbean region and middle Magdalena valley of northern Colombia, and present the first records west of the Andes for one bird species heretofore known to occur only in the lowlands and foothills east of the Eastern Cordillera. All records are based on field observations, and museum specimens support two of them. Finally, we discuss some possible causes mediating the presence of these species in the west of the Andes.

Materials and methods

We gathered field records during different surveys in several localities in departments of Cesar, Norte de Santander and Santander, among 2004 and 2011. In most localities, we made visual and auditory records during extensive observations (1-5 km), supplemented by mist-net captures and tape-recordings. However, some records correspond to opportunistic observations or were gathered in non-systematic surveys. Therefore, sampling is not equivalent in time or effort at all localities. A few voucher specimens were collected and deposited at Instituto de Ciencias Naturales (ICN) in the Universidad Nacional de Colombia, Bogotá.

Museum specimens of *Polytmus guanumbi* from the Chocó department, kept in the bird collection of Instituto Alexander von Humboldt (IAvH-A), were compared with Orinoco specimens housed at ICN with the aim of assessing for possible phenotypic differences at the populational level. Details on geographic coordinates and elevation for all localities are presented in Table 1. Nomenclature and phylogenetic order follow Remsen *et al.* (2013).

Table 1. List of 17 localities across the Eastern Cordillera, middle Magdalena valley and Chocó referenced in the text(in brackets). Localities are numbered in ascending order of latitude, south to north.

	Locality	Department	Coordinates (N, W); elevation (m)	Fieldworkers
1	Tibanica wetland (Bosa; Bogotá D.C.)	Cundinamarca	4°32′, 74°10′; 2850	ABO (2000)
2	Reinita Cielo Azul reserve (Serranía de los Yariguíes; Mun. San Vicente de Chucurí)	Santander	6°51′, 73°21; 1500-2100	Freeman *et al.*, (2012)
3	Mun. Piedecuesta	Santander	6°59′, 73°03′; 1000	JEA
4	El Humedal (vereda El Pantano; Mun. Girón)	Santander	7°00′, 73°13′; 1300	JEA
5	Quebrada las Tapias (Paramito, vereda Ruitoque; Mun. Floridablanca)	Santander	7°01′, 73°04′; 1100-1200	JOCH
6	Quebrada la Judía (vereda La Judía; Mun. Floridablanca)	Santander	7°05′, 73°02′; 1500	JEA & ERBL
7	Cañaverales/El Puente farms (corregimiento de Portugal; Mun. Lebrija)	Santander	7°09′; 73°17; 1100-1200	JEA
8	Villa Vista farm (vereda El Aburrido; Mun. Bucaramanga)	Santander	7°14′, 73°05′; 1700	JEA & ERBL
9	Los Andes farm (vereda Honduras; Mun. Rionegro)	Santander	7°16′, 73°05′; 1750	JEA & ERBL
10	Buenos Aires farm (vereda Bremen; Mun. Matanza)	Santander	7°20′, 73°05′; 1700	JEA & ERBL
11	Tangarra (right margin of the Atrato River; Mun. Turbo)	Antioquia	7°48′, 77°08′; 0-50	IAvH-A
12	Hacienda Sautatá (left margin of the Atrato River; Mun. Riosucio)	Chocó	7°50′, 77°04′; 0-50	IAvH-A
13	Vereda Peye (left margin of the Atrato River; Mun. Riosucio)	Chocó	7°54′, 77°05′; 0-50	IAvH-A
14	Pueblo Nuevo (vereda El Cauca; Mun. Ocaña)	N. de Santander	8°09′, 73°25′; 700-900	Freeman *et al.*, (2012)
15	La Mesita farm (Mun. Convención)	N. de Santander	8°28′, 73°20′; 1180	JEA
16	Casacará River (vereda Las Vegas; Mun. Agustín Codazzi)	Cesar	9°59′, 73°03′; 1400	JEA & DARG
17	Mun. Agustín Codazzi	Cesar	10°02′, 73°14′; 200	JEA & DARG

Results

White-tailed Goldenthroat (Polytmus guainumbi)

This hummingbird has a large distribution in South America ranging the savannas, surrounding the Amazon basin, from Argentina to Venezuela and Trinidad and Tobago. To the north of the Amazon River, it inhabits the savannas (Llanos) of Colombia and Venezuela from the eastern foothills of the Eastern Cordillera and the Mérida Andes to the Guianas and northern Brazil (Schuchmann, 1999). It favors damp or marshy grasslands mainly, and pastures especially in vicinity of water, from sea level to 600 m, reaching 1,500 m south the Orinoco in Venezuela (Hilty, 2003). Seven specimens (IAvH-A 3116-21, 4458) of this species were collected in the Chocó Biogeographic region of northwest Colombia. It was found at three localities (11-13) along the margins of the Atrato River, at Los Katíos National Park by staff of INDERENA, during 1975-79 (Fig. 1). Although this population was reported by Rodríguez-Mahecha (1982), these records have been overlooked by recent publications (Hilty and Brown 1986; Schuchmann, 1999; Restall *et al.,* 2006; McMullan *et al.,* 2010). Two more trans-Andean records came from the foothills of west slope of Eastern Cordillera, in Santander. JEA observed this species at the swamp known as El Humedal (4) on 29 November 2006 hovering around small flowering shrubs in the middle of the swamp, but did not observe it in gallery forests, grasslands or pineapple crops around the swamp. Close to this locality, JOCH observed one individual along Las Tapias stream (5) on 10 July 2008 foraging from an exotic plant (*Spathodea campanulata*). Recently, Freeman *et al.,* (2012) recorded the species on 23 May 2010 below Ocaña (14) (c. 700 m), department of Norte de Santander, in the west slope of the Cordillera. These records suggest that, in addition to its widespread occurrence east of the Andes, the species has a local distribution in the Atrato and middle Magdalena valley, apparently restricted to riverine habitats and freshwater swamps from sea level to 1,300 m.

Spectacled Thrush (Turdus nudigenis)

This species is found in gallery forest borders, semi-open areas with scattered groves of trees and semi-urban areas east of the Andes from Colombia to the Guianas and northeast Brazil (Hilty, 2003). It ranges in the lowlands east of the Andes in Colombia, from the

Figure 1. Ventral, lateral and dorsal views of two male specimens of *P. guainumbi,* from Colombia. Left: ICN 30998 from Campamento Caño Limón, Arauca, collected on March 27 1991. Right: IAVH-A 3116 from vereda Peye, P.N.N. Los Katíos, Riosucio, Chocó, collected on August 3 1976.

Catatumbo region in Norte de Santander to the Llanos in Meta department, with the highest records at mid-elevations (1,500-1,600 m) on the east slope of the Eastern Cordillera (Hilty and Brown, 1986). The species was collected near to the east ridge of the Cordillera, in a cultivated area at Convención (15), Norte de Santander (ICN 35345), on 24 March 2004. However, confirmed trans-Andean records of *T. nudigenis* came from one specimen (ICN 35807) and single individuals observed from May to November 2005 at small forest patches at the Cañaverales and El Puente farms (7), in Santander. In addition, the northernmost record west of the Cordillera corresponds to an individual observed on 4 June 2011 close to shrubs in pasture lands on the west slope of Serranía de Perijá at the Casacará River (16), Cesar department. The southernmost record comes from Reinita Cielo Azul reserve (2) in the west slope of the Serranía de los Yariguíes, Santander, where it was recorded on July 2010 and August 2011 (Freeman *et al.,* 2012).

Magpie Tanager (Cissopis leverianus)

This tanager is widely distributed in the lowlands, up to 1,200 m east of the Andes from northeast Argentina to the Andes of Venezuela, where it ranges up to 2,000 m (Isler and Isler, 1999). It inhabits shrubby and regenerating clearings in humid forests, open woodlands, river edges, and also plantations (Isler and Isler, 1999; Hilty, 2003). It occurs in the lowlands east of the Eastern Cordillera from Norte de Santander south to Amazonas departments (Hilty and Brown, 1986). ERBL and JEA recorded groups of 3-5 individuals of this species at four localities (6, 8-10) along the west slope of the Cordillera in the department of Santander, between 2004 and 2007. All records were made along forest borders or in grasslands with scattered trees between 1,500 m and 1,750 m. Recently, DARG and JEA observed a pair on 1-4 June 2011 visiting tall bushes and forest borders close to pastures on the west slope of Serranía de Perijá at the Casacará river (16).

Carib Grackle (Quiscalus lugubris)

This grackle is commonly known from the Llanos, in Eastern Colombia, to the Guianas, the mouth of Amazon in Brazil, and the Lesser Antilles, with some populations introduced in Tobago and Aruba, and vagrants recorded in Bonaire (Restall *et al.,* 2006). It favors open and semi-open habitats with scattered trees, urban and seaside areas, and also the edges of gallery forests from the sea level to 850 m (Hilty, 2003; Restall *et al.,* 2006). Recent evidence suggests that it is spreading to the west of the Andes through two distinct routes due to deforestation. One is along the Caribbean coast of northern Venezuela, in Falcón state (Hilty, 2003), possibly resulting in the recent colonization of the Guajira peninsula and Caribbean coast in Colombia (Strewe *et al.*, 2006). The species was recorded along the Santa Marta and Barrancabermeja highway, during February 2011, with the southernmost record at Puerto Boyacá, department of Boyacá (Freeman *et al.,* 2012). The most recent records come from a group of three males and six females that visited some bushes scattered in grasslands at 1,400 m on the west slope of Serranía de Perijá, in the Casacará River (16), Cesar department. After five minutes foraging, the group flew to the low and more deforested part of the River. The species was also observed in the urban area of Agustín Codazzi (17), where it is apparently common. Moreover, JEA observed a pair on 27 September 2011 at the urban area of the municipality of Piedecuesta (3), Santander. Besides, four individuals of *Q. lugubris* were recorded at the Tibanica wetland (1) in the Altiplano Cundiboyacense region (ABO, 2000).

Discussion

The records brought here are into two classes: grassland-restricted species previously unrecorded west of the Andes or overlooked in museums (*P. guainumbi*), and open-country species (*T. nudigenis*, *C. leverianus,* and *Q. lugubris*) that have presumably expanded their distributions recently. The former group includes one species of savanna grasslands (*P. guainumbi*). Haffer (1967) hypothesized the expansion of grasslands through the northern tip of the Andes (i.e. the Guajira peninsula). According to him, during several dry climatic periods of the Pleistocene and post-Pleistocene the northern tip of the Andes was a possible route ("bypassing the Andes") for the colonization of non-forest species in the Caribbean lowlands of northern Colombia. Sea levels were lower and lowland grassland areas were more extensive during these periods (Ramírez-Barahona and Eguiarte 2013). Indeed, the lack of phenotypic differences between cis- and trans-Andean populations (F. G. Stiles pers. com.) could make this scenario more likely than an earlier vicariant event. Dispersal through open environments associated with watercourses is possible in *P. guainumbi*, because species associated with these habitats are expected to show better dispersal capabilities than closed-forest species, allowing them to track the seasonal dynamics of riverine environments (Cadena *et al.,* 2011). Alternatively, the trans-Andean populations could correspond to relicts isolated during the Andean uplift. The scarcity of records of *P. guainumbi* in the trans-Andean region is similar to that of other widely distributed cis-Andean species

that have been recently recorded to the west of the Andes (*Dromococcyx pavoninus* (Hilty and Brown, 1986; Cuervo *et al.,* 2008; Freeman *et al.,* 2012, Donegan 2012) and *Megascops guatemalae* (Freeman *et al.,* 2012)).

These species have been overlooked possibly due to shortcomings in ornithological samplings, coupled with the local and apparently low abundance of their trans-Andean populations. Whether the trans-Andean populations of *P. guainumbi* are the result of a demographic expansion during the Pleistocene/post-Pleistocene or were isolated from the Amazonian populations during the uplift of the Andes, represent two mutually exclusive hypotheses that can be tested through phylogeographic and coalescent methods.

The second group of records (*T. nudigenis*, *C. leverianus* and *Q. lugubris*) corresponds to range expansions of open-country species probably facilitated by deforestation. Indeed, birds inhabiting forest edge are less sensitive to habitat disturbance. They are more prone to crossing habitat gaps and open areas than their counterparts restricted to the understory (Şekercioğlu *et al.,* 2002). Moreover, recent evidence suggests that canopy-midstory species have higher dispersal propensity, on average, than understory birds due to several factors such as their heterogeneous habitat preferences, less dietary specialization and greater fluctuations in local and seasonal abundance (Burney and Brumfield, 2009). These factors combined with the current maximum altitudinal range of *T. nudigenis* and *C. leverianus*, c. 1,200-1,600 m on the east slope of the Eastern Cordillera, suggests that colonization of the west slope and of the middle Magdalena valley could have occurred through low mountain passes such as the depression (c. 1,400 m) that connects the Serranía de los Motilones with the rest of the Eastern Cordillera, in Ocaña, Norte de Santander. Both species have been recorded there. Supporting this cross-Andean dispersal at the Ocaña depression are recent records at the west slope of several east slope species such as Scaled Piculet *Picumnus squamulatus*, Red-crowned Ant Tanager *Habia rubica* and Burnished-buff Tanager *Tangara cayana* (Freeman *et al.,* 2012).

As *T. nudigenis* is a popular cage bird in the Llanos (F. G. Stiles pers. com.) and escaped individuals of *C. leverianus* have been observed in Antioquia (A. M. Cuervo pers. com.), It arises questions like whether the west slope records in the Eastern Cordillera correspond to introduced or escaped birds. We consulted databases on illegal trade bird species in the Santander department during the past fourteen years (data from CDMB and CAS environmental government corporations). Most of the confiscated birds by these corporations are usually released. However, we did not find any record of illegal trade or release of *T. nudigenis* or *C. leverianus*. In the case of *C. leverianus*, ERBL and others conducted 25 inquiries in 2004 with families in vereda La Judía where the species was first recorded. The results showed that *C. leverianus* was seen for the first time in the area in 2003-2004. None of those consulted families admitted to have kept this species as a cage bird. Therefore, the available data do not show evidence of a possible introduction of these species, at least, in Santander department.

The presence of *Q. lugubris* on the Altiplano Cundiboyacense is more complex to explain. If the species crossed the Andes via a low pass, the nearest is Las Cruces (Andalucía) Pass (c. 1,200 m) in Huila department. As a result, several populations might be expected along the eastern foothills of the upper Magdalena valley, where it has not been recorded till now. Alternatively, the species could have ascended the Andes from the Llanos. Indeed, the species may have moved up the dry Río Negro valley (east slope of the Cordillera) as it has been recorded near Cáqueza (c. 800 m); but this implies that it has crossed a considerably higher pass (El Boquerón de Chipaque, c. 3150 m) in the Cerros Orientales of Bogotá (F. G. Stiles pers. com.). Therefore, a process of introduction is a more plausible hypothesis for explaining the presence of *Q. lugubris* on the Altiplano. The arriving of *Molothrus bonariensis* on the Sabana de Bogotá (Jiménez and Cadena, 2004) stands this hypothesis. However, the Perijá and Cáqueza records show that *Q. lugubris* has the potential to colonize higher elevations than previously were known. The species is known for making local movements in the Llanos (Restall *et al.,* 2006). Dispersal to the highlands could be enhanced through a stepping-stone process tracking open or fragmented habitats along the Andean slopes. Indeed, many low-elevation species from the west slope of the Cordillera seem to have colonized the Altiplano following this process, for the last 10-30 years (ABO, 2000). The records from Piedecuesta (this study) and Puerto Boyacá (Freeman *et al.,* 2012) are noteworthy in showing the high dispersal ability of this species, which has expanded its range to the middle Magdalena valley by c. 600 km in six years, since it was recorded for first time in Magdalena department (Strewe *et al.,* 2006).

There is increasing evidence of range expansions by deforestation in the middle Magdalena and Cauca valleys (Stiles *et al.,* 1999, Garcés-Restrepo *et al.,* 2012), the Chocó (Johnston-Gonzáles *et al.,* 2006), and the Amazonian foothills (Salaman *et al.,* 2002). There is also evidence of expansions of lowland species recently es-

tablished in the Altiplano Cundiboyancese (ABO, 2000; Zuluaga-Bonilla, 2006). Previous to these records, just one cross-Andean expansion had been reported in Colombia. The Scrub Tanager (*Tangara vitriolina*) has colonized the east slope of the Eastern Cordillera, possibly through the head of the Magdalena valley (Salaman *et al.,* 2002). However, the records brought here suggest that cross- and bypass-Andean expansions could become more common in the next decades, due to the current fragmentation of the Andean forests, the accelerated transformation of natural ecosystems in the lowlands of the Amazon, Pacific and the savannas of the Orinoco plains (Etter and van Wyngaarden, 2000), and projected effects of global warming on the range of species in Colombia (Velásquez-Tibatá*et al.,* 2012).

In fact, a recent meta-analysis found that the distribution of many terrestrial organisms has shifted recently to higher elevations at a median rate of 11.0 m per decade, and to higher latitudes at a median rate of 16.9 km per decade (Chen *et al.,* 2011). It is assumed that these shifts result because species track their optimal habitat in response to the rearrangement of climate zones. As climate warming displaces climate zones uphill, lowland forest specialists or poor dispersal species could be greater affected in comparison with generalists or high dispersal species (Warren *et al.,* 2001; Velásquez-Tibatá *et al.,* 2012). For specialists, uphill or northward dispersal will depend on the availability of suitable habitat patches and their ability to cross through fragmented or open habitats. Therefore, uphill expansion in specialists could mean a cost in population size due to range reduction and fragmentation (Gaston, 1994). In contrast, the higher resilience to habitat fragmentation and greater dispersal abilities of generalist species could help them to track their habitat requirements. Therefore, it is expected that future bird range extensions, crossing or bypassing the Andes, is led for generalist species mainly (i.e. open-country, savanna, and freshwater species). In sum, the records discussed here highlight the importance of monitoring fragmented habitats in order to understand the dynamics of landscape transformation, bird colonization and population viability, as well as the need for continuing field work in areas considered relatively well-sampled in Colombia (e.g. middle Magdalena and Atrato valleys).

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