

Arid valleys as dispersal barriers to high-Andean forest birds in Ecuador

Niels Krabbe

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Los patrones de distribución de aves en los Andes son complejos como su topografía. Nuestro conocimiento sobre las barreras (geográficas, ecológicas) que limitan la distribución de las especies es todavía incipiente. Sin embargo, aquí presento algunos ejemplos de especies cuyos rangos se interrumpen por los ríos que intersectan la cordillera andina. La barrera más importante al este de los Andes es al parecer el río Zamora, mientras en la cordillera occidental los valles secos de los ríos Mira y Chimbo-Chanchán son los más sobresalientes. Con esta nota espero contribuir al entendimiento de la distribución de aves en los Andes ecuatorianos y, sobre todo, a incentivar estudios más profundos.

The altitudinal range of the Andean slopes is so wide (c.1,000–6,000 m) that large expanses of humid forest have been able to persist through historical climate fluctuations by 'simply' moving up and down the slopes. This has permitted the evolution of a number of sedentary species with poor flying abilities or a reluctance to cross unsuitable habitat. High-elevation forests, which also expand latitudinally during cold climates, possess a greater ability to spread across dry valleys than do many such birds.

At present, the climate in the high Andes is fairly uniform along the Pacific slope from Colombia to south-central Ecuador, and along the Amazonian slope from Venezuela to Bolivia. That many high-Andean bird species occur in forests with several different soil types and yet have very limited geographical distributions, might indicate that history has played an important role in shaping their present ranges.

Apart from gaps in suitable habitat, latitudinal dispersal may be hindered by presence of competitors, usually closely related species, as perhaps best exemplified by *Scytalopus tapaculos*², but is also seen in many other families. The suture zones ('ceasefire lines') between such species-pairs may be temporarily sited in uniform habitat, but unless altitudinal or niche segregation of the species evolves, the sutures eventually come to coincide with minor or major dispersal barriers. One could define a major dispersal barrier as a habitat gap too wide to cross even in the absence of a closely related competitor on the other side³.

Although absence of a species from an area with seemingly suitable habitat may have been caused by local extinction, one might still infer from absence that the area is sufficiently isolated to hinder recolonisation or slow it down considerably. In the following, I focus on some dry valleys in the high Andes of Ecuador that mark limits to present-day bird distributions, and discuss their roles as minor or major dispersal barriers. Most of these

forest gaps have been discussed to a varying degree in previous literature^{1,3-6}.

Some of the broadest dry valleys in the Ecuadorian Andes run north-south. They divide the Andes into an eastern and a western chain in much of the country. The two chains are connected by several transverse ridges ('nudos¹'), but these are drier than the outer slopes, and only a few appear to have functioned as corridors between eastern and western faunas, and only for a limited number of species. That more than 20 widespread forest species occurring on a variety of soil types in the high parts of the East Andes are missing from similar habitats in the West Andes, where they are not replaced by ecologically similar species, strongly suggests that these ridges have also possessed unsuitable habitat during other climates, and that the central dry valleys should be considered a major dispersal barrier to a number of species. The colonisation of the Cajas plateau by certain east-slope species is briefly mentioned below, but has previously been discussed in much greater detail⁵.

Further, several dry valleys intersect the humid forests on the outer slopes and coincide with present-day north-south boundaries of bird distributions. On the east slope, the only dry valley that should be considered a major dispersal barrier is that of the río Zamora¹. It forms a distributional boundary to several bird species. The strongest case for considering it a major barrier is that of the Crescent-faced Antpitta *Grallaricula lineifrons*⁶, which species replaces its close relative Slate-crowned Antpitta *G. nana* above 2,900 m throughout its range. South of the río Zamora, however, where Crescent-faced is absent, Slate-crowned ascends all the way to treeline, strongly suggesting a competitive release resulting from the río Zamora Valley being a true dispersal barrier to *lineifrons*. In addition, the valley forms the southern boundary of the ranges of Agile Tit-Tyrant *Uromyias agilis* and Black-backed Bush Tanager

Urothraupis stolzmanni. In particular, the former is widespread where it occurs, and seemingly suitable habitats for both species exist south of the valley. Finally, the valley forms the boundary between the species-pair Viridian *Metallura williami* and Neblina Metaltails *M. odomae*, and between two distinct populations of Páramo Tapaculo *Scytalopus canus*.

Another dry valley on the east slope, that of the río Paute, may have presented a major dispersal barrier during cooler and drier climates, but is currently only a minor barrier. It does form the modern boundary between two species-pairs: Tourmaline *Heliangelus exortis* and Flame-throated Sunangels *H. micraster* and White-chinned *Schizoeaca fuliginosa* and Mouse-coloured Thistletails *S. griseomurina*. However, for some other species-pairs the suture lies in seemingly uniform habitat just south of the valley, without coinciding with it, which suggests that they are results of recent colonisation across the valley. These are Andean *Penelope montagnii* and Bearded Guans *P. barbata*, Spillmann's *Scytalopus spillmanni* and Chusquea Tapaculos *S. parkeri*, and Slaty *Atlapetes schistaceus* and Northern Rufous-naped Brush Finches *A. latinuchus*. In the small areas of overlap, the guans replace each other altitudinally, whereas the brush finches have undergone a partial niche shift, *schistaceus* moving more rapidly and foraging higher in the vegetation and further out on branches than *latinuchus* (pers. obs.). The suture between the tapaculos has not been located. Several species appear to have an endpoint or break in their distribution at this river, but for at least some of them, this may be ecologically determined rather than the result of the valley serving as a dispersal barrier. It should be noted that the Sangay region is relatively little studied, and some species thought to be absent, such as Black-eared Hemispingus *Hemispingus melanotis* and Metallic-green Tanager *Tangara labradorides*, may prove to occur there after all.

Parts of the west slope of the Andes are drier than the east slope, and the humid forests are intersected by a larger number of dry valleys, including those of the Mira, Chimbo, Chanchán, Jubones, Puyango and Catamayo rivers, all of which on present knowledge appear to mark endpoints in bird distributions. Others might be added, but some parts of the west slope are ornithologically poorly known, in particular the outer slope of Cordillera Toisán in Esmeraldas province, the region between the Toachi and Chimbo rivers, and the higher parts between the Jubones and Puyango rivers. In the northern part of the west slope only two dry valleys may qualify as major dispersal barriers: the río Mira and río Chanchán (and Chimbo) valleys.

The río Mira Valley marks the southern limit on the west slope of several species, perhaps most notably Viridian Metaltail and Páramo Tapaculo, both of which are widespread in the East Andes, where they occupy a wide range of habitats. However, the isolated occurrence on the west slope in Carchi of Sulphur-bellied Tyrannulet *Mecocerculus minor*, a species capable of at least some sustained flight, may suggest the fairly recent presence of a habitat bridge between the East and West Andes in southernmost Colombia and/or northernmost Ecuador³.

The Chanchán and Chimbo river valleys have long been recognised as dispersal barriers¹. Despite the presence of suitable habitat and absence of closely related competitors south of the valleys, several species only range south to the río Chanchán Valley, including Buff-winged Starfrontlet *Coeligena lutetiae*, Ocellated Tapaculo *Acropternis orthonyx*, Barred Fruiteater *Pipreola arcuata*, Plain-tailed Wren *Thryothorus euophrys* and Glossy Flowerpiercer *Diglossa lafresnayi*.

Elevations below 2,500 m on the Pacific slope in Azuay are ornithologically relatively poorly known, and some of the species thought to be absent, such as Collared Inca *Coeligena torquata*, Striped Treehunter *Thripadectes holostictus*, Long-tailed Antbird *Drymophila caudata*, Rufous-headed Pygmy Tyrant *Pseudotriccus ruficeps*, Rufous-crowned Tody-Flycatcher *Poecilotriccus ruficeps*, Yellow-bellied Chat-Tyrant *Ochthoeca diadema*, Barred Becard *Pachyramphus versicolor*, Capped Conebill *Conirostrum albifrons*, Hooded Mountain Tanager *Buthraupis montana* and Grass-green Tanager *Chlorornis riefferii* might occur.

Some of the East-Andean species that have crossed over to the Cajas plateau in Azuay⁵ have spread around or over the plateau to the Pacific slope. Two of these, Grey-breasted Mountain Toucan *Andigena hypoglauca* and Mouse-coloured Thistletail are replaced north of the río Chanchán Valley by closely related competitors: Plate-billed Mountain Toucan *Andigena laminirostris* and White-chinned Thistletail. Meanwhile, Lacrimose Mountain Tanager *Anisognathus lacrymosus*, which in view of its fairly widespread distribution in the eastern Andes must be considered to have well-developed dispersal abilities, has no apparent competitor north of the valley.

Characterisation of the río Chimbo Valley as a major dispersal barrier is supported by the distribution of a distinctive subspecies of Rainbow Starfrontlet *Coeligena iris hesperis*. This hummingbird is endemic to the Cajas area and the forest between the Chimbo and Chanchán valleys, yet does not appear to have very specific habitat requirements. The Chimbo Valley also marks the southern limits of Rufous Wren *Cinnycerthia unirufa*, Nariño Tapaculo *Scytalopus vicinior* and

perhaps Moustached *Grallaria alleni* and Chestnut-naped Antpitta *G. nuchalis*, all species of relatively poor flight.

As stated above, the higher parts of the Chilla Mountains between the Jubones and Puyango rivers are so poorly known ornithologically that it is difficult to ascertain the effect of the Jubones Valley as a dispersal barrier. The presence in the Chilla Mountains of Yellow-bellied Chat-Tyrant and Hooded Mountain Tanager, both apparently absent from the Pacific slope in Azuay, suggests that the Chilla Mountains may have served as a bridge for dispersal from the East Andes to the Pacific slope. Lacrimose Mountain Tanager, which on the west slope only occurs in the areas immediately north and south of the río Puyango, may have crossed this way or via the 'Cañar bridge', to subsequently spread across the Jubones Valley, or via both bridges. The Chilla range merits extensive research in order to elucidate bird distribution patterns in the region.

Further south, between the valleys of the Puyango and Catamayo rivers, the Celica Mountains lie very isolated. They barely exceed 2,600 m and hence lack many high-elevation species, but a large number of birds of lower temperate and subtropical climates are also missing; a fact difficult to explain except by the continued aridity of the wide and deep valleys surrounding them, and thereby serving as major dispersal barriers. Despite morphological resemblance to the nearest other populations, Northern Rufous-naped Brush-Finches from the Celica mountains differ by as much as 1.6% in mitochondrial DNA sequences (J. García-Moreno unpubl.), suggesting that they have been isolated for an extended period of time.

In conclusion, there are still so many gaps in our knowledge that it remains a challenge to future ornithologists to reliably determine the distributional limits of many Ecuadorian birds.

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Niels Krabbe

E-mail: NKKrabbe@snm.ku.dk.