Biogeographic Barriers in the Andes: Is the Amotape—Huancabamba Zone a Dispersal Barrier for Dry Forest Plants?

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BIOGEOGRAPHIC BARRIERS IN THE ANDES: IS THE AMOTAPE–HUANCABAMBA ZONE A DISPERSAL BARRIER FOR DRY FOREST PLANTS?[1]

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Abstract

We investigate whether the Amotape–Huancabamba zone in the Andes acts as a barrier or corridor for plant species migration. We test this hypothesis based on data on trees, shrubs, and herbs collected in dry inter-Andean valleys (DIAVs) of Ecuador. We found that 72% of the species cross the Amotape–Huancabamba zone in a north–south direction and 13% of the species cross the Andes in an east–west direction. Southern DIAVs concentrate the highest numbers of endemic species. At the regional level we found that 43% of the species are exclusively Andean, while the remaining 57% are found in the Pacific lowlands, the Caribbean, and Mesoamerica. These results showing many species crossing the Amotape–Huancabamba zone in a north–south direction and also frequently found in neighboring lowland and highland ecosystems suggest that the Amotape–Huancabamba zone acts as a corridor for species migration of dry inter-Andean flora.

Key words: Amotape–Huancabamba zone, Ecuador, endemism, IUCN Red List, species ranges.

Many recent studies point to the role of Andean orogeny in shaping the evolution and biogeography of the Neotropical flora, emphasizing its effects on climate, the direction of flow of major rivers, and as a dispersal barrier (Hoorn, 1993; Antonelli et al., 2009). Dispersal barriers may shape species ranges, which are dynamic over time and thought to depend on the dispersal capacity of the species (Shmida & Wilson, 1985). Literature discussing the Andean cordillera as a dispersal barrier emphasizes the north–south orientation of the mountain chain (Antonelli et al., 2009) and how that orientation isolates the narrow lowland Pacific coastal plain on the western side of the continent from the vast lowlands to the east.

In what is now southern Ecuador and northern Peru the Andean orogeny has been least pronounced, resulting in the lowest altitudes in the tropical Andes. In addition, the eastern and central cordilleras were eroded by the Chamaya and Marañon rivers, and although the western cordillera does extend from Peru to Ecuador, its lowest parts never reach above 2145 m altitude (Weigend, 2002). This low saddle in the Andes was called the Amotape–Huancabamba zone by Berry (1982) and was described in more detail by Weigend (2002, 2004). It has also been called the Huancabamba deflection by those who emphasize the knee or changing orientation of the cordillera, or the northern Peruvian low, or the Piura divide (Molau, 1988). In this paper we use the term Amotape–Huancabamba zone, which has become widely used in phytogeographical studies (Berry, 1982; Weigend, 2002, 2004).

Although other parts of the Andes were already uplifted by the time of the Eocene, it is thought that the Huancabamba area was then at sea level and invaded by marine incursions. This western Andean portal was closed by the Middle Miocene by the growing Andean mountain chain, but its effect as an early dispersal barrier for lowland plants has been suggested by the geographical structure of the phylogenies of extant groups (e.g., Rubiaceae; Antonelli

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et al., 2009). In addition, the orthodox view of the Amotape–Huancabamba zone as a more recent biogeographic barrier for montane plant groups is evidenced by taxa exhibiting centers of endemism to both its north and south (e.g., Campanulaceae, Calceolariaceae, Tropaeolaceae; reviewed by Antonelli et al. [2009] and Antonelli and Sanmartín [2011]), despite earlier authors indicating that it does not seem to have been a major dispersal barrier for highland groups such as Passifloraceae, Grossulariaceae (Weigend, 2002), and Onagraceae (*Fuchsia* L.; Berry, 1982).

In this context, the Amotape–Huancabamba zone, situated in southern Ecuador and northern Peru, has also been considered as a barrier for the north–south dispersal of both highland (Molau, 1988; Weigend, 2002; Antonelli & Sanmartín, 2011) and lowland plant taxa (Antonelli et al., 2009).

Here we use a new dataset of 63 plant inventories made in seasonally dry tropical forest (SDTF) vegetation from dry inter-Andean valleys (DIAVs) in Ecuador to investigate species distribution ranges in an area crossed by a biogeographic barrier, the Amotape–Huancabamba zone. Our approach is to look at the flora of a particular ecosystem in the DIAVs, rather than particular taxonomic groups as in previous studies, so our surveys cover the entire flowering plant community that stretches along a north–south latitudinal gradient extending ~600 km in the Ecuadorian Andes, spanning from the center of the Amotope–Huancabamba zone (ca. 6°S) to well beyond its northern limit at 3°S, allowing an assessment of how many species end their range at its northern limit. In addition, we use distribution information for all native species to assess whether their ranges are limited by the Amotape–Huancabamba zone.

We address the following questions: (1) How many species in our northern surveys have ranges that cease at the boundary of the Amotape–Huancabamba zone? (2) Are most of DIAV species also found to the east and west of the Andes? (3) Are there more endemic species inside the Amotape–Huancabamba zone than north of its limit? (4) How large is the geographic distribution of the DIAV species across the Neotropics?

Answering these questions addresses the nature of the Amotape–Huancabamba zone as a biogeographic barrier in the Andes for the SDTF flora.

Methods

study area and vegetation

Our inventories span from the Amotape–Huancabamba zone stretching from 1°N, across the Girón–Paute valley into the higher cordillera at 5°S where DIAVs are found between the eastern and western Andean cordilleras. Seasonality is pronounced in these valleys, and their mean annual precipitation is usually less than 1600 mm with a

prolonged dry season of more than five months. In the driest valleys, the precipitation is as low as 430 mm per year and the vegetation is made up of cactus scrub dominated by spiny trees, mostly *Vachellia macracantha* (Humb. & Bonpl. ex Willd.) Seigler & Ebinger and *Tara spinosa* (Feuillée ex Molina) Britton & Rose, and a few species of grasses that form the ground cover (Quintana et al., 2017). In less dry valleys, with ~850 mm annual precipitation, the vegetation is semi-deciduous forest with a closed canopy dominated by *Inga insignis* Kunth, *Tecoma stans* (L.) Juss. ex Kunth, and *Schinus molle* L. All these vegetation types fall within the concept of the SDTF biome, which is patchily distributed from northwestern Mexico to northern Argentina. Within this large area, SDTF occupies dry Andean valleys in Colombia, Ecuador, Peru, and Bolivia; the dry coastal lowlands of Ecuador and Peru; as well as central and southwestern Brazil (Pennington et al., 2009; Linares-Palomino et al., 2011; DRYFLOR et al., 2016). These forests have a 3- to 6-month dry season and rich soils that support deciduous vegetation (Murphy & Lugo, 1986; Sánchez-Azofeifa et al., 2005).

The northern starting point of the Amotape–Huancabamba zone is located in southern Ecuador at around 2°30′–3°S (Weigend, 2002), coinciding with the Girón–Paute valley (Jørgensen & Ulloa Ulloa, 1994). North of this valley the mountains are tall, reaching altitudes of almost 6000 m. To the south, the tallest peaks do not exceed 4000 m and the eastern and western cordilleras—which are so obvious farther north—are no longer recognizable as separate mountain chains (Hall, 1977; Hall & Calle, 1982). DIAVs north of the Girón–Paute valley lie between 1300 and 2800 m above sea level, while southern DIAVs found within the Amotape–Huancabamba zone are found between 800 and 2100 m (Quintana et al., 2017).

data collection

Fieldwork was carried out from January to April 2014. We established 63 transects, each measuring 5 × 100 m, along a north–south latitudinal gradient extending ~600 km in the Ecuadorian Andes (Fig. 1). We placed our transects in sites least impacted by human activities. In each transect all mature trees and shrubs were identified and counted to determine their abundance. Specimens of all species were collected and vouchers were deposited in QCA of the Pontificia Universidad Católica del Ecuador. The coverage of terrestrial herbs was estimated in each 500 m² transect on an ordinal scale from 1 to 5 (1 = ≤ 100 m², 2 = 101 ≤ 200 m², 3 = 201 ≤ 300 m², 4 = 301 ≤ 400 m², 5 = 401 ≤ 500 m²).

analyzing the distributions of diav species

The 314 species encountered were grouped into four categories (Table 1). Within the latitudinal range of our
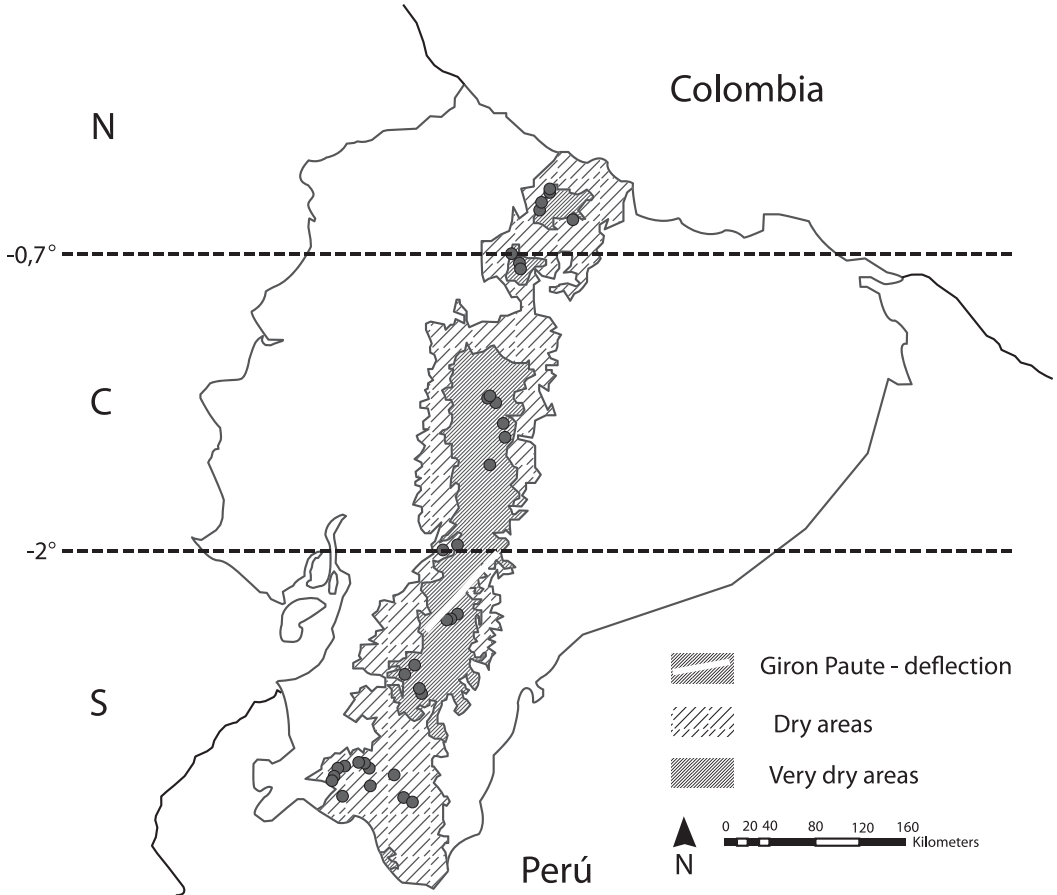
Sample localities of Ecuadorian DIAVs

Figure 1. Map of Ecuador. Black dots represent the location of 63 transects in the dry inter-Andean valleys. The Girón–Paute deflection (GPD) is shown with a white line. Dry areas are 5 to 9 months with precipitation < 100 mm; very dry areas are > 9 months < 100 mm. Black dotted lines show Ecuadorian divisions for north (N), center (C), and south (S). Modified from Quintana et al. (2017).

study (~6°), we categorized species as distributed either in the northern or southern parts of the study area, following a dividing line at the Girón–Paute valley, which forms a diagonal line at ~2°30′S (Fig. 1). For practical reasons and following the distribution patterns shown by most of the species, we defined "northern species" as those recorded exclusively north of 2°S and "southern species" as those recorded south of that line. Apart from the species with restricted distribution north or south of 2°S, there were widespread species covering the whole latitudinal range and species with disjunct distributions with a gap between 0.7 and 2°S (Table 1). To place species in latitudinal categories we evaluated distribution maps of the 314 DIAV species to determine if they cross the Girón–Paute valley (~2°30′S). We used maps provided by Tropicos® (<http://www.tropicos.org>). If the distribution of the species starting

at a northern or southern point continued farther north or south from the Girón–Paute valley, we concluded that the species crosses the Amotape–Huancabamba zone. If the distribution of the species stopped before a northern or southern point from the Girón–Paute valley, we

Table 1. Distribution patterns of dry inter-Andean valleys (DIAVs) at different elevations and latitudes in Ecuador.

Distribution pattern	Elevation (m)	Latitude
North	1300–2800	north of 2°S
South	800–2100	south of 2°S
Disjunct	800–2800	north of 0.7°S and south of 2°S
Wide	800–2800	covering the range 1°N–5°S

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concluded that the species did not cross the Amotape–Huancabamba zone. This analysis was not applied to introduced species, as their geographical range is artificial.

The species occurring in DIAVs may also grow to the east or west of the Andes as well as at higher and lower altitudes. For our analysis we recognized five ecosystems defined by their geographic position and altitude: (1) Amazon lowlands (east of the Andes), (2) dry inter-Andean, (3) eastern montane forest, (4) Pacific lowland forest (west of the Andes), and (5) western montane forest (Table 2). We used the designation "ALL" for plants found in all ecosystems. When the western or eastern ranges of montane forest species were uncertain (7.3% species), we assigned them to a sixth category of montane forests and páramo.

We listed all 314 species recorded in the transects (including four infraspecific taxa) and determined their regional and global distribution (Table S1; <https://www.puce.edu.ec/portal/content/Proyectos/547?link=oln30.redirect>). We used the TROPICOS® database (<www.tropicos.org>) together with local herbarium databases (AAU, QCA, and LOJA; acronyms follow Thiers, 2016) and related literature to establish total species ranges at local, regional, and global scales. For the regional distributional ranges we modified and simplified Linares-Palomino's (2011) categories, and we recognized the Bolivian Andes as an additional category because they are floristically distinct (López, 2003; Linares-Palomino et al., 2011). The literature- and database-derived occurrences were supplemented with our own observation in the field.

We defined our endemic species as those restricted to Ecuador, based on their geographic distribution as recorded in the *Catalogue of Vascular Plants* (Jørgensen & León-Yánez, 1999) and the updates summarized in the latest version of the *Libro Rojo de las Plantas Endémicas del Ecuador* (León-Yánez et al., 2011).

RESULTS

SPECIES CEASING THEIR RANGES AT THE BOUNDARY OF THE AMOTAPE–HUANCABAMBA ZONE

Of the 314 species encountered in our survey, 72% cross the Amotape–Huancabamba limits in a north–south direction. Shrubs contribute 40% of the species, followed by the herbs with 38% and 22% of trees (Table S1).

SPECIES FOUND TO THE EAST AND WEST OF THE ANDES

In a west–east direction, 13% of the species cross the Andes at the Amotape–Huancabamba zone. The herbs and shrubs each contribute 39% of the species, while the trees contribute 22% (Fig. 2, Table 2). Southern DIAVs situated within the Amotape–Huancabamba zone have the highest species numbers (106 spp.) and they share most species with the Pacific and Amazon lowlands (Fig. 2, Table 2). Northern DIAVs do not share many species with the Pacific and Amazon lowlands. Of the species found in the northern DIAVs, only *Cestrum megalophyllum* Dunal is also found in the Amazon and Pacific lowlands (Fig. 2, Table 2). There are more than twice as many DIAV species reaching the eastern montane forests compared to those reaching the western montane forest for all distributions, except in

Table 2.   Ecosystems adjacent to dry inter-Andean valley (DIAV) in Ecuador and the number of DIAV species found in them that are documented with botanical records (vouchers deposited in herbaria or authors' observations). Lowland forests are coastal west of the Andes or Amazonian east of the Andes, whereas montane forests are located on the Andean slopes. They can be west, east, or inter-Andean. The total number of species was 314, which were recorded in 63 transects established in DIAVs between 1°N and 5°S. North (N) and south (S) regions depart from ~2°S.

| Ecosystem (abbreviations used in Table 4)	Description	Altitudinal range	No. of species
Amazon lowlands (AL)	evergreen, non-seasonal Amazonian forest	< 600 m	27
Dry inter-Andean (DRY)	dry vegetation and seasonally dry forests located on the inter-Andean valleys, between 1°N and 5°S	1300–2800 m (N) 800–2100 m (S)	137
East montane forests (EMF)	humid or wet forests on the slopes of the eastern cordillera	600–3500 m (N) 600–2900 m (S)	69
Montane forests and páramo (MF–P)	humid or wet forests and grassland vegetation with sometimes seasonally dry forests fragments that grow higher in the Andes located on inner slopes of the Andes, facing the inter-Andean valleys	2200 > 3500 m (N) 800 > 2900 m (S)	23
Pacific lowland forests (PL)	Most are semi-deciduous and dry forests located in the coastal plains, particularly south of 0.7°N. To the north the forests are wet.	< 400 m	51
West montane forests (WMF)	Humid or wet forests on the west slopes of the western cordillera. Less humid forests are more frequent in the south.	600–2500 m (N) 400–1800 m (S)	32
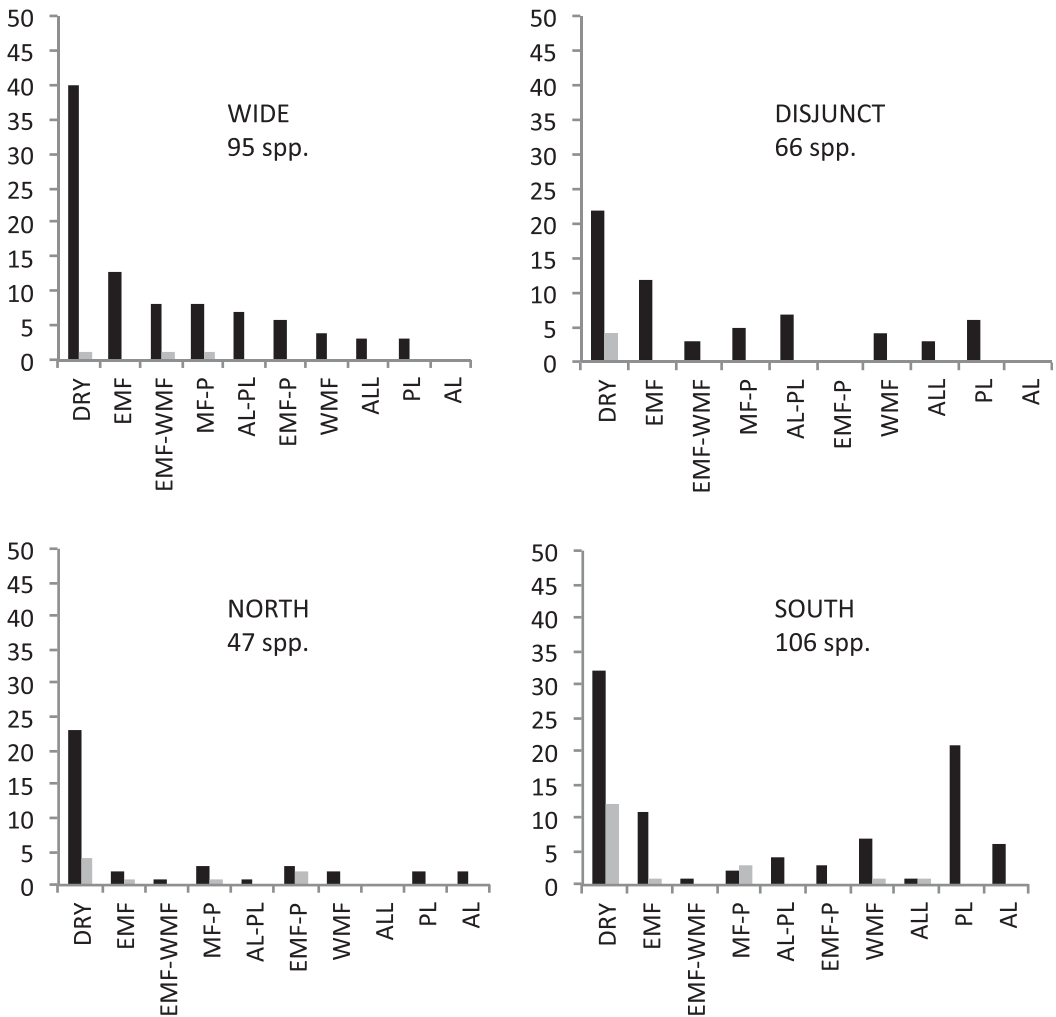
Figure 2.   Ecological ranges of 314 plant species (including four subspecies) found in 63 transects established in Ecuadorian dry inter-Andean valleys (DIAVs). Species were grouped into four categories according to their latitudinal occurrence in DIAVs: wide = widespread, disjunct = > 0.7°N and < 2.5°S, north = > 2°S, and south = < 2°S. Vegetation types where the species have been recorded besides dry forests (DRY): ALL= species found in all ecological regions and ecosystems, AL= Amazon lowlands, AL–PL= Amazon and Pacific lowlands, DRY= exclusively dry inter-Andean region, EMF= east montane forest, EMF–P= east montane forest and páramo, EMF–WMF = east and west montane forest, MF–P= montane forest and páramo (> 2100 m in the south; > 2800 m in the north), PL= Pacific lowlands, WMF= west montane forest. Gray bars represent species endemic to Ecuador.

the north, where there are almost the same number of DIAV species reaching the eastern and western montane forest, respectively (Fig. 2).

ENDEMIC SPECIES IN THE NORTHERN LIMITS OF THE AMOTAPE–HUANCABAMBA ZONE

Of the 314 species registered in our study, 33 were endemic to Ecuador, and, of these, 18 species (55%) occurred in southern DIAVs and eight species (24%) were found in the northern DIAVs, whereas four species

(12%) were disjunct and three species (9%) were widely distributed (Fig. 2, Table 3). Only southern endemic species were recorded in all latitudinal categories and in other ecosystems like páramos and Amazon and Pacific lowlands (Table 3). Regarding northern endemics, four species were found in the northern montane forests and four were exclusive to northern dry areas. There were 21 endemic species confined to DIAVs (Fig. 2, Table 3): 12 occurred exclusively in the south, four were found exclusively in the north, four had disjunct distributions, and only one (*Opuntia soederstromiana* Britton & Rose)

Table 3.   Distribution and conservation status of endemic species in dry inter-Andean valleys (DIAVs). South and north divide was at 2°S (see Methods). Disjunct species were those growing north of 0.5°N and south of 2°S. Widespread species grow all over the latitudinal gradient. Vegetation types include: ALL= species found in all ecological regions and ecosystems, DRY= exclusively dry inter-Andean region, EMF= east montane forest, EMF–P= east montane forest and páramo, MF–P= montane forest and páramo (> 2100 m in the south; > 2800 m in the north), WMF= west montane forest. Conservation status follows León-Yánez et al. (2011). Relative frequency (Fre) corresponds to the proportion of transects where the species occur, individuals per hectare (Ind/ha) applies to trees and shrubs, whereas relative dominance (Dom) corresponds to the area covered by herbs.

Family	Species	Vegetation type	Life form	Fre (%)	Ind/ha	Dom (%)	Conservation status
Only south							
Amaryllidaceae	*Eucrosia mirabilis* Pax	DRY	herb	13.3		3	Endangered
	Phaedranassa schizantha Baker	DRY	herb	26.7		1.75	Endangered
Araliaceae	*Oreopanax rosei* Harms	DRY	tree	10	3		Vulnerable
Asteraceae	*Barnadesia aculeata* (Benth) I. C. Chung	ALL	shrub	3.33	4		Vulnerable
	Calea harlingii H. Rob.	DRY	shrub	3.33	5		Vulnerable
	Verbesina barclayae H. Rob.	MF–P	shrub	3.33	1		Endangered
Begoniaceae	*Begonia froebelii* A. DC.	DRY	herb	6.66		5	Near Threatened
Bromeliaceae	*Puya eryngioides* André	DRY	herb	3.33		3	Least Concern
	Tillandsia aequatorialis L. B. Sm.	MF–P	herb	3.33		3	Vulnerable
Cactaceae	*Armatocereus godingianus* (Britton & Rose) Backeb. ex E. Salisb.	DRY	shrub	6.66	18		Vulnerable
	Cleistocactus leonensis Madsen	MF–P	shrub	3.33	12		Endangered
	Espostoa frutescens Madsen	DRY	shrub	3.33	8		Least Concern
Euphorbiaceae	*Croton fraseri* Müll. Arg.	WMF	shrub	20	203		Endangered
	Croton lehmannii Pax	DRY	shrub	3.33	50		Endangered
Fabaceae	*Bauhinia stenantha* Diels	DRY	tree	10	4		Endangered
Oxalidaceae	*Oxalis elegans* Kunth	DRY	herb	3.33		4	Vulnerable
Primulaceae	*Myrsine sodiroana* (Mez) Pipoly	EMF	tree	3.33	3		Vulnerable
Selaginellaceae	*Selaginella carinata* R. M. Tryon	DRY	herb	6.66		3.5	Vulnerable
Only north							
Amaryllidaceae	*Phaedranassa tunguraguae* Ravenna	DRY	herb	3.33		1	Endangered
Bromeliaceae	*Puya aequatorialis* André	DRY	herb	6.06		3	Least Concern
	Puya glomerifera Mez & Sodiro	MF–P	herb	6.06		2.5	Least Concern
Euphorbiaceae	*Croton elegans* Kunth	DRY	shrub	18.2	122		Least Concern
Fabaceae	*Coursetia dubia* (Kunth) DC.	EMF–P	shrub	18.2	175		Near Threatened
	Coursetia gracilis Lavin	EMF–P	shrub	9.09	167		Vulnerable
Lamiaceae	*Salvia humboldtiana* F. Dietr.	DRY	shrub	18.2	94		Near Threatened
Orchidaceae	*Epidendrum brevivenium* Lindl.	EMF	herb	18.2		16	Least Concern
Disjunct							
Bromeliaceae	*Puya dodsonii* Manzan. & W. Till	DRY	herb	3.64		3	Least Concern
Euphorbiaceae	*Croton pavonis* Müll. Arg.	DRY	shrub	1.82	22		Endangered
	Croton wagneri Müll. Arg.	DRY	shrub	18.2	487		Near Threatened
	Croton menthodorus Benth.	DRY	shrub	25.5	1056		Near Threatened
Widespread							
Campanulaceae	*Burmeistera sodiroana* Zahlbr.	EMF–WMF	herb	3.33		1	Least Concern
Cactaceae	*Opuntia soederstromiana* Britton & Rose	DRY	shrub	39.7	307		Deficient Data
Lamiaceae	*Salvia quitensis* Benth.	MF–P	shrub	4.76	46		Least Concern

was widely distributed in DIAVs (Fig. 2, Table 3). Three of these exclusive species have the status of threatened in the IUCN system (Table 3). Of the endemics, 40% crossed the Girón–Paute valley, 18% of shrubs and herbs, and just one tree species (*Myrsine sodiroana* (Mez) Pipoly).

GEOGRAPHIC DISTRIBUTION OF THE DIAV SPECIES ACROSS THE NEOTROPICS

Of the 314 DIAV species, 43% are restricted to the Andean region while large proportions are shared with the Bolivian Andes (151 species), the Pacific lowlands (116 species), the Caribbean region (96 species), and

Mesoamerica (100 species). The number of species shared with the Brazilian region is the lowest (Table 4).

Discussion

SPECIES CEASING THEIR RANGES AT THE BOUNDARY OF THE AMOTAPE–HUANCABAMBA ZONE

The number of species that cross the Amotape–Huancabamba zone both in a north–south and a west–east direction (see below) shows that for dry forest species this zone is not a barrier but a bridge. Similar findings are reported for species of the genera *Nasa* Weigend, *Urtica* L., and *Ribes* L. where the Amotape–Huancabamba zone is not a barrier and concentrates high numbers of restricted-range species (Mutke et al., 2014). It seems that DIAV species have physiological tolerances for the different environmental conditions farther north or south of the Amotape–Huancabamba zone. Northern DIAVs are drier (Quintana et al., 2017), with taller mountains formed of andesitic and dacitic rocks and with intense volcanic activity until the present, while southern DIAVs are formed of rhyolitic rocks, with a volcanic activity that ceased in the Pliocene (Hall, 1977; Hall & Calle, 1982; Hall & Wood, 1985).

SPECIES FOUND TO THE EAST AND WEST OF THE ANDES

The high number of species shared between the Pacific lowlands and the Andes regions reinforces the hypothesis of a migration route through the Amotape–Huancabamba zone (Linares-Palomino et al., 2011). The DIAVs in southern Ecuador shared 31 species with lowland forests, particularly in the western Pacific lowlands. Five species also grew in lowland forests on both sides of the Andes. This demonstrates that in southern Ecuador a significant proportion of the DIAV species reaches both the highlands and the lowlands

more easily than in northern Ecuador, where the mountains are higher and the slopes are steeper. The lower elevation of the Andes as well as the similar climatic condition in the Pacific lowland region of southern Ecuador and northern Peru, where the vegetation is dry forest, may explain this result. These findings correspond well with the theory that the Amotape–Huancabamba zone is a migration route or natural corridor between the eastern and western sides of the Andes (Bridgewater et al., 2003; Stern et al., 2008).

The high number of species shared with neighboring ecosystems (57%) may reflect dispersal among them. In DIAVs, rivers and streams can create ecotones and microclimates, allowing the persistence of species that demand humidity. Examples are species of *Begonia* L. that are abundant in montane forests. Because of their abundance in neighboring habitats and their high reproductive rates, some propagules reach dry forests and become established in areas where water and shady environments favor their survival. Mass effect (Shmida & Wilson, 1985), in this case the flow of individuals from humid mountain forests to dry areas, may be involved in increasing species richness in DIAVs. The DIAV species restricted to this ecosystem (43%) tended to be more abundant than species shared with other ecosystems, especially among the shrubs. The abundance of exclusive species was two to three times as high as the abundance of shared species (Quintana et al., 2017). The patterns found in DIAVs, with the majority of species shared with neighboring habitats but the minority of ecological specialized species as dominants in terms of abundance, has also recently been documented for palm swamp forests (Pitman et al., 2013) and white sand forests (García-Villacorta et al., 2016) in Amazonia. Dispersal from neighboring ecosystems is fundamental in shaping DIAV species composition, which is also true for Amazonian forests, where dispersal from non-white sand forests is fundamental in

Table 4. Number of dry inter-Andean Valley (DIAV) species shared with other seasonal dry tropical forest (SDTF) regions in North and South America. The analysis included 314 species recorded in 63 transects established in Ecuadorian DIAVs. The Andean region includes Andean areas of Colombia, Ecuador, and Peru. Bolivian Andes contains Bolivian highlands. Brazil comprises records found in Brazilian territory; Caribbean includes Caribbean islands; Mesoamerica includes Mexico and Central America; South South America includes geographic areas of Argentina, Chile, Paraguay, and Uruguay; and Equatorial Pacific includes areas of Ecuador and Peru close to the Pacific coast. Boldface values show the highest numbers of shared species.

	Andean	Bolivian Andes	Brazil	Caribbean	Mesoamerica	South South America	Equatorial Pacific
Andean	314	**151**	56	96	**100**	83	**116**
Bolivian Andes		151	52	87	87	76	76
Brazil			58	47	45	33	34
Caribbean				98	72	61	64
Mesoamerica					103	60	60
South South America						84	50
Equatorial Pacific							122

the species composition of Amazonian white sand forests (García-Villacorta et al., 2016).

DIAVs located in the northern limits of the Amotape–Huancabamba zone have the highest numbers of species endemic to Ecuador. This could be due to the peculiar geology and geography of southern DIAVs (wetter climate, lower mountains formed of rhyolitic rocks, with a volcanic activity that ceased in the Pliocene), as well as an overlap of northern and southern floristic groups (Weigend, 2002). Many of these endemics will be the result of prolonged geographic isolation and dispersal limitation in DIAVs (Särkinen et al., 2012).

GEOGRAPHIC DISTRIBUTION OF THE DIAV SPECIES ACROSS THE NEOTROPICS

The significant numbers of DIAV species shared with other areas of Neotropical SDTF, especially adjacent Andean areas, reinforce the picture of the Amotape–Huancabamba zone as a bridge rather than a barrier for the dry forest flora. The high number of species shared between the Bolivian Andes and the central Andean region was already commented on by Linares-Palomino et al. (2011), who found a strong floristic similarity between these two regions. Vicariance and long-distance dispersal events in combination have been discussed as the basis of widespread distributions of Neotropical SDTF species (Prado & Gibbs, 1993; Pennington et al., 2006; Symmank et al., 2011; Pennington & Lavin, 2016).

CONCLUSIONS

Drought-adapted DIAV species in northern and southern Ecuador use the Amotape–Huancabamba zone as a dispersal corridor, not as a barrier. We also document that 57% of the species found in Ecuadorian DIAVs are shared with neighboring ecosystems, mainly with montane and tropical Amazon lowland forests. The pattern found for species shared with neighboring ecosystems is similar for Amazonian forests, where shared species are less abundant than exclusive ones, but there are more shared species. The Amotape–Huancabamba zone in southern Ecuador therefore acts as a corridor for both north–south and east–west migration of plant species.

In the Ecuadorian DIAVs, small remnants shelter an important number of species, including endemics, whose distribution patterns suggest an active and complex exchange with neighboring ecosystems. Some 10% of the species are restricted to Ecuador and occur nowhere else on the planet and ~5% (nine species) are restricted to the Ecuadorian DIAVs alone. We believe this ecosystem deserves the highest conservation priority, not only because of its unique endemism but also because it is a natural corridor between neighboring ecosystems.

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