



CHANGES IN SEED DISPERSAL SPECTRUM ALONG THE ALTITUDINAL GRADIENT BETWEEN WET AMAZONIAN AND ANDEAN FORESTS IN COLOMBIA

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Guacamayas como mienndo frutos y dispersando semillas. Mitú cachivera (Vaupes).

ABSTRACT

In this study we aimed to identify the patterns of change in the seed dispersal spectrum along the altitudinal gradient between Amazon and Andean forests in Colombia. The main research questions addressed were: 1. Are there differences in the seed dispersal spectrum of tree communities in tropical forests along the altitudinal gradient of Amazonian-Andean forests? 2. If so, what are the main mechanisms in relation to this variation between forest types or biogeographical regions? 3. What are the main implications for forest conservation? We recorded and collected all tree species (DBH > 10cm) in 10-ha plots at four sites, one in the Amazon Forest (100 m.a.s.l) and three in the Central Andean Cordillera at 1712, 2051 and 3027 m.a.s.l. Four seed dispersal modes were identified: mammalochory (by mammals), ornithochory (by birds), anemochory (by wind), and autochory (self-dispersion). The 4th-corner method was used to evaluate the relationship between site altitude and dispersal modes. The relationship between dispersal mode and altitude was significant ($p=0.002$). Mammal-dispersed species became less frequent at higher altitudes, where species dispersed by wind or birds became more important. The systematic pattern of change in the dispersal spectrum along the altitudinal gradient was similar to that

found on other plant traits, such as wood density and body size, which could be seen as a response of forest functioning to the variations in the amount of energy available. However, the remaining small population size of large mammals in the Colombian Andean forests could be mirroring the relative decrement of tree species dispersed by these vectors. In the Andean Mountains, dispersal by birds could be an advantage, since the switch of the dispersal spectrum from mammalochory to ornithochory may be a response to global change and defaunation of large mammals.

Key words:

Seed dispersal mode, 4th-corner method, conservation, functional traits.

RESUMEN

Se analizaron los patrones de cambio en el espectro de dispersión de semillas de bosques húmedos a lo largo de un gradiente altitudinal en las regiones de los Andes y la Amazonia en Colombia. Las preguntas de investigación fueron: 1. ¿Hay diferencias en el espectro de dispersión de semillas de comunidades arbóreas tropicales a lo largo del gradiente altitudinal Amazonia-Andes? 2. Si es así, ¿cuáles son los mecanismos

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asociados a esa variación entre tipos de bosque o regiones biogeográficas? 3. ¿Cuáles son las principales implicaciones para la conservación de los bosques? Se tomaron las especies arbóreas (DAP > 10 cm) en 10 ha, en cuatro sitios, las cuales incluyen un sitio en la Amazonia (100 msnm) y tres sitios en los Andes, en la Cordillera Central, a 1712, 2051 y 3027 msnm. Los mecanismos de dispersión fueron mamalocoria (por mamíferos), ornitocoria (por aves), anemocoria (por viento) y autocoria (autodispersión). Se usó el método de la cuarta esquina para evaluar la relación entre la altitud de los sitios y los mecanismos de dispersión. La relación entre los mecanismos de dispersión y la altitud fue globalmente significativa ($p = 0.002$). Las especies dispersadas por mamíferos fueron predominantes en elevaciones bajas, mientras que especies dispersadas por aves y el viento lo fueron en elevaciones altas. El cambio en el espectro de dispersión a lo largo de un gradiente altitudinal fue similar a lo reportado para otras características funcionales de las plantas (densidad de la madera y altura); esto podría ser visto como respuesta del funcionamiento del bosque a variaciones en la cantidad de energía disponible. Sin embargo, el pequeño remanente de las poblaciones de grandes mamíferos en los bosques andinos podría estar asociado con el decrecimiento relativo de especies dispersadas por este vector. En los Andes, la dispersión por aves podría ser una ventaja, como respuesta al cambio global y la pérdida de grandes mamíferos.

Palabras claves:

Espectro de dispersión, 4th-corner, cambio global, características funcionales de las especies.

INTRODUCTION

In tropical forests, between 70 and 90% of the tree species produce fleshy fruits adapted for consumption by birds (ornithochory) or mammals (mamallochory) (Howe & Smallwood, 1982). Wind dispersal (anemochory) has generally been considered as an adaptation of canopy trees and vines (Gentry, 1982), and a very small number of species show self-dispersion (autochory; Willson, 1993). However, little is known about how those seed dispersal modes vary along complex environmental gradients, such as alti-

tudinal gradients, or where habitat loss has reduced large mammals and birds to minimal quantities or even made them prone to extinction. This is the case, for instance, in the northern part of the Andes, which has been considered as one of the most threatened ecosystems on Earth (Myers *et al.*, 2000).

The mechanism used by plants to move away from parent plants and establish themselves in other sites is known as seed dispersal mode. The range of seed dispersal modes in a particular forest type is known as the seed dispersal spectrum. It has profound implications on the ability of species assemblages to migrate over geographical distances and time to avoid extinction from fragmentation or as a result of climate change (Corlett, 2009; Engler *et al.*, 2009). Therefore, awareness of how mechanisms of seed dispersal modes work in plant communities contributes to the understanding of local and regional ecology. These mechanisms may help to identify those principal factors that determine the floristic composition and structure of tropical forests (Howe & Westley, 1988). For example, in lowland forests of the Malaysian Peninsula, it was found that larger seeds or animal-dispersed species had a less clustered pattern than the wind-dispersed ones, while smaller seeds dispersed by birds had a more clustered pattern than mammal-dispersed species (Seidler & Plotkin, 2006). This type of information will certainly support environmental planning and conservation.

Colombia, located in northern South America, is characterized by its wide environmental variation largely determined by the three Andean mountain ranges and by humidity from the Amazon basin. The Amazon region represents about 33% of the country's area. This region is covered by a natural tropical rain forest that could be considered as one of the best-preserved forests in the world, still harbouring a high diversity of large mammals (Emmons, 1999) and birds (Hilty & Brown, 1986). The fact that a large part of this forest remains in good condition is mainly due to the lack of infrastructure and to low population density in the region. The Andes covers about 25% of the country's area. There have been historical pressures on the area's natural ecosystems due to the establishment of large urban centres, resulting in remaining forest areas that represent less than 30% of the origi-



Semilla Lecythidaceae

nal cover (Myers *et al.*, 2000; Rodríguez *et al.*, 2004). The Colombian Andean region contains some of the most threatened animals of the country, including large mammals such as the Andean bear (*Tremarctos ornatus*), the jaguar (*Pantera onca*) and the mountain tapir (*Tapirus pinchaque*) (Lizcano *et al.*, 2002; Jorgenson & Sandoval-A, 2005). Altitudinal differences in the diversity and distribution of animals between Andean and Amazonian regions have been reported for birds, frogs and bats (Kattan *et al.*, 2004; Kattan & Franco, 2004). All these features are considered to be responsible for shaping the seed dispersal spectrum of plant communities in the Neotropics.

Therefore, expected changes in the seed dispersal spectrum along the Amazon-Andes altitudinal gradient might be framed within one or some of the following scenarios: (1) Mammalochory and ornithochory play a more prominent role in lowlands than in highlands due to their high relative species diversity and abundance; (2) Since woody plant species richness from lowlands to highlands also follows an inverse relationship with the altitudinal gradient parallel to that of mammals and birds, in relative terms (%), the dispersal spectrum may be similar between forest types; (3) Finally, due to wind intensity, which has been found to be stronger in highlands than in the lowlands (B. Sampurno, pers. comm.), we expected a more important impact from this factor affecting seed dispersal structuring plant communities in the high mountains.

In order to test those predictions, we analysed changes in the seed dispersal spectrum along an environmental gradient in Colombia. We characterized the seed dispersal spectrum linked to the floristic composition in this Amazonian-Andean forest transect, including one site in Amazonia at 100 m.a.s.l, and three sites in the Central Cordillera at 1712, 2051 and 3027 m.a.s.l. Once all locations had been classified as humid forests, our principal hypothesis to be tested was whether the seed dispersal spectrum varies according to altitude, and according to temperature.

However, due to main differences in the conservation state of these two contrasting biogeographical regions, the effect from habitat disturbance and forest fragmentation is also faced indirectly. Therefore, our research questions were: 1. Are there differences in the seed dispersal spectrum of tree communities in tropical forests along the altitudinal gradient Amazonian-Andean forests? 2. If so, what are the main mechanisms in relation to this variation between forest types or biogeographical regions? 3. What are the main implications for forest conservation? With this study, we hope to provide new insights on how seed dispersal modes can help to explain the tree species assemblages along such complex gradients in order to promote forest management and conservation in these two neotropical biogeographical regions.

Study area

This study was carried out in Colombia along an altitudinal gradient between the Amazon and the Andes. The Colombian Amazonian is the country's least populated region and it is characterized by well-preserved forests with very low (10%) signs of recent large scale disturbances including human intervention, and with a high species diversity (Duque *et al.*, 2009). In contrast, the Andean Mountain Region has historically been the centre of human settlement in Colombia. As a result, most of the region's natural forests have been seriously affected, with just 30% of the original vegetation cover remaining. Unlike the Amazonian Forest, Andean ecosystems are characterised by a higher degree of forest fragmentation and environmental degradation (Rodríguez *et al.*, 2004).

The first study site was located in the Amazonian region at the Colombian Amacayacu National Park (3°49' S, 70°19' W), at 100 m.a.s.l in terra-firme forests, where the annual average rainfall is 3000 mm (for more details see Barreto *et al.*, 2010). The following three study sites form part of the regional system of protected areas located in three different natural reserves: 1) La Forzosa (6°58' N, 75°09' W), located at 1750 m.a.s.l; with an annual average rainfall of 2400 mm. 2) El Romeral (6°9,5' N, 75°42' W), located at 2100 m.a.s.l; with an annual average rainfall of 2900 mm. 3) Belmira (6°35' N, 75°32' W), located at 2800 m.a.s.l; with an annual average rainfall of 2100 mm (see López & Duque, 2010).

METHODS

Vegetation sampling

In the Amazonian forests, plant species composition was obtained from a floristic survey carried out in a 5-ha plot (100 x 500 m), which was set up to study and monitor terra-firme forests within the Colombian Amacayacu National Park. The Andean sites comprised five scattered 1-ha plots (100 x 100 m each) located in different sites, as follows; two of them were located in Anorí (Reserva La Forzosa), one in Angelópolis (Reserva El Romeral), and two in Belmira. In

both regions, coordinates and altitude were obtained with a GPS and maps, respectively.

In all plots, we tallied and collected all trees, palms and tree ferns with a diameter at breast height (DBH) equal or larger than 10 cm, following the methodology proposed by Condit (1998). Each site delivered at least one botanical voucher from each species. However, plant species richness was estimated according to abundance in each location and defined as rare when there were two or less individuals per species, otherwise it was considered as abundant. At least three vouchers were collected for every individual rare species and a subset of a minimum of two individuals for abundant species. Amazonian samples were processed and identified at Herbario Amazónico Colombiano (COAH), while Andean samples were identified at the Herbarium of Universidad de Antioquia (HUA). Botanical samples were dried and then identified by comparing them to the collections, using monographs or consulting specialists. Samples that could not be identified to the species level (morphospecies) were excluded from the analysis: 29% in Amacayacu, 36% in Anorí, 31% in Angelópolis, and 17% in Belmira.

Floristic characterization

A species-site matrix of presence/absence values was used to recognise potential patterns of floristic composition in the 1-ha plots. In order to analyse patterns of species distribution in our plots, we used a Detrended Correspondence Analysis (DCA by segment without any transformation of data). All analyses were carried out using the software CANOCO 4.5 (Ter Braak & Šmilauer, 1998). The degree of floristic change amongst sites was assessed by measuring the distance in standard deviations along the ordination axes.

Seed dispersal modes

Seed dispersal modes were deduced from the morphology of the diaspores (seeds and fruits), using the criteria proposed by Ridley (1930), Van der Pijl (1982) and Ausgpurger (1986). In addition, the information was complemented with former studies

on processes and dispersal modes (Mori & Brown, 1994) as well as with information available in databases from Kew Botanical Garden (Liu *et al.*, 2008). Main characteristics of the diaspores were obtained from Gentry (1993), Del Valle (1973), Vásquez (1997), Vargas (2002), Toro & Alzate (2003), Rudas & Prieto (2005), as well as information from the databases of the Center for Tropical Forest Science (<http://www.ctfs.si.edu>). Four seed dispersal modes were defined: mammalochory (by mammals), ornithochory (by birds), anemochory (by wind), and autochory (self-dispersion). Diaspores assigned to animal dispersal were those with flesh or succulent aril. Colourful small fruits or seeds were assigned to bird dispersal, while odiferous (if available) and large diaspores (2 cm or more) were assigned to larger and terrestrial mammals. The anemochory dispersal mode was assigned to plants with winged, hairy or plumed diaspores or to sizes <2 mm that did not present any other evident feature corresponding to another dispersal mode. Autochory or auto-dispersal, which included gravity dispersal, was assigned to big or heavy diaspores without modification that did not favour a different dispersal mode. This classification was assumed regardless of the fact that secondary dispersal modes like myrmecochory can occur in some of these species. All species were assigned to one or more dispersal modes per forest, using 1 for presence and 0 for absence.

Dispersal modes and altitudinal variation

The 4th-Corner Method (Legendre *et al.*, 1997) was used to evaluate the relationship between dispersal modes and habitat characteristics. This method uses four matrices that share rows and columns, which offer a way to test for direct relationships between variables. Matrix A contains zeroes and ones and matrices B and C share the nominal or quantitative data to be related in matrix D ($D = CA'B$) (Legendre *et al.*, 1997). The method uses the statistics chi-square, G or F to measure the association and estimate significance according to the type of variable (nominal, quantitative, etc.). Matrix A contains the presence/absence of all the species in each location (528 species x 4 sites). No dispersal mode could be assigned to the species *Piptocoma*

discolor (Kunth) Pruski, so it was eliminated from the analysis. In matrix B, an indicator matrix, the four dispersal modes studied, mammalochory (n=262), ornithochory (n=291), anemochory (n=62), and autochory (n=56), were registered. In cases where the same species had more than one dispersal mode, in order to run the 4th-corner analysis, it was always recorded as 1 (and 0 when the species did not belong to that classification). The final dimension of this matrix was 528 species and 4 modes. Matrix C contained data about the altitude (m.a.s.l) of each site, which was found as the elevation average above sea level of the plots representing a site. Altitude increased in the following order: Amacayacu, Anorí, Angelópolis and Belmira, with 100, 1712, 2051 and 3027 m.a.s.l, respectively. In order to use the 4th-corner method, altitude values were converted into an ordinal scale from 1 to 4, considered as quantitative data for the sake of the analysis (1 x 4 matrix), following the altitudinal increase of the sites (see Legendre *et al.*, 1997). The analysis was run using the statistic software *4thcorner* (http://www.bio.umontreal.ca/casgrain/en/labo/4th_corner.html). To relate altitude (m.a.s.l) with dispersal modes, we calculated the global F-statistic, the homogeneity statistics D and correlation *r* (Legendre *et al.*, 1997). The permutation model used consisted in random permuting the occurrence of the species within rows in matrix A (Model 1; Legendre *et al.*, 1997), to test the hypotheses that changes in altitude promote alterations in the environmental conditions that determine the likelihood of species establishment.

RESULTS

Floristic composition patterns. The total of individuals recorded and identified for the species level was 5315, out of which 43, 18, 27 and 12% belong to Amacayacu, Anorí, Angelópolis and Belmira, respectively. The number of species identified at each site was 338 in Amacayacu, 105 in Anorí, 87 in Angelópolis, and 45 in Belmira. The number of exclusive species in each site was 317, 75, 65 and 32, respectively, whereas 40 species were found at more than one site, giving a total of 529 species. The first DCA axis showed a clear difference from left to right between Amazonian and Andean sites, following the altitudinal

gradient from lowlands to highlands (Figure 1). It is notable that the highlands species change in association with the amplitude of gradient among the different sites, which in almost all the cases was over four standard deviations (Table 1).

As expected, species distribution followed a contrasting pattern between lowlands and high mountain ecosystems. In lowlands, the dominance of families having a diversity center in Amazonia, such as Lecythidaceae, Sapotaceae, Burseraceae and Chrysobalanaceae, among others, was constant. In highlands, the high abundance of Holarctic and Austral-Antarctic elements such as *Quercus humboldtii* (Fagaceae), Magnoliaceae, Winteraceae, and Cunnoniaceae, respectively, emphasises the differences with lowlands. However, Andean forests were also clearly structured by having different species assemblages. The con-

fluence of elements coming from both Amazonian and Andean biogeographical provinces at an intermediate altitude, which was the case of Anorí's forests, was striking. There, typical species of Andean montane forests, such as *Q. humboldtii* and *Weinmania spp.*, coexist with *Pouteria torta*, *Tapirira guianensis*, *Protium spp.*, *Qualea spp.*, characteristic and abundant in Amazonian forests. This confluence of some species at this site supposes high species plasticity and mobility, both from lowlands and highlands, which help to explain the high diversity found in these Andean forests located in the corridor between South and Central America.

Dispersal modes. Seed dispersal modes were assigned to 528 species. According to the site dispersal spectrum, animals constituted the most important dispersal vector at all sites. However, birds dispersed the

FIGURE 1. DCA ORDINATION DIAGRAM BASED ON PRESENCE-ABSENCE OF TREE SPECIES IN DIFFERENT FOREST TYPES ALONG AN ALTITUDINAL GRADIENT IN COLOMBIA.

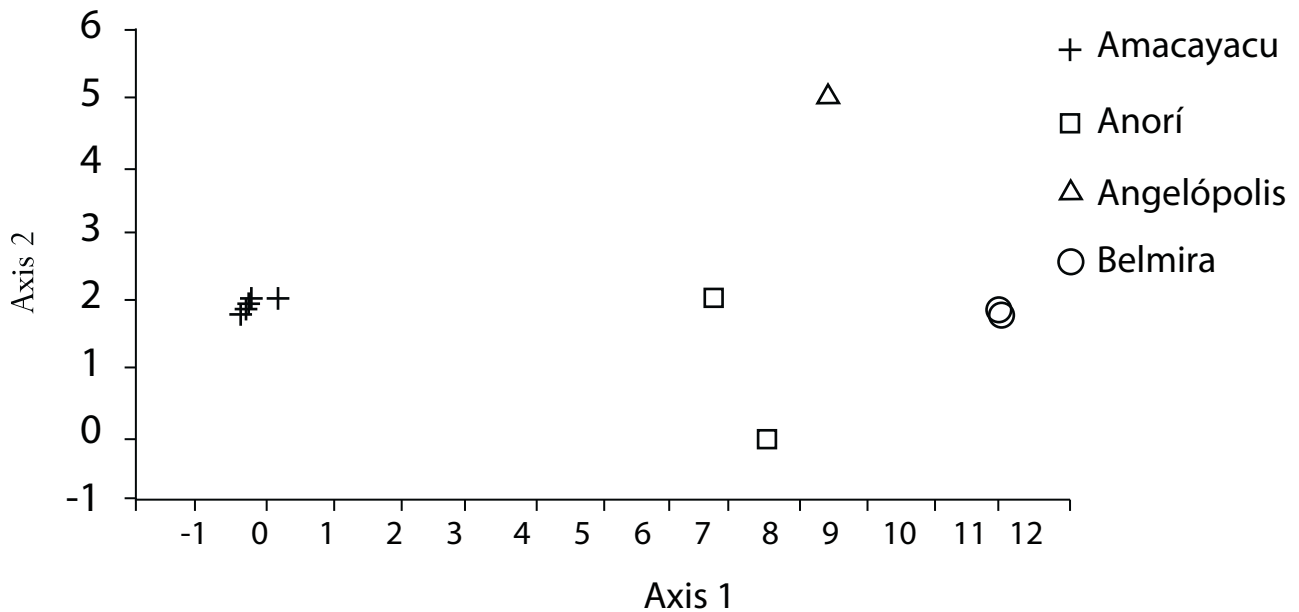


TABLE 1. SUMMARY TABLE OF DETRENDED CORRESPONDENCE ANALYSIS (DCA) OF TREE SPECIES IN 10 (1-HA) PLOTS LOCATED IN DIFFERENT FOREST TYPES ALONG AN ALTITUDINAL GRADIENT IN COLOMBIA.

	Axis 1	Axis 2	Axis 3	Axis 4	TOTAL INERTIA
EIGENVALUES	0.976	0.260	0.246	0.189	3,779
LENGTH OF GRADIENT (SD UNITS)	10,947	4,972	1,546	1,600	
SUM OF ALL EIGENVALUES					3,779

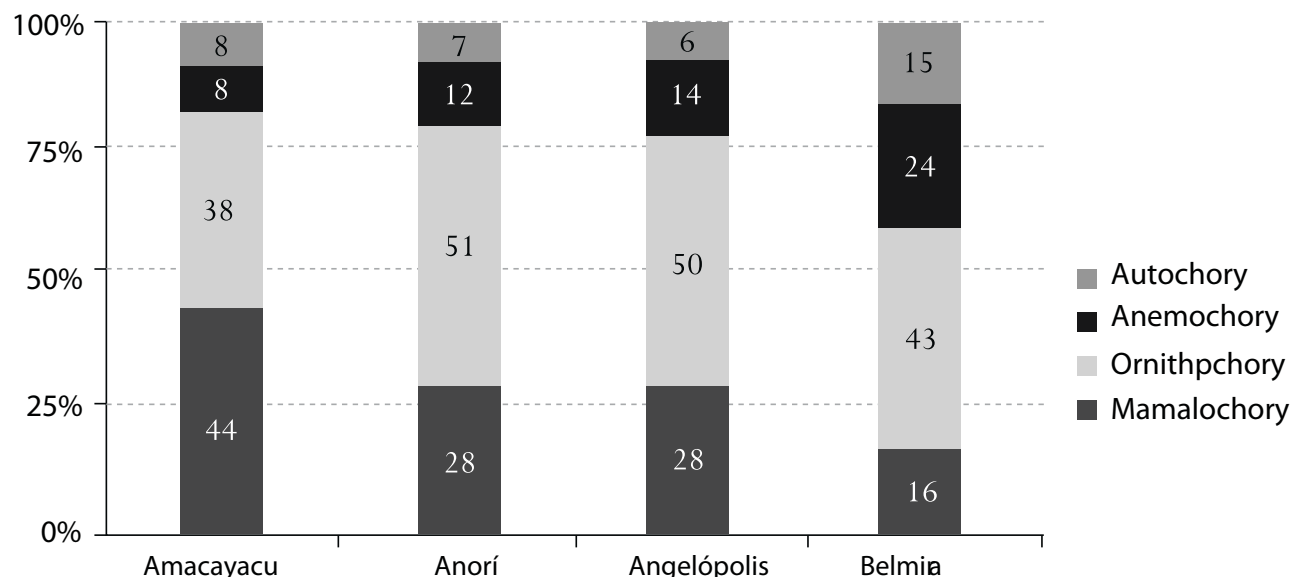
higher percentage of species at the Andean sites, while mammals were more important at the Amazonian site. With regard to altitude, anemochory showed a positive relationship with elevation, while mammalochory showed the opposite. Anorí and Angelópolis, which were the closest sites in terms of altitude, showed a very similar dispersal spectrum despite having large differences in their floristic composition. Autochory was rare at all sites and did not follow any specific trend neither regarding altitude nor between Amazonian and Andean regions (Figure 2). The relationship between dispersal modes and altitude was globally significant ($F = -33.02, p = 0.002$). With regards to the mammal-dispersed species, these showed a negative correlation with altitude, positively associated

to lower sites. In contrast, the species dispersed by wind exhibited a significant and positive relationship with sites of higher altitude; species dispersed by birds were marginally significant (Table 2).

DISCUSSION

The dispersal spectrum along the altitudinal gradient. The results of this study agreed with others carried out in tropical forests, where animal-dispersed species were the most important components of the dispersal spectrum (Gentry, 1982; Ibarra-Manríquez & Oyama, 1992; Yockteng & Cavelier, 1998). It has previously been demonstrated that mammals and birds promote long-distance seed dispersal (Kitamura *et*

FIGURE 2. SEED DISPERSAL SPECTRUM OF DIFFERENT FOREST TYPES ALONG AN ALTITUDINAL GRADIENT IN COLOMBIA



Altitude increases from left to right. Values within blocks are the percentage of species belonging to a particular dispersal mode.

TABLE 2. SUMMARY TABLE OF THE FOURTH CORNER ANALYSIS.

	DISPERSAL MODE			
	MAMMALOCHORY	ORNITHOCHORY	ANEMOCHORY	AUTOCHORY
ALTITUDE (D = HOMOGENEITY; R = FOURTH-CORNER CORRELATION STATISTICS; P = PROBABILITY)				
D(1,j)	0.3813	0.5515	0.1561	0.1205
P	0.001	0.562	0.999	0.923
R(1,j)	-0.1840	0.0642	0.1384	-0.0146
P	0.001*	0.06	0.001*	0.382
F = -33.0242 P (999 PERM.) = 0.002				

Significance was tested after running 999 permutations following the model 1. *: $p < 0.05$.

al., 2007; Guimaraes *et al.*, 2008), which becomes an important mechanism for the maintenance of diversity and species coexistence (Terborgh *et al.*, 2002). However, the dispersal spectrum reported here for humid neotropical forests changed along the altitudinal gradient, emphasizing the differences between geographic regions. Mammalochory diminished as the altitude increased and had a significant positive association with the Amazonian region, while ornithochory had a marginally significant and positive relationship with altitude, being the dominant mechanism in the Andean region. Anemochory was significant, and tended to increase with altitude as well. This systematic pattern of change in the dispersal spectrum along the altitudinal gradient was similar to that found in other plant characteristics, such as wood density (Swenson & Enquist, 2008) and body size (Aiba & Kitayama, 1999), which could be seen as a response in forest functioning to the variations in the amount of energy available across different natural systems (Brown, 1995).

The average seed dispersal distance achievable by mammals ranges between 10 m and more than 10 km, depending on the size of the dispersal vector (Corlett, 2009). Thus, in the Amazonian region, the high abundance of large mammals (Tobler *et al.*, 2010) may promote a wider distribution of plant species (see *i.e.* Pitman *et al.*, 1999). In contrast, at high elevations in the Andean Mountains, large mammals have naturally been less diverse and abundant than in lowlands (Emmons, 1999), supporting the observed switch in dominance from mammalochory to ornithochory with altitude. However, in the Colombian Andean Mountains, large-scale forest loss of up to 70% of the original cover has occurred mainly during the last 50 years (Rodríguez *et al.*, 2004). Although the forest remnants studied here were selected on the basis of being part of a protected area in order to ensure a good degree of conservation, the observed trend of the dispersal spectrum, could also be reflecting the effect from past and current habitat fragmentation. The remaining small population size of large mammals in the Colombian Andean forests (Lizcano *et al.*, 2002; Jorgenson & Sandoval-A, 2005), which might include some of the most threatened animals on earth, could be mirroring the relative decrease of tree species dispersed by this

vector. Nevertheless, to differentiate the effect from defaunation or from evolutionary processes upon the dispersal spectrum along this altitudinal gradient can be difficult, mainly because it is masked by historical influence from human intervention (Nogués-Bravo *et al.*, 2008).

In the Andean Mountains, ornithochory was by far the dominant seed dispersal mode for all different species assemblages. This is a striking feature given that we know alpha diversity of birds in highlands to be significantly lower than in lowlands (Renjifo *et al.*, 1997; Kattan & Franco, 2004). It would appear that this result suggests that bird-dispersed species have a much greater chance of surpassing geographical barriers in order to be able to maintain viable population sizes after forest fragmentation. In other words, in the Andean Mountains, dispersal by birds seems to be an evolutionary advantage, since the switch of the dispersal spectrum of these humid forests along the altitudinal gradient may be a response to global change and defaunation of large mammals. Finally, since wind-dispersed species belong primarily to pioneer species, their observed increment with altitude can be seen as a simple consequence of a higher degree of disturbance in some of these forests, and could continue to increase if deforestation in Andean Mountains follows the current trend.

Lessons learned regarding forest management and conservation? Our results have important implications regarding both the maintenance of species diversity and the adaptation of tropical forests to climate change. Terra-firme forests in Amazonia, such as those studied in Amacayacu National Park, have been recognised as being one of the richest in species in the world (Duque *et al.*, 2009). The high amount of large-seeded species is located in the well-preserved status of this forest, currently under official protection. The existence of a high variety of dispersers in this forest suggests that most species have a large chance of colonizing other suitable spots, thereby diminishing their risk of extinction by isolation. Regarding climate change, and assuming an average increase in temperature up to 5°C in the next century (IPCC, 2007), the impact on this forest type would not be major. Furthermore, this non-seasonal forest

growing on relatively fertile soils might have a good resilience to changes in rainfall seasonality and regular droughts as previously reported (Phillips *et al.*, 2009), which would be largely beneficial to the dominance of large-seeded species such as those belonging to the Lecythidaceae and Leguminosae families (Barreto *et al.*, 2010). In this way, and in contrast to the case reported for Tropical East Asia (Corlett, 2009), humid lowland neotropical forests seem to be less threatened by climate and global change than their mountain counterparts.

In the Andean region, the relative increase of wind-seeded species in an ecosystem with such a low amount of large seed predators and game species, contradicts the expected increase of tree species with large seeds (Wright *et al.*, 2007). This result confirms that habitat fragmentation, driven by an estimated deforestation rate of 1.05% per year (26 000 ha-year⁻¹) in the study region (Yepes *et al.*, in prep), surpasses the effect from hunting and along with climate change becomes the major factor influencing species extinction in Andean Mountain forests. Our results suggest that in the Andean region of Colombia, the expected increase in temperature, which might lead to a likely change in the position and rate of cloud formation (Bush *et al.*, 2007), will certainly pose a real threat to the maintenance of diversity and species coexistence.

Understanding characteristics such as dispersal syndromes as well as seed size and wood density (Ter Steege *et al.*, 2006) along complex and altitudinal gradients, could serve as a good indicator of the state of conservation of tropical forests. Furthermore, the dispersal spectrum and its capability to respond to global climate change have profound implications for the carbon dynamics and carbon storage in this particular ecosystem. According to this study, species diversity and carbon stocks in humid neotropical forests might have a higher probability to adapt and respond to climate change in lowland forests than in their highland counterparts (but see Corlett, 2009). Therefore, in Colombia, different strategies in terms of conservation are needed, but priority must be focused on the Andean Mountain ecosystems.

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