Distribution of black flies (Diptera: Simuliidae) along an elevational gradient in the Andes Mountains of Colombia during the El Niño Southern Oscillation

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ARTICLE INFO

ABSTRACT

Vector ecology is a key factor in understanding the transmission of disease agents, with each species having an optimal range of environmental requirements. Scarce data, however, are available for how interactions of local and broad-scale climate phenomena, such as seasonality and the El Niño Southern Oscillation (ENSO), affect simuliids. We, therefore, conducted an exploratory study to examine distribution patterns of species of Simuliidae along an elevational gradient of the Otún River in the Colombian Andes, encompassing four ecoregions. Larval and pupal simuliids were sampled at 52 sites ranging from 1800 to 4750 m above sea level in dry and wet seasons and during the La Niña phase (2011–2012) and the El Niño phase (2015–2016) of the ENSO; physicochemical measurements were taken during the El Niño phase. Twenty-seven species in two genera (*Gigantodax* and *Simulium*) were collected. Species richness and occurrence in each ecoregion were influenced by elevation, seasonality, and primarily the warm El Niño and cool La Niña phases of the ENSO. The degree of change differed among ecoregions and was related to physicochemical factors, mainly with stream discharge. Some putative simuliid vectors of *Leucocytozoon*, such as *G. misitu* and *S. muiscorum*, markedly changed in distribution and occurrence, potentially influencing parasite transmission.

1. Introduction

The Simuliidae have received considerable attention for their hematophagous habits that can cause nuisance problems and sometimes host deaths, and can result in host diseases from transmission of parasites such as *Leucocytozoon*, *Mansonella*, *Onchocerca*, and *Trypanosoma* (Adler, 2005). The immature stages, which develop in running water, are an important component of stream ecosystems throughout the world (McCreadie and Adler, 1998; Hamada et al., 2002; Malmqvist et al., 2004; McCreadie et al., 2005; Srisuka et al., 2015; Ya'cob et al., 2016a). Each vector species requires different environmental conditions to complete its life cycle (Santiago-Alarcon et al., 2012). An understanding of abiotic and biotic factors that determine the presence of different vector species can provide insight into the dynamics of parasite transmission. Gaps in basic biological knowledge for most vector species, however, can lead to generalizations about a vector's biology based on the knowledge of only a few species (Huff, 1938; Santiago-Alarcon et al., 2012).

The El Niño Southern Oscillation (ENSO) involves oceanic and atmospheric interactions typically expressed in warm (El Niño) and cool (La Niña) phases with worldwide climatic influence. In the Colombian Andes, El Niño is associated with decreases in rainfall, soil humidity, river flow, and glacial area, whereas La Niña is associated with their respective increases (Poveda et al., 2002; IDEAM, 2012). Seasonality (wet and dry seasons) can become intensified during the ENSO. Environmental variations driven by the ENSO influence resource availability and, thus, have been associated with changes in the population dynamics of animals and plants (Holmgren et al., 2006; Beaumont et al., 2016). Accordingly, El Niño and La Niña provide an opportunity to study the effects of environmental changes on species distributions.

Elevational gradients offer a means of understanding the influence of climatic factors on species distributions and diversity. Thus, species distributions and long-term responses to factors, such as temperature, can be studied under natural conditions (Malhi et al., 2010). The Andes Mountains support unique highland ecosystems, such as glaciers, páramo, and cloud forests (Castaño-Uribe, 2002; Célleri and Feyen, 2009; Rangel-Ch, 2015). These unique systems favor high rates of

speciation in relatively short periods of time (Madriñán et al., 2013), making them hotspots for biodiversity and endemism (Myers et al., 2000).

In Colombia, 70 species of Simuliidae in two genera (*Gigantodax* and *Simulium*) have been reported (Wolff et al., 2016). Most simuliid studies in Colombia have focused on taxonomy, with only some biological characterizations of vectors for *Mansonella* and *Onchocerca* in lowlands (Tidwell et al., 1980; Corredor et al., 1998). Few studies have examined the ecology of simuliids in the Andean Mountains, perhaps because of a lack of human-pathogen transmission. However, the presence of *Leucocytozoon* parasites in non-migratory birds in the high Colombian Andes, and the infections with *Leucocytozoon* spp. in some highland simuliids (Lotta et al., 2016), indicate the need for multifaceted studies that characterize the species richness, seasonality, and ecology of simuliids, particularly vectors, at high elevations.

We present the first investigation of distributional patterns of simuliid species during the ENSO in the Andes Mountains. Our aim was to identify factors associated with species distributions across ecoregions and elevations in the Colombian Andes during El Niño and La Niña periods.

2. Materials and methods

2.1. Study area

Our study was conducted in the Colombian central cordillera from 1800 to 4750 m above sea level (masl). The area (69.7 km^2) included five sectors at different elevations in the high basin of the Otún River, encompassing the following four ecoregions, or life zones (Fig. 1) (Cuatrecasas, 1958; Rangel-Ch, 1994):

The snow-capped mountain ecoregion (4500–4950 masl) is covered by ice and lichen-encrusted rocks, with areas of accumulation and ablation; the nearest glacier to the study area is the Nevado Santa Isabel. However, the glacier's contribution to the main discharge of the Otún River is only 0.27%; most of the water is collected by Lake Otún (Llinás and Meneses, 2004).

The páramo ecoregion (3700–4200 masl) has an uniform landscape, with open areas and shrubby vegetation, frailejones (Asterales: Asteraceae) (certain plants of the sunflower family adapted to highland conditions), and grasses. The temperature is highly variable during the day. Glaciers from the Pleistocene and the Santa Isabel and Santa Rosa volcanoes sculpted the geomorphology of this ecoregion. Lake Otún gives rise to the Otún River as a subterranean flow through this ecoregion. Two of our sampled streams in the páramo were influenced by glacial melting; the others originated from wetlands and pools.

The Andean forest ecoregion (2480–3500 masl) is characterized by steep slopes and uneven, broken terrain dominated by paddocks, with remnants of high Andean forest in sheltered rocky areas, high areas, and near water bodies. Private farms have livestock operations in the study area. The Otún River resurfaces in this ecoregion.

The subandean forest ecoregion (1800–2480 masl) consists predominantly of paddocks, herbaceous vegetation, and secondary forests of native and introduced plants in different stages of succession. Some waterfalls are present. The area is associated with the highest species richness of animals and plants (Rangel-Ch, 1994). Much of the area belongs to the Pereira Water Company and the regional autonomous corporation (CARDER) and national institute (*Otún Quimbaya* Flora and Fauna Sanctuary) for environmental conservation.

2.2. Sampling and taxonomic identifications

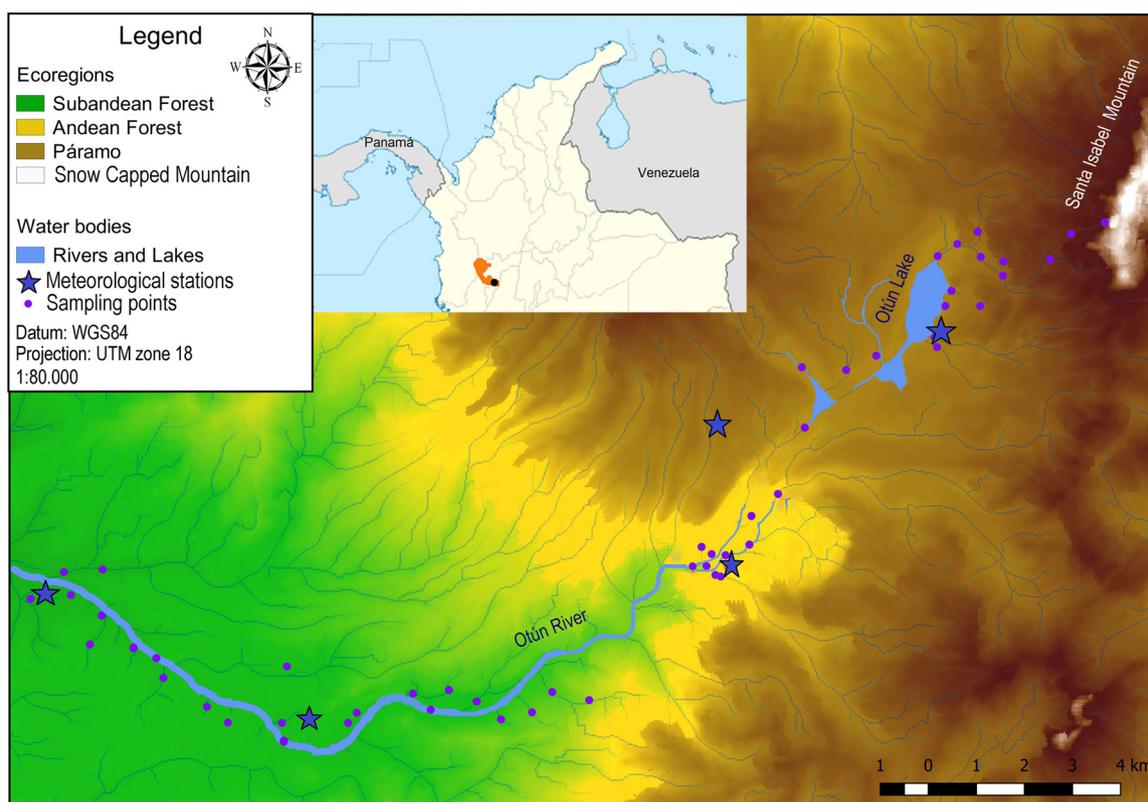We sampled at five elevations along the main channel of the Otún

Fig. 1. Map of the high basin of the Otún River, created from a digital elevation model, using QGISv.2.18. The black point in the Colombian map shows the location of the sampling area in Risaralda Department (grey).

River and in 46 tributaries for a total of 52 sampling sites: 3 in the snow-capped mountains (directly influenced by the glacial border), 15 in the páramo, 10 in the Andean forest, and 24 in the subandean forest. Simuliid larvae and pupae were collected with forceps by one researcher, from all substrate types (e.g., leaves, stones, and trailing vegetation) at each site while walking bank to bank along a 5-m stream reach. Total sampling time at each site averaged 60 min. Each stream was sampled once (evening) per month; sampling of all sites required one month. Streams were resampled during wet and dry months as follows: April (wet), July (dry), October (wet), and December (dry) 2011; March (wet), July (dry), and December (dry) 2012; April (wet), July (dry), and December (dry) 2015; and January (dry) 2016. The years 2011–2012 were classified as a weak La Niña and 2015–2016 as a strong El Niño (Null, 2016).

All specimens were fixed in the field in 80% ethanol at ambient temperature. Representative specimens were cleared in hot 85% lactic acid, dissected in glycerin, identified, and stored in microvials. Taxonomic identifications were based on characters and keys by Muñoz de Hoyos et al. (1993), Muñoz de Hoyos and Coscarón (1999), Coscarón and Coscarón Arias (2007), Hernández-Triana (2011), and Mantilla et al. (2013). For known species complexes, we recognized a separate morphospecies when larvae, pupae, and associated adults differed morphologically from the original description of the species. Voucher specimens were deposited in the Instituto de Ciencias Naturales, Bogotá, Colombia and in the collection Grupo de Estudio Relación Parásito Hospedero (GERPH), Department of Biology, Universidad Nacional de Colombia (accession no. IN-00001 to IN-00145).

2.3. Measurements of physicochemical variables

For all samplings in April, July, and December 2015 and January 2016, canopy cover, riparian vegetation, and streambed-particle size were quantified according to the rankings by McCreadie et al. (2006). Stream depth and width were measured with a measuring tape. Velocity was estimated as the time a cork moved over a predetermined distance. Discharge was calculated as the product of stream depth, width, and velocity; and conductivity, dissolved oxygen, percent oxygen saturation, pH, and temperature were measured with a portable Multiparameter Hach HQ30d meter (Hach Co., Loveland, CO, USA), using different IntelliCAL probes. Factors were selected for their ease of measurement in the field and their demonstrated power in predicting simuliid distributions among streams (McCreadie and Adler, 1998, 2012; Ya'cob et al., 2016a, 2016). Precipitation was obtained from five nearby meteorological stations (Fig. 1), and solar radiation was available from one of these meteorological stations (Fig. 1) administered by IDEAM and Red Hidroclimatológica de Risaralda (http://redhidro.org/home/).

2.4. Statistical analysis

Differences in physicochemical factors among ecoregions were assessed by discriminant analysis, using the function 'qda' (quadratic discriminant analysis) in MASS package (Venables and Ripley, 2002; Ripley et al., 2016). A biplot was made with the function 'scatterplot' from the package 'car' (Fox et al., 2016), using R Wizard version 2.1 (Guisande et al., 2014). A multivariate one-way ANOVA model was used to test the null hypothesis that physicochemical factors were identical across ecoregions. Differences between dry and wet seasons and differences in simuliid species richness (number of species) were evaluated using the package 'car' (Fox et al., 2016), with the software R version 3.2.5 (R Development Core Team, 2005).

Percent species occurrence in each ecoregion was determined as the number of streams in which a species was found divided by the number

of streams sampled in each ecoregion. Species with the highest percentage of occurrence were defined as "common" and those with the lowest percentage as "uncommon". Dry and wet seasons and years were distinguished.

Generalized linear models (GLM) provide a flexible generalization of ordinary linear regression, allowing the use of response variables without normal distributions (Nelder and Wedderburn, 1972). For our data set, the response variables were counts of species and individuals; hence, a Poisson distribution with a log-link function was used. GLM was used to describe the spatiotemporal trends of species richness and relative abundance (number of individuals collected per sampling effort as time/person) associated with ecoregions, seasonality, and ENSO phases, simultaneously testing the effect of the variables. The same analysis was done using the physical and chemical measurements as independent variables. These measurements were also evaluated with respect to presence and absence of species that occurred at more than 20% of the streams along the transect, as a binomial variable with a logit-link function. GLM analyses were performed with the function 'glm' in MASS package (Venables and Ripley, 2002; Ripley et al., 2016). For selected variables, the variance inflation factor (VIF) was used with the package 'usdm' (Naimi et al., 2014; Naimi, 2015), with VIF values greater than 10 suggesting multicollinearity. We used R Wizard version 2.1 (Guisande et al., 2014) for the analyses.

Canonical correspondence analysis (CCA) was conducted with pupal relative abundance of species that occurred at more than 10% of the streams along the transect, against the different physical and chemical variables for the streams, using the package 'candisc' (Friendly and Fox, 2016) and the package 'car' (Fox et al., 2016), with the software R Wizard version 2.1 (Guisande et al., 2014). In contrast to our other analyses, only pupae were used for CCA because, as the last stage in the stream, the pupa more nearly indicates the potential presence of adults in each ecoregion.

Beta diversity (similarity by the Sørensen index) was evaluated using the package 'vegan' (Oksanen et al., 2016), with the software R version 3.2.5 (R Development Core Team, 2005)

Data were checked for the normal or Poisson distribution, and variables were log-transformed when necessary. In general, significance was set at $P < 0.05$.

3. Results

3.1. Characterization of ecoregions

Streams differed in physicochemical factors among the four ecoregions (Fig. 2). Discriminant analysis correctly classified 90.1% of the streams, and a multivariate ANOVA of all physical and chemical variables showed significant differences among ecoregions (F value = 13.73, $P < 0.001$) (Table 1). All variables were inversely related to elevation (Fig. 2). The most significant variables in distinguishing ecoregions, according to multivariate ANOVA, were canopy cover (F value = 30.88, $P < 0.001$), conductivity (F value = 48.5, $P < 0.001$), riparian vegetation (F value = 49.27, $P = 2.2 \times 10^{-16}$), and temperature (F value = 254.7, $P < 0.001$). The Andean and subandean forests were the most similar ecoregions (Fig. 2 Table 1). The snow-capped mountains (and one stream in the Andean forest) had the lowest pH (< 4.0). Precipitation differed significantly among ecoregions (F value = 9.9, $P < 0.001$). All parameters differed significantly between dry and wet seasons (F value = 32.29, $P < 0.001$).

3.2. Seasonal effects on streams conditions

Seasonality affected physical and chemical parameters of the sampled streams. In general, the size and discharge of the streams and the
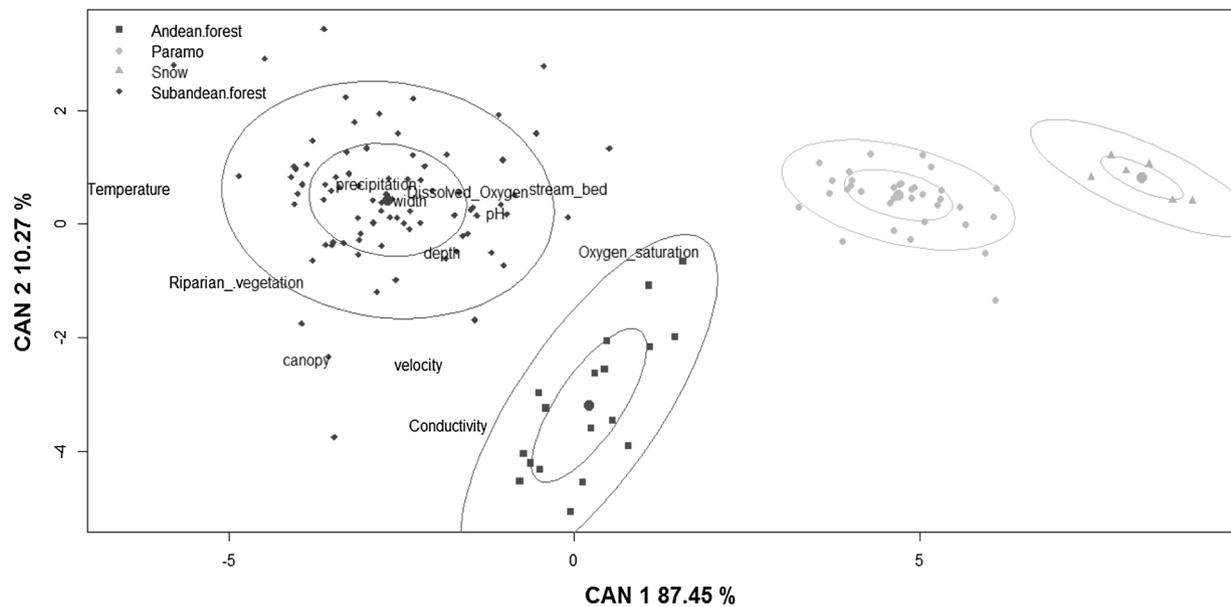
Fig. 2. Discriminant analysis of physical and chemical stream factor for ecoregions in the Colombian Andes, showing the first two canonical axes; large ovals indicate the variance of the data for each ecoregion.

acidity of the water increased during the wet season, whereas temperature, conductivity, and oxygen saturation increased during the dry season (Fig. 3). However, water temperature increased during the wet season, with respect to the dry season for the snow-capped mountain, páramo, and Andean ecoregions (Table 1).

3.3. Species

We collected 3970 larvae and pupae representing 27 species in two genera: *Gigantodax* (10 species) and *Simulium* (17 species). *Simulium* was represented by four subgenera: *Aspathia* (1 species), *Psilopelmia* (*sensu* Shelley et al., 2010) (13 species), *Pternaspatha* (1 species), and *Trichodagmia* (2 species). Forty-five (88.2%) of 51 streams were positive for simuliids. No simuliids were found in the snow-capped mountains, whereas 100% of streams in the subandean and Andean forests and 60% in the páramo had simuliids.

Species richness per stream ranged from 0 to 6, with a mean of 1.5. The number of species per ecoregion decreased with elevation: subandean forest (16 species), Andean forest (13), páramo (5), and snow-capped mountains (0).

3.4. Seasonal effects on Simuliidae

No significant effect of dry and wet seasons was observed on species richness (Table 2); however, changes in the percentage of occurrence

and relative abundance were observed (Fig. 4, Table 2). *Gigantodax misitu* was favored in the wet season, whereas other páramo species, such as *S. quimbayum* and *S. machetorum*, were most common during the dry season in both sets of years (2011–2012 and 2015–2016) (Fig. 4). In the subandean region in 2011–2012, *G. multituberculatus*, *S. near roquemayu*, and *S. pifanoi* showed the highest occurrence during the wet season (Fig. 4), whereas *G. flabellus*, *S. ignescens* sp 1, *S. ignescens*, and *S. muiscorum* were more common during the dry season. In 2015–2016, *S. ignescens* sp 1 and *G. multituberculatus* were most common during the wet season, whereas *S. muiscorum* showed the highest occurrence during the wet season.

In 2011–2012 (La Niña), the most common species was *S. ignescens*, with 47.8% of the total occurrence, and the least common species were *S. furcillatum, S. lutzianum,* and *S. near townsendi*, each with 2.2% of the total occurrence. *Simulium near townsendi* was most similar to *S. townsendi sensu stricto*, but the terminalia of pharate females from our collections differed sufficiently to suggest that our material is not conspecific with the type figured by Hernández-Triana (2011). In 2015–2016 (El Niño), the most common species was *S. ignescens* (52.9%), and the least common were *G. misitu, G. ortizi, S. albanense, S. bicoloratum,* and *S. (Psilopelmia) sp*, each with 1.9% of the total occurrence. These patterns of occurrence were similar in each ecoregion (Fig. 4). *Simulium ignescens* showed a high degree of morphological and ecological variation and was treated as two morphoforms. *Simulium ignescens* corresponded with the original species description, and *S.*

Table 1

Seasonal values (mean ± standard deviation) of physical and chemical factors of streams for four ecoregions sampled for simuliids in the Colombian Andes.

| Region	Season	Temperature (C°)	Conductivity (µS cm)	pH	Oxygen saturation (%)	Discharge (m³/s)	Riparian vegetation	Canopy cover
Snow-capped mountain	Dry Wet	1.5 ± 0.25	2.6 ± 0.2	5.9 ± 0.48	99.0 ± 0.5	14196 ± 3196	0.0	0.0
		2.2 ± 0.32	4.5 ± 1.3	4.1 ± 0.54	92.0 ± 2.0	65015 ± 1891		
Páramo	Dry Wet	7.9 ± 1.53	60.1 ± 26.4	6.9 ± 0.34	98.9 ± 3.5	22717 ± 69392	1.0	1.0
		8.3 ± 1.33	64.1 ± 49.7	6.4 ± 0.09	90.5 ± 12.2	54778 ± 19306		
Andean	Dry Wet	10.9 ± 1.63	251.7 ± 111.3	6.9 ± 1.58	96.4 ± 5.6	213915 ± 268124	2.3 ± 0.7	2.3 ± 0.4
		11.7 ± 1.53	223.2 ± 124.9	7.0 ± 1.67	95.5 ± 5.2	291324 ± 182547		
Subandean	Dry Wet	15.7 ± 2.24	126.3 ± 103.8	8.45 ± 1.04	95.5 ± 15.0	871239 ± 1100046	2.4 ± 0.7	2.1 ± 0.7
		15.2 ± 1.74	83.6 ± 71.7	6.95 ± 0.4	86.6 ± 7.8	531784 ± 1611555		

Canonical scores　　　　　**Structure**
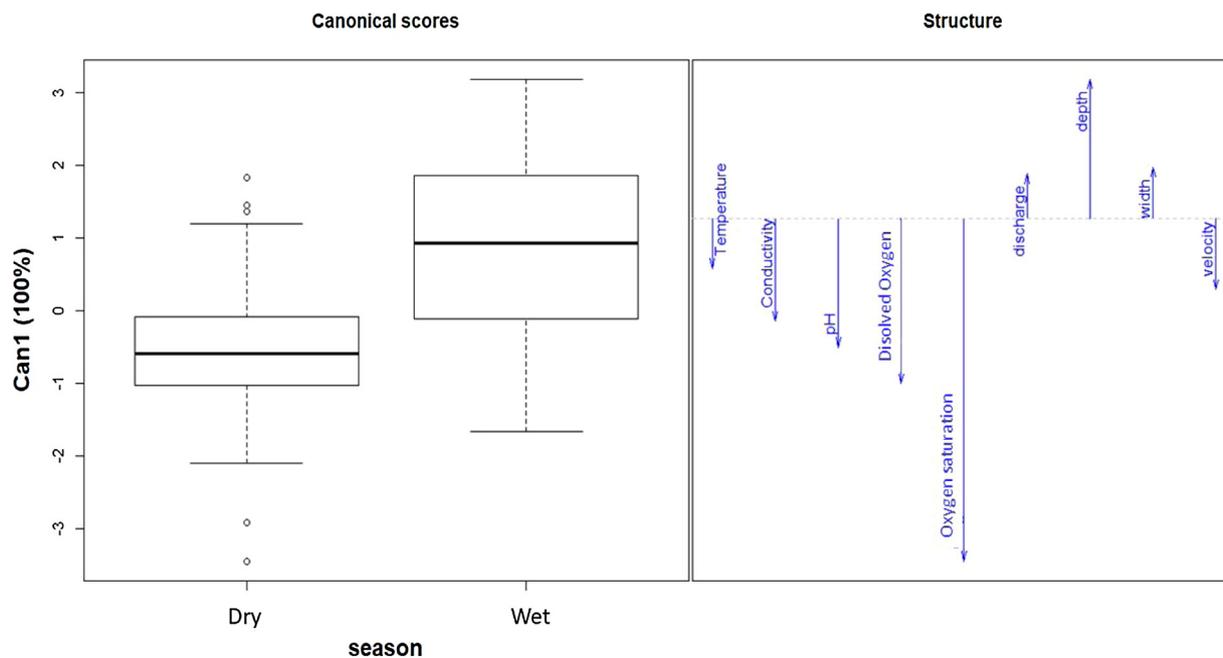
Fig. 3. Discriminant analysis of streams based on physical and chemical variables, comparing dry and wet seasons; the number of correctly classified streams by cross validation was 76%. Upward arrows correspond to variables that increased during the wet season, whereas downward arrows represent variables that increased during the dry period.

ignescens sp 1 was morphologically distinct. *Simulium ignescens* was more prevalent at low elevations, whereas *S. ignescens* sp 1 was prevalent at high elevations, a pattern that intensified under El Niño (Fig. 4).

3.5. El Niño Southern Oscillation (ENSO)

Precipitation decreased and solar radiation increased (Student's *t*-test, P < 0.001) in 2015–2016 (El Niño), compared with 2011–2012 (La Niña). The páramo was the most-affected ecoregion; four of the sampled páramo streams disappeared completely. According to the GLM, El Niño had a significant negative effect on species richness (Table 2). All variables (ENSO, season, and ecoregion) had a significant effect on simuliid relative abundance, with the wet season and El Niño being positively related to the increase in simuliid relative abundance.

The effects could be observed by comparing changes in species occurrence (Fig. 4). In the páramo, the most remarkable change was observed for *G. misitu*. In 2011–2012, it was the most common species, independent of season (Fig. 4), but in 2015, it almost disappeared. In contrast, *G. arrarteorum*, *G. basinflatus*, *S. machetorum*, and *S. quimbayum* increased in relative abundance during El Niño, at least during

the dry season (Fig. 4). In the Andean and subandean forests, *S. ignescens* and *S. ignescens* sp 1 remained the most common species. However, the effect of the dry and wet seasons on the occurrence of *S. ignescens* sp 1 changed between La Niña and El Niño; the species became more restricted to the Andean forest during El Niño. *Simulium pifanoi* and *S.* near *roquemayu*, although common in the Andean forest during La Niña, disappeared from this ecoregion and remained only in the subandean forest during El Niño. Uncommon species (*S. furcillatum* and *S. tolimaense*) in the Andean and subandean forests during La Niña were not found during El Niño.

3.6. Simuliid composition across ecoregions

The Sørensen index differed among ecoregions (Fig. 5). In 2011–2012 (La Niña), the páramo did not share any species with ecoregions at lower elevations, whereas the Andean and subandean regions shared species (Fig. 5A). However, in 2015–2016 (El Niño), the páramo shared species with the Andean and subandean regions, whereas the number of species shared between the Andean and subandean regions decreased (Fig. 5B).

Three species shifted their elevational ranges between the

Table 2
Generalized linear model (GLM), using a Poisson distribution, to test simuliid species richness and relative abundance against the El Niño phase, ecoregion, and season in the Colombian Andes.

|	Richness				Relative Abundance			
	Estimate	Std. error	t-value	P-value[a]	Estimate	Std. error	t-value	P-value[a]
(Intercept)	0.902	0.141	6.37	**0.000**	2.272	0.065	34.813	0.053
El Niño	−0.372	0.121	−3.058	**0.002**	0.407	0.061	6.6	**0.000**
Páramo	−0.324	0.170	−1.907	0.056	−1.117	0.076	−14.614	**0.000**
Snow-capped mountains	−1.637	0.720	−2.271	**0.023**	−2.019	0.263	−7.672	**0.000**
Subandean	0.006	0.146	0.043	0.965	−0.632	0.058	−10.89	**0.000**
Wet season	0.016	0.114	0.14	0.889	0.459	0.049	9.254	**0.000**

[a] Significant P values are in bold.
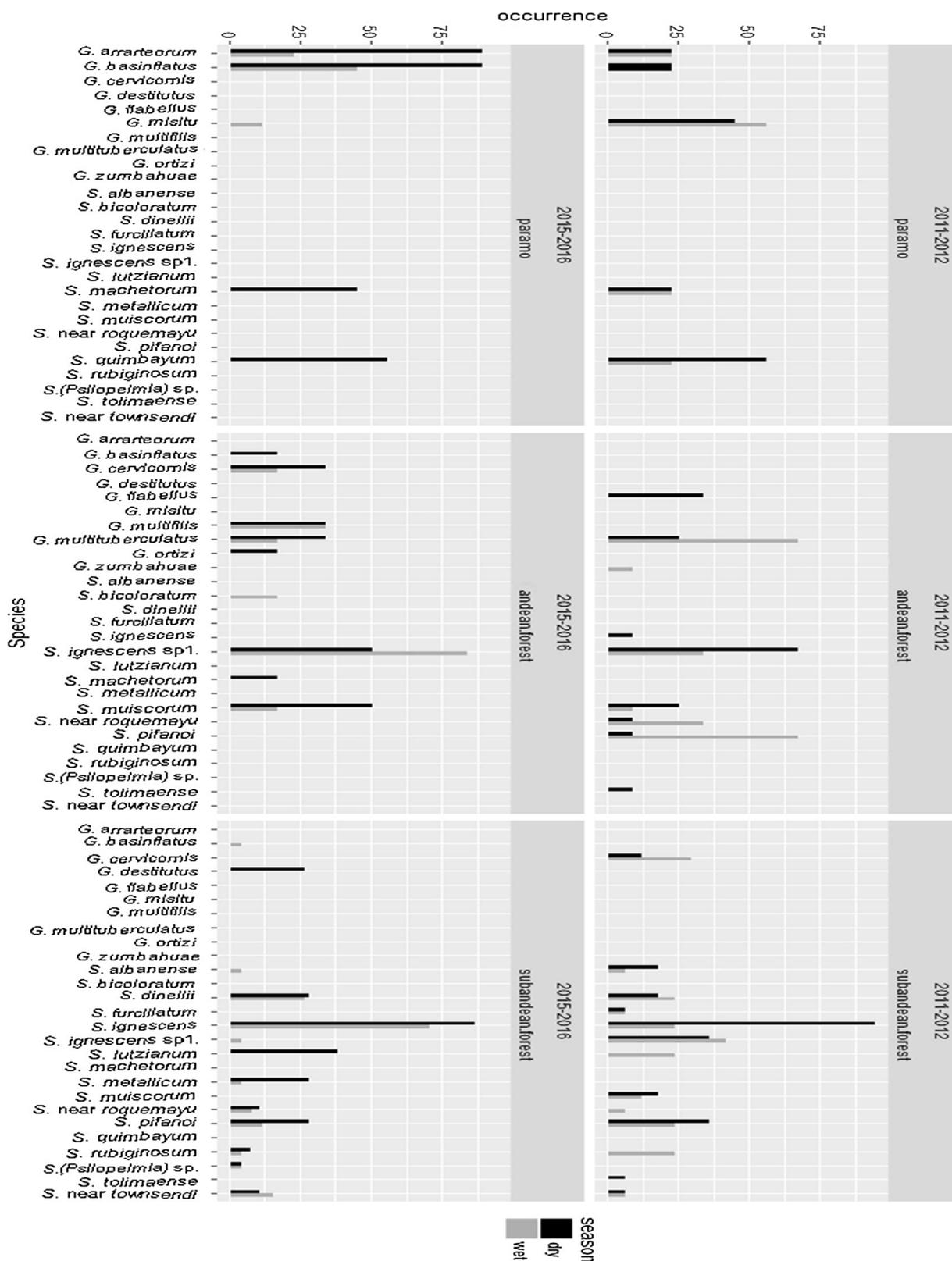
Fig. 4. Percentage of species occurrence by ecoregion (number of streams in which the species occurred divided by the number of streams sampled per ecoregion) and by season for simuliids in the Colombian Andes. Black bars indicate the dry season and gray bars indicate the wet season; the right section of the graph corresponds to La Niña and the left section to El Niño.
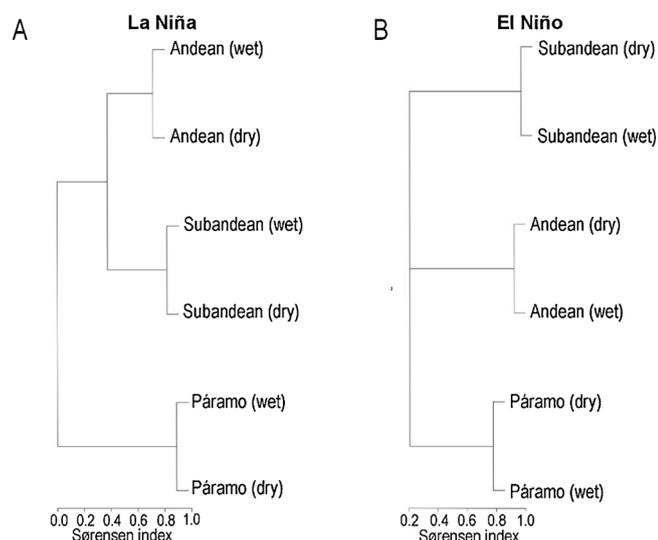
Fig. 5. Dendrograms of ecoregions and season of collection (wet and dry) for simuliids in the Colombian Andes, comparing differences between La Niña (A) and El Niño (B), based on the Sørensen index. Branch length is associated with the Sørensen index (0.0–1.0); shorter branches indicate more shared species.

2011–2012 La Niña and the 2015–2016 El Niño – two to lower elevations and one to higher elevations. *Gigantodax basinflatus* and *S. machetorum,* which were restricted to the páramo in 2011–2012, were found at the lowest elevations in 2015–2016. The situation was especially acute for *G. basinflatus*, which was found as low as 2450 masl. In contrast, *S.* near *townsendi*, which was found only in the subandean forest (< 2100 masl) in 2011–2012, moved to higher elevations (2400 masl) in 2015–2016. Additionally, *S. muiscorum*, a species morphologically similar to *S.* near *townsendi* (both in subgenus *Trichodagmia*), became highly restricted in elevation. In 2011–2012, it was found in the subandean and Andean forests (2200–3400 masl), but in 2015–2016, it was found only in the Andean forest (3100–3300 masl).

3.7. Relationship of species richness and abundance to physicochemical variables

The GLM with a Poisson distribution between species richness and the physicochemical variables and precipitation gave an R^2 of 0.7. The most significant variables were canopy cover, stream depth, discharge, pH, and riparian vegetation; however, the significant intercept indicated that factors not evaluated in our study might have affected

species richness (Table 3). For relative abundance, the model gave an R^2 of 0.57, and the significant variables were canopy cover, conductivity, stream depth, oxygen saturation, pH, precipitation, and riparian vegetation (Table 3).

3.8. Relationship of simuliid species to physicochemical stream conditions

For species with more than 10% occurrence along the transect, CCA was conducted. The first three canonical axes accounted for 86.1% of the variance (Fig. 6, Appendix A). The first axis was influenced principally by temperature; the second by canopy cover and percent oxygen saturation and negatively by temperature; and the third mostly by canopy cover. The first axis indicated that *S. lutzianum* and *S. metallicum* were relatively more abundant at higher water temperatures, whereas *G. basinflatus* and *S. quimbayum* were more abundant at lower water temperatures. For the second axis, the relative abundance of *S. ignescens* sp. 1 and *S. pifanoi* were positively related to higher levels of oxygen and canopy cover, whereas the relative abundance of *G. basinflatus* and *G. arrarteorum* were related to low levels of dissolved oxygen and canopy cover.

By analyzing the factors that explain the presence of species with more than 20% occurrence, we found that the presence of *G. arrarteorum* was associated with reduced precipitation and stream discharge, whereas the presence of *G. basinflatus* was associated with high elevations and low water conductivity. Despite their morphological similarities, *S. ignescens* was present in streams at lower elevations and with less canopy cover than those with *S. ignescens* sp. 1. Additionally, *S. ignescens* was associated with increased precipitation and oxygen saturation, whereas *S. ignescens* sp.1 was associated with high discharge, conductivity, and large streambed particles (Table 4).

4. Discussion

Our principal findings indicate that (1) elevational distributions and relative abundance of Andean simuliid species change over the course of the ENSO, (2) species composition differs between dry and wet seasons, and (3) simuliid species are differentially affected by the ENSO and seasons, with the greatest effects on the páramo species.

Associations between simuliid species assemblages and elevation, such as the negative relation between species richness and elevation reported here, have been documented in other zoogeographic regions and attributed to differential tolerance of the species to environmental factors (Ya'cob et al., 2016b). The association of species-richness patterns with physicochemical conditions (e.g., stream size) in our study agrees with reports for other zoogeographical areas, such as the Nearctic, Oriental, Palearctic, and lowland Neotropical regions

Table 3
General linear model (GLM), using a Poisson distribution, for physical and chemical variables in streams of the Colombian Andes.

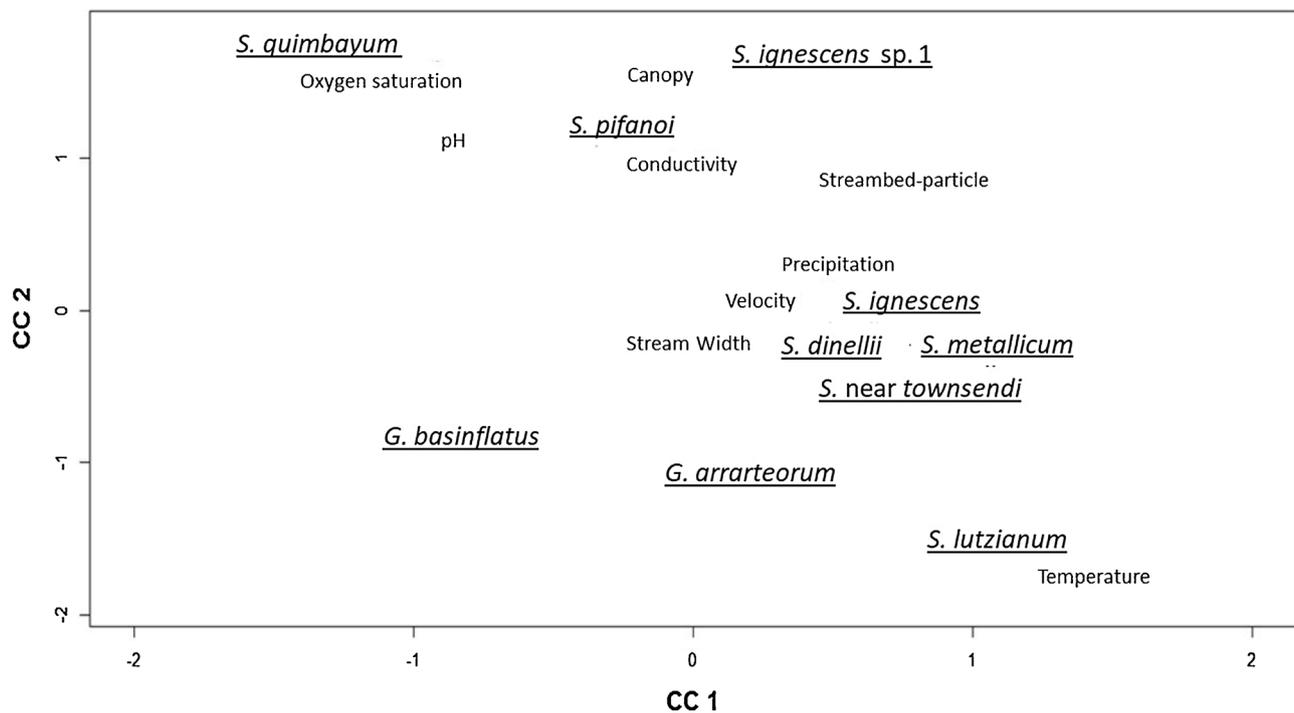|	Species Richness				Relative Abundance			
	Estimate	Std. error	t-value	P-value[a]	Estimate	Std. error	t-value	P-value[a]
(Intercept)	−6.311	1.465	−4.307	**0.000**	−8.477	4.297	−1.973	**0.048**
Precipitation	0.001	0.001	0.863	0.388	5.027	3.436	14.63	**0.000**
Streambed-particle size	0.037	0.096	0.388	0.698	−2.559	3.121	−0.082	0.934
Riparian vegetation	−0.300	0.125	−2.405	**0.000**	−2.554	4.038	−6.325	**0.000**
Canopy	0.767	0.111	6.922	**0.000**	3.773	4.753	7.937	**0.000**
Temperature	0.026	0.026	0.964	0.335	−1.305	9.689	−1.347	0.178
Conductivity	0.002	0.001	1.662	0.097	3.984	2.768	14.39	**0.000**
pH	0.152	0.047	3.240	**0.001**	9.041	1.311	6.898	**0.000**
Oxygen saturation	0.021	0.012	1.698	0.090	1.455	3.961	3.674	**0.000**
Discharge	0.000	0.000	1.866	**0.042**	2.18	2.914	0.748	0.455
Depth	−0.039	0.010	−4.062	**0.000**	−8.61	3.291	−2.616	**0.009**

[a] Significant P values are in bold.

Fig. 6. Canonical correspondence analysis for relative abundance of simuliid species found in more than the 10% of sampled streams in the Colombian Andes, and selected chemical and physical parameters of the streams. Species are underlined.

Table 4
General linear model (GLM), using a binomial distribution, to test the presence-absence of simuliid species found in more than 20% of sampled streams and their relation to chemical and physical variables in 52 streams of the Colombian Andes.

Species	Variables	Estimate	P-value	AIC	Percentage well classified[a]
G. arrarteorum	Precipitation	−1.85	**0.05**	54.7	27.3
	Streambed-particles	−2.00	0.99		
	Discharge	−1.90	**0.05**		
G. basinflatus	Elevation	0.94	**0.004**	66.9	50
	Streambed-particles	−0.76	**0.02**		
	Oxygen saturation	0.11	0.14		
	Conductivity	−0.04	0.06		
S. ignescens	Elevation	−0.001	**< 0.001**	113	56.1
	Precipitation	0.01	**0.001**		
	Canopy	−0.92	**0.01**		
	Oxygen saturation	0.07	**0.04**		
	Discharge	0.01	0.1		
S. ignescens sp.1	Elevation	5.01	**0.01**	40.9	75
	Precipitation	1.39	0.15		
	Streambed-particles	2.55	0.01		
	Canopy	4.86	**0.006**		
	Riparian vegetation	2.63	**0.02**		
	Conductivity	−7.03	0.17		
	Discharge	1.65	0.07		

[a] Refers only to species presence.

(McCreadie and Adler, 1998; Malmqvist et al., 1999; Hamada et al., 2002; Figueiró et al., 2008; Pramual and Wongpakam, 2010). Additional environmental associations with Andean simuliids might be expected with the inclusion of other factors, such as the quality of

dissolved organic matter (DOM), biochemical oxygen demand (BOD), dissolved minerals, and presence of other macroinvertebrates, algae, and microorganisms.

Although the ecoregions in our study were originally established largely on the basis of floristic composition, they are useful in predicting simuliid species distributions. An association between simuliid species assemblages and ecoregions was also found in the Nearctic Region (McCreadie and Adler, 2006) and the Australasian Region (Craig et al., 2012). The association of members of species complexes with ecoregion has also been documented (Adler et al., 2017).

Seasonal changes that affect precipitation (dry–wet seasonality) and, therefore, flow rates, have profound effects on simuliid distributions and relative abundance (Pramual and Wongpakam, 2010; Srisuka et al., 2015). In our study, seasonal effects differ for each species and change between La Niña and El Niño. Previous studies have shown the effect of El Niño and La Niña on hydrological factors, such as discharge and temperature, in Andean ecosystems, driven largely by the influence of the ENSO on precipitation and atmospheric temperature (Blanco, 2003; Ríos-Pulgarín et al., 2016). These factors probably influence the observed faunistic shifts in distributions and relative abundance between El Niño and La Niña.

Our findings contrast with those of Ríos-Pulgarín et al. (2016), who found no significant changes in *Simulium* abundance during the ENSO, and attributed the results to a putative high tolerance of environmental conditions. The discrepancy might lie in the level of taxonomic refinement. Ríos-Pulgarín et al. (2016) evaluated simuliids at the generic level, obscuring the responses of ecologically and evolutionarily unique species (McCreadie and Adler, 1998), whereas we identified simuliids to species level. Further insights into species-level responses might be expected with more refined taxonomy of the Andean simuliid fauna. For example, the mean species richness per stream in our study (1.5) is lower than that in other areas, typically 2.3–4.8 (McCreadie et al., 2005), where the simuliid fauna has been analyzed at chromosomal and molecular levels, revealing hidden biodiversity (Adler and Crosskey, 2015). The contrasting habitat associations of *S. ignescens* and *S.*

ignescens sp. 1, which we suspected of being distinct species, suggest that further investigation of cryptic species is warranted.

During La Niña, species in the páramo were not found in other ecoregions, suggesting that elevation can be a barrier for some species (Mantilla et al., 2013). However, when the same streams were inspected in the dry and wet months of El Niño, two species previously in low occurrence in the páramo were found in other ecoregions; *G. basinflatus* was found as low as 2450 masl (extended ca. 12.6 km) and changed from a rare to a common species in the páramo. Elevational shifts in distribution were documented for *S.* near *townsendi* and to some extent for *S. muiscorum*, which became restricted to the highest elevation of its distribution during El Niño.

The elevational shifts in both directions could be explained by changes in oviposition choices of the females – the primary, though poorly studied, factor determining distributions of the immature stages – or egg and larval drift in some cases (McCreadie and Adler, 1998, 2012; Mantilla et al., 2014). We note that species inhabiting larger, swifter streams (e.g., members of the subgenus *Trichodagmia*) are under selection to locate habitats with adequate discharge. As streams drop below acceptable discharge levels for swift-stream species, they, nonetheless, could become suitable for small-stream species, such as many members of the genus *Gigantodax,* as we observed for *G. arrarteorum*. Thus, under changing conditions of precipitation, different species of simuliids might be expected to move up or down in elevation, depending on the availability of species-specific optimal habitats and release from competition with species less tolerant to environmental changes.

Oviposition behavior of the female flies (McCreadie and Adler, 2012) is influenced by dispersal ability (Winemiller et al., 2010), which, in turn, is affected by the availability of suitable hosts for blood meals (Crosskey, 1990). One of the most obvious changes during the dry season in our study was the reduction of the level of Lake Otún (páramo ecoregion) and, with it, a decrease in populations of water birds. Similar changes have been reported previously for water birds in the same area (Gil-Ospina et al., 2010). A reduction of avian hosts might influence elevational distributions of some simuliids. In Sweden, for example, the distribution of the immature stages of *S. annulus* is related to the presence of the principal avian hosts (*Gavia*) of the female flies (Malmqvist and Hoffsten, 2000).

Previous research in our study area indicates that *G. misitu* and *S. muiscorum* are probable vectors of *Leucocytozoon*, suggesting that they are using birds as their blood sources (Lotta et al., 2016). Furthermore, the observed changes in simuliid species composition across ecoregions could affect the transmission dynamics of *Leucocytozoon* spp., the only Haemosporida parasites that have been found infecting wild resident birds of Lake Otún. This possibility would be especially acute for species such as *G. misitu*, which experienced a significant decrease during El Niño. This scenario illustrates the importance of ecological characterization of vector species at local scales, rather than generalizations about their behavioral and ecological responses. Characterization of the local ecology of putative vectors, therefore, could produce more accurate ecoepidemiological information and help establish the contribution of each vector to transmission dynamics.

Simuliids in the páramo develop in small streams with reduced canopy cover and high exposure to ultraviolet radiation (Laurion et al., 2000; Kelly et al., 2003; Clements et al., 2008). The adults of numerous páramo species have denser, longer hair and darker coloration than do lower-elevation species (Wygodzinsky and Coscarón, 1979). The adults of *S. machetorum*, for example, are among the darkest and most pilose species in the subgenus *Psilopelmia* and have been found at the highest elevations (> 3900 masl) of any member of the subgenus (Mantilla et al., 2013). In contrast, among species in other ecoregions of our study, only species of the genus *Gigantodax* and the subgenus *Trichodagmia* have dark adults. Increased pigmentation (e.g., melanin) in adults, as well as larvae, is associated with cooler temperatures and protection from UV radiation (Donahue and Schindler, 1998; Adler et al., 2004; Loayza-Muro et al., 2013).

The pupal cocoon of *S. machetorum* has a large, broad dorsal prolongation, a character attributed to desiccation resistance when water levels drop after pupae have been fixed to a substrate by the cocoon (Mantilla et al., 2013). We observed that larvae and pupae of *G. arrarteorum*, which are whiter than other páramo species, were found only under stones. Similar behavior has been reported for *Austrosimulium unicorne, A. bicorne*, and *A. tonnoiri* in New Zealand as a strategy to protect them from UV radiation and desiccation (Craig et al., 2012). This strategy might explain the increased occurrence of *G. arrarteorum* in páramo streams during El Niño. Perhaps the absence of lower-elevation species in the páramo is attributable to an absence of structural and behavioral characteristics associated with life in extreme conditions of the páramo.

The lack of simuliids near the glacier might be associated with the low temperature, low discharge, and reduced particulate organic matter of the meltwater. Our results are consistent with studies of simuliids in other mountains of Colombia, which document a lack of *Simulium* species above the páramo (i.e., in the super páramo) (Muñoz and Miranda, 2000). Simuliids adapted to glacial meltwater habitats are typically found in the Northern Hemisphere and are members of older cold-adapted lineages (e.g., *Prosimulium*) and include some taxa (e.g., *Gymnopais*) that have lost their labral fans over evolutionary time, instead browsing periphyton from in-stream substrates (Adler et al., 2004). In addition to temperature and particulate load, factors such as UV radiation, probably limit simuliid distributions at higher elevations.

Our results emphasize the dynamic nature of simuliid communities over space and time. Studies of how simuliids respond to El Niño and La Niña can provide a window into the effects of global climate change (Finn and Adler, 2006). Following the response of simuliid communities through future ENSO phases could provide insights into the influence of global climate change on high-elevation ecosystems and the ability of the various simuliid species to adapt or face local extinction.

Appendix A

See Table A1.

Table A1

Contribution of physical and chemical factors to the first three canonical components and their relation to the most common species of Simuliidae in the Colombian Andes, according to canonical correspondence analysis.

Variable[a]	First canonical axis	Second canonical axis	Third canonical axis
Precipitation	0.386	0.232	−0.004
Size of streambed particles	0.524	0.804	0.383
Canopy cover	−0.065	1.513	1.495
Temperature	1.021	−1.886	−0.710
Conductivity	−0.036	0.923	0.103
pH	−0.621	1.087	0.597
Oxygen saturation	−0.813	1.515	−1.126
Stream width	0.070	−0.299	−0.369
Water velocity	0.212	−0.0286	−0.349
Common Species			
Gigantodax arrarteorum	−0.075	−0.566	−0.521
Gigantodax basinflatus	−0.769	−0.430	−0.353
Simulium dinellii	0.290	−0.073	−0.182
Simulium ignescens	0.366	0.094	−0.592
Simulium ignescens sp 1	0.083	0.970	0.150
Simulium lutzianum	0.626	−0.804	1.452
Simulium pifanoi	−0.323	0.646	0.372
Simulium quimbayum	−1.201	1.006	0.947
Simulium near townsendi	0.221	−0.041	−0.629
Simulium metallicum	0.559	−0.095	−0.0518

[a] Variables were selected according to the percentage of explanation of the variance in the canonical analysis.

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