



UNIVERSIDAD NACIONAL DE COLOMBIA

# **Local and regional determinants of vascular epiphytes mortality in the Andean mountains of Colombia**

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Medellín, Colombia

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*A Vicky y Amalia porque sin ellas esto no hubiera sido posible de la misma forma.*

*A mis padres Omaira Zapata y Adalberto Zuleta por su amor y apoyo incondicional. Junto con Juan Ma, Amalia y Vicky continuarán siendo el motor de mi vida.*

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## Resumen

Se presenta el primer censo de mortalidad de comunidades epífitas vasculares llevado a cabo a gran escala en el noroccidente de los Andes colombianos. Nuestro objetivo fue identificar los principales modos de muerte y las variables que determinan la mortalidad de epífitas. Durante un año seguimos el destino de 4.247 epífitas hospedadas por 116 forofitos de 10 bosques localizados entre 60 y 2900 m.s.n.m. Nuestros resultados sugieren que la sobrevivencia de las epífitas es limitada principalmente por la dinámica del sustrato, constituyendo un riesgo de extinción para aquellas especies con ciclos de vida lentos ante la imposibilidad de colonizar nuevos sustratos rápidamente. El papel de la evapotranspiración en la mortalidad de epífitas indica el impacto directo (limitando el metabolismo) e indirecto (incrementando la mortalidad por factores mecánicos) que puede tener el cambio climático en la dinámica de las epífitas. La influencia de determinantes locales clarificó el efecto del microclima en la dinámica de estas plantas.

**Palabras clave:** Bosques montanos; Dinámica de comunidades epífitas; Evapotranspiración; Microclima del bosque; Supervivencia.

## Abstract

In this study we present the first census of mortality of vascular epiphyte communities carried out at large-scale in mountains of the Andes. Our goal was to identify the main modes of death and the determinants variables on epiphytes mortality. During one year, we went behind the fate of 4,247 epiphytes in 10 forests (116 host trees) located from 60 to 2900 m a.s.l. Our results suggested that the survival of epiphytes is limited primarily by the instability of substrate constituting a possible risk of extinction for those species with slow life cycles because of the impossibility to colonize new substrates quickly. The role of ET in the probability of death of the epiphytes indicated both the direct (limitation of the metabolism) and indirect impact (increasing the mechanical mortality) that climate change could have on the vascular epiphytes dynamics. The influence of local determinants clarified the effect of the microclimate in the dynamics of this non-tree growth component of the forest.

**Keywords:** Epiphytes community dynamic; Evapotranspiration; Forest microclimate; Montane forest; Survival.

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# 1. Introduction

In tropical forests, vascular epiphytes (*i.e.*, non-parasitic plants that use other plants as support) can represent up to 50% of the total richness of vascular species (Kelly *et al.* 2004; Benavides *et al.* 2005). However, at a regional scale, we know very little about the causes of the mortality of vascular epiphytes (hereafter simply referred to as epiphytes). The establishment and survival of epiphytes depends primarily on various factors that operate at different spatial scales. On the one hand, the macroclimatic variation generates the main environmental filter for species adaptation, which defines the species distribution patterns at regional scales (Gentry & Dodson 1987; Wolf 1994). On the other hand, the forest structure and microclimate variation may fine-tune the niche-partitioning associated with the humidity, light, and temperature variability within each type of forest (Johansson 1974; Benzing 1995; Krömer, Kessler & Gradstein 2007). An improvement of our understanding regarding the role played by climatic variation at different spatial scales in determining epiphyte mortality will aid in developing conservation and management programs that aim to avoid species loss and the extinction of this particular growth form (Pereira *et al.* 2010; Mondragón 2011).

As a consequence of the continuing increase in temperature and recurrence of extreme climatic events, such as drought and storms (IPCC 2012), it is anticipated that epiphytes will be negatively affected (Foster 2001; Colwell *et al.* 2008). The high sensitivity of

epiphytes to the supply of water appears to be one of the most common causes of death (Nieder *et al.* 2000; Zotz & Hietz 2001). In highlands of tropical montane forests (TMF), the effect of climate change should be more severe than in lowlands due to the upward changes in cloud-based formations and likely increase in evapotranspiration rates (Pounds, Fogden & Campbell 1999; Still, Foster & Schneider 1999; Ruiz *et al.* 2008; Ruiz, Martinson & Vergara 2012; Zotz *et al.* 2010). For example, in montane forests of Costa Rica, experimental studies reported that a decrease in the incidence of fog resulted in an increase in mortality and a reduction in leaf longevity and production (Nadkarni & Solano 2002). However, a high proportion of epiphytes display water-saving crassulacean acid metabolism (CAM), which must favor their ability to resist strong droughts (Winter & Smith 1996; Benzing 1998). In fact, severe droughts have been shown to indirectly increase epiphyte mortality by increasing the mortality of the host trees (i.e., the phorophyte) rather than by constraining the normal metabolism of the epiphytes. For instance, during the El Niño Southern Oscillation (ENSO) between 1997-1998 in the lowlands of Panama, the epiphyte mortality was largely driven by external mechanical events associated with the tree dynamics, such as fallen trees and branches, rather than by negative effects on epiphyte metabolism (Zotz & Schmidt 2006; Laube & Zotz 2007; Zotz & Bader 2009). Therefore, the study of the main causes of epiphyte mortality in tropical forests along broad climatic gradients could inform us about the expected effect of global warming on this quite diverse component of tropical forests.

In forests, the vertical distribution of epiphytes is strongly determined by changes in microhabitat characteristics along the tree profiles (Johansson 1974; Benzing 1995; Zotz



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2007). Overall, species that inhabit the canopy are subjected to higher temperatures, radiation, and wind intensity, and to a reduced availability of water and nutrients, as compared with species that are established in the understory (Chazdon & Fetcher 1984; Freiberg 1997; Krömer *et al.* 2007). The internal microclimates also vary between phorophytes in relation to the individual size, architecture, and bark characteristics (Benzing 1990; Mehltreter, Flores-Palacios & García-Franco 2005; Wagner, Mendieta-Leiva & Zotz 2015; Woods, Cardelús & DeWalt 2015). For example, variations in leaf area can affect stemflow along the trunks (Hölscher *et al.* 2003), and external branches can be drier than central ones (Wagner, Bogusch & Zotz 2013). Furthermore, the tree microclimate can also vary over time. In the tropics, falling branches (van der Meer & Bongers 1996; Hietz 1997; Gillman & Ogden 2005), bark characteristics (López-Villalobos, Flores-Palacios & Ortiz-Pulido 2008), and tree phenology (Einzmann *et al.* 2014) are factors that should affect the likelihood of epiphyte death.

Here, we present the first assessment of epiphyte mortality conducted on a large scale in the tropical Andean mountains and surrounding lowlands. Using two epiphyte surveys performed along a complex environmental gradient in the northwest of Colombia, we aimed to quantify the extent to which local and regional factors determine the mortality of vascular epiphytes. The main research questions to answer were as follows: 1) How much of the total mortality rates can be attributed to either mechanical or natural factors? 2) What are the main local and regional environmental determinants of the observed epiphyte mortality rates? We hope to improve knowledge regarding the dynamics of this growth

form, which has been identified as a potentially highly threatened species in this region as a consequence of global change (Duque *et al.* 2014).

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## 2. Methods

### 2.1 Study region

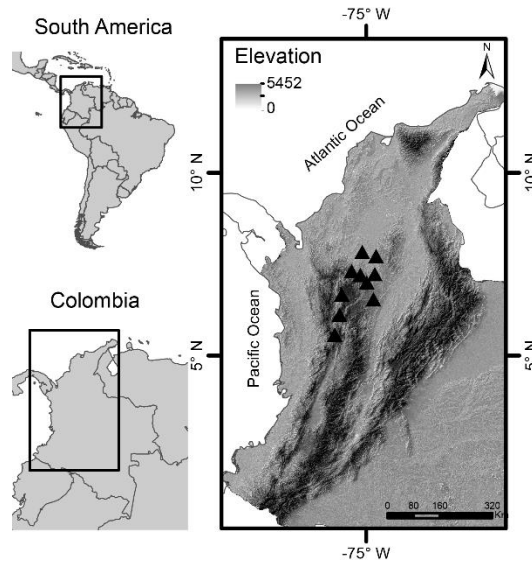
The study area is located in the northwest region of Colombia between 5°50' and 8°61' N and 74°61' and 77°33' W. This region encompasses an altitudinal gradient from sea level to 4000 m a.s.l. and is highly variable in terms of its topography, climate and soil. The annual precipitation in this region ranges from 1000 mm to almost 7000 mm. Likewise, the topography and geology are highly variable because of the presence of two mountain ranges that influence the patterns of drainage, rainfall and soil fertility on local scales (Instituto Geográfico Agustín Codazzi - IGAC 2007). This study was conducted using data collected from 10 sites that overlap with 10 permanent 1-ha tree inventory plots. The permanent plots were distributed across a large geographical area encompassing approximately 64 000 km<sup>2</sup>, mostly in the province of Antioquia. The plot locations span an altitudinal gradient from 60 to 2900 m a.s.l. (Table 1). Overall, the current forest cover only accounts for approximately 30% of the original vegetation (Duque *et al.* 2014).

**Table 1.** Geographical and environmental description of the 10 study sites of epiphytes surveyed in Andean forests.

Site location	Altitude (m a.s.l.)	Annual Precipitation (mm yr <sup>-1</sup> )	Annual mean temperature (°C)	Coordinate N	Coordinate W
Caucasia	62	3298	28.0	8.13367	-74.94286
El Bagre	67	4260	28.9	7.65606	-74.81517
Segovia	769	3244	24.7	7.11142	-74.73145
Amalfi	1006	2946	23.0	6.77662	-75.07618
Maceo	1023	2886	22.9	6.45800	-74.78675
Anorí	1783	3255	19.6	6.98711	-75.14333
Valdivia	2080	3213	18.5	7.07990	-75.47592
Angelópolis	2183	2221	16.8	6.12092	-75.69156
Jardín	2525	2841	15.2	5.49247	-75.89862
Belmira	2887	2723	12.8	6.61203	-75.65433

## 2.2 Epiphytes sampling and assessment of mortality

To assess the mortality rates, vascular epiphytes were tallied twice (2013-2014) at 10 different sites encompassing a large geographical area that includes the northern part of the Andean mountains in Colombia (Fig. 1). At each site, the minimum time that elapsed between censuses was 12 months. To sample the epiphytes, we adapted the SVERA method proposed by Wolf, Gradstein & Nadkarni (2009), which in principle aims to assess the epiphyte richness and abundance. Overall, we explored 512 trees using a nested sample at each site consisting of 35 host trees (loading epiphytes). The 35 phorophytes were distributed in the following six size classes: 10 trees with a diameter at breast height (DBH) > 30 cm and 25 trees in five classes with a smaller size (5-10, 10.1-15, 15.1-20, 20.1-25, 25.1-30 cm DBH). We included host trees with smooth, hard or sloughing bark, and we checked cases in which the selected tree did not have epiphytes as a measure of the occupation frequency at each site.



**Figure 1.** Location of the 10 sites surveyed in the northwest of Colombia.

The epiphytes were mapped using binoculars, and in all possible cases, they were collected either by climbing or with poles and ladders in the surroundings of the tallied host trees. For each phorophyte, all of the vascular epiphytes (i.e., epiphytes, nomadic vines, primary hemiepiphytes, facultative epiphytes, accidental epiphytes; Benzing 1990; Zotz 2013) were mapped, recorded, and in some cases photographed. Groups of plants that grew in colonies that were spatially differentiated were considered to be different individuals because the distinction of the ramets in the field carries a high degree of uncertainty and logistical effort (Nadkarni 1984). For each individual epiphyte plant, we recorded the following characteristics: azimuth, height above ground at the attachment site, size, and the *i*-th branch of the tree in which it was found. We only included plants with an approximate size that was greater than or equal to 5 cm because they are difficult to identify, but orchids of all sizes were included. Although all of the individuals were assigned to taxonomic morphotypes, the botanical resolution of the dataset employed to assess the mortality rate was 57.6% at the species level, 38.3% at the genus level, 2.4% at the family level, and 1.6% unidentified. All of the collected vouchers were deposited in the Herbarium of the University of Antioquia (HUA).

The plant demography greatly depends on the sampling size. Therefore, we applied two filters before analyzing the epiphyte mortality in each phorophyte to avoid sampling noise and bias due to a small sample size. First, during the second census, we classified all of the branches and stem sections as reliable or non-reliable according to the visual accuracy from the ground for each stem section or branch. Only those branches classified as reliable, which indicates that we were able to check the location of all of the plants with a certainty of approximately 95% or more, were selected. Second, after selecting all of the reliable branches, we included only those phorophytes that had loaded 10 or more epiphytes. Therefore, 116 of 350 phorophytes were used to analyze mortality at a regional scale after applying these two filters. None of the phorophytes from one site could be included after applying the two filters, and therefore, that site was eliminated from the analysis. For each phorophyte, we recorded the geographical position, the DBH, the total height (HTree), and the number of branches (BranchNum).

Two types of mortality were defined. 1) Natural mortality consisted of all of the plants that perished in situ. In most cases, they were identified as plants or the parts of plants without photosynthetically active tissue by the naked eye. 2) Mechanical mortality was defined as mortality caused by mechanical factors such as falling branches or entire plants, detached bark, or any external factor such as the effects of animals or winds. These individuals were considered dead because the likelihood of surviving on the forest floor is very small (Matelson, Nadkarni & Longino 1993).

### **2.3 Local and regional determinants of epiphytes mortality**

The forest structure variability was employed as a surrogate for the microclimate on a local scale. All of the variables were obtained from 1-ha permanent plots, which, excluding one site (Angelópolis), overlapped the location of the phorophytes. All of the plots were 100 m x 100 m. In each plot, all of the woody plant individuals (shrubs, trees, palms, and tree

ferns) with a DBH  $\geq 10$  cm were mapped, tagged, and measured. All individuals with a DBH between 1 and 10 cm were counted in a 40 x 40 m subplot located near the center of each plot. The structural variables that were considered as likely determinants of epiphyte mortality were as follows: basal area of individuals with a DBH  $\geq 5$  cm (AB:  $\text{m}^2 \text{ha}^{-1}$ ); number of canopy individuals (DBH  $\geq 10$  cm; Ind10); number of understory individuals ( $5 \leq \text{DBH} < 10$  cm); and maximum height (Hmax). Hmax was calculated as the average of the 10 largest trees in each plot. At the individual phorophyte level, we also included the following as likely explanatory factors: HTree, BranchNum, mean height of epiphytes in the phorophyte (MHP) and estimated mean size of epiphytes (MSP) (see Table S1 in Supporting Information for details).

As likely regional determinants of epiphyte mortality, we used the main climatic variables estimated at each site at a spatial resolution of 30 arc-s (c. 1 X 1-km resolution). The variables employed were as follows: actual evapotranspiration (AET,  $\text{mm yr}^{-1}$ ); mean diurnal temperature range (MDT: mean of the monthly range (max temp - min temp)); temperature seasonality (TS: standard deviation \* 100); annual temperature range (ATR); annual precipitation (AP); precipitation in the driest month (PDM); and precipitation seasonality (PS: coefficient of variation)). The actual evapotranspiration was obtained from the Global Soil Water Balance Geospatial Database (<http://www.cgiar-csi.org>; Trabucco & Zomer 2010) and is referred to as the loss of water from the soil by evaporation and transpiration. All of the other climatic variables were downloaded from the WorldClim Database (<http://www.worldclim.org>; Hijmans *et al.* 2005) (see Table S1 for details).

## 2.4 Data analysis

The annual mortality rates were estimated at the individual phorophyte level. For each phorophyte we estimated the annual mortality rate, the natural mortality rate and the mortality rate due to mechanical factors. We estimated the mortality rate in each

phorophyte using the equation recommended by Sheil, Burslem & Alder (1995) in relatively short periods (~1 year) defined as follows:

$$m (\% \text{ yr}^{-1}) = 1 - (N_1/N_0)^{1/t},$$

where  $N_0$  and  $N_1$  are the number of epiphyte individuals found in the initial and final census, respectively, and  $t$  is the average annualized time that elapsed between the two censuses. The overall difference between the mechanical and natural mortality was evaluated using the Mann-Whitney test ( $\alpha = 0.05$ ).

To investigate the local and regional determinants of the epiphyte mortality rates, a generalized linear model (glm) was constructed (Zuur *et al.* 2009). A logistic regression analysis for proportional data with a binomial distribution of the error was applied to determine whether the probability of death was related to the explanatory variables. We fitted the same model for total mortality (mechanical and natural factors together), only mechanical, and only natural factors. Due to a greater number of zeros than ones in the probability of death (i.e., many phorophytes with a low rate of epiphyte mortality), we used the complementary log-log link function (clog-log) as suggested by Zuur *et al.* (2009). To avoid incorrect conclusions, we analyzed outliers, homogeneity, normality, collinearity, interactions, and the independence of covariates and data (Zuur, Ieno & Elphick 2010). To obtain a set of explanatory variables without collinearity, we calculated the variance inflation factor (VIF) by removing one variable at a time and recalculating the VIF values. This process was repeated until variables with VIF values less than 3 were attained (Zuur *et al.* 2009). In addition, we considered the second order interactions between all of the selected covariates and performed the variable selection again, according to the collinearity. Given the high collinearity between the variables that were initially considered to build the final models, we based all of the analyses on only four climatic variables (MDT, TS, ATR, AET), one variable related to forest structure (Ind10), four phorophyte variables (MHP, MSP, HTree, BranchNum), and the interaction between



MSP and BranchNum. Therefore, the initial glm to test our hypothesis regarding the determinants of mortality was follows:

$$(P_i) = \beta_0 + \beta_1 (\text{MDT}) + \beta_2 (\text{TS}) + \beta_3 (\text{ATR}) + \beta_4 (\text{AET}) + \beta_5 (\text{Ind10}) + \beta_6 (\text{MHP}) + \beta_7 (\text{MSP}) + \beta_8 (\text{HTree}) + \beta_9 (\text{BranchNum}) + \beta_{10} [(\text{MSP}) \times (\text{BranchNum})] + \varepsilon,$$

where  $P_i$  is the probability of death in the  $i$ -th phorophyte, and  $\beta$  values are model parameters.

The most parsimonious model was selected using the backward stepwise model selection procedure based on the Akaike Information Criterion (AIC) (Crawley 2012). The analysis of residuals in the final model was performed for the residuals of the deviance, which is recommended for data with many zeros in the response variable (Pierce & Schafer 1986). One phorophyte was removed from the analysis because it was classified as highly influential in accordance with the Cook distance (larger than 1; Fox 2002). The removed phorophyte was a fallen tree for which the mortality rate was 100%. To analyze the effect of each significant explanatory variable that remained in the final model, we conducted a sensitivity analysis to predict the probability of death within the observed range of values while maintaining the other explanatory variables fixed at their average. Finally, we used the *geoR* package in R (Diggle & Ribeiro Jr 2007) to perform a variogram analysis to assess the spatial autocorrelation in the residuals. All of the analyses were conducted using R 3.1.2 (R Core Team 2014).



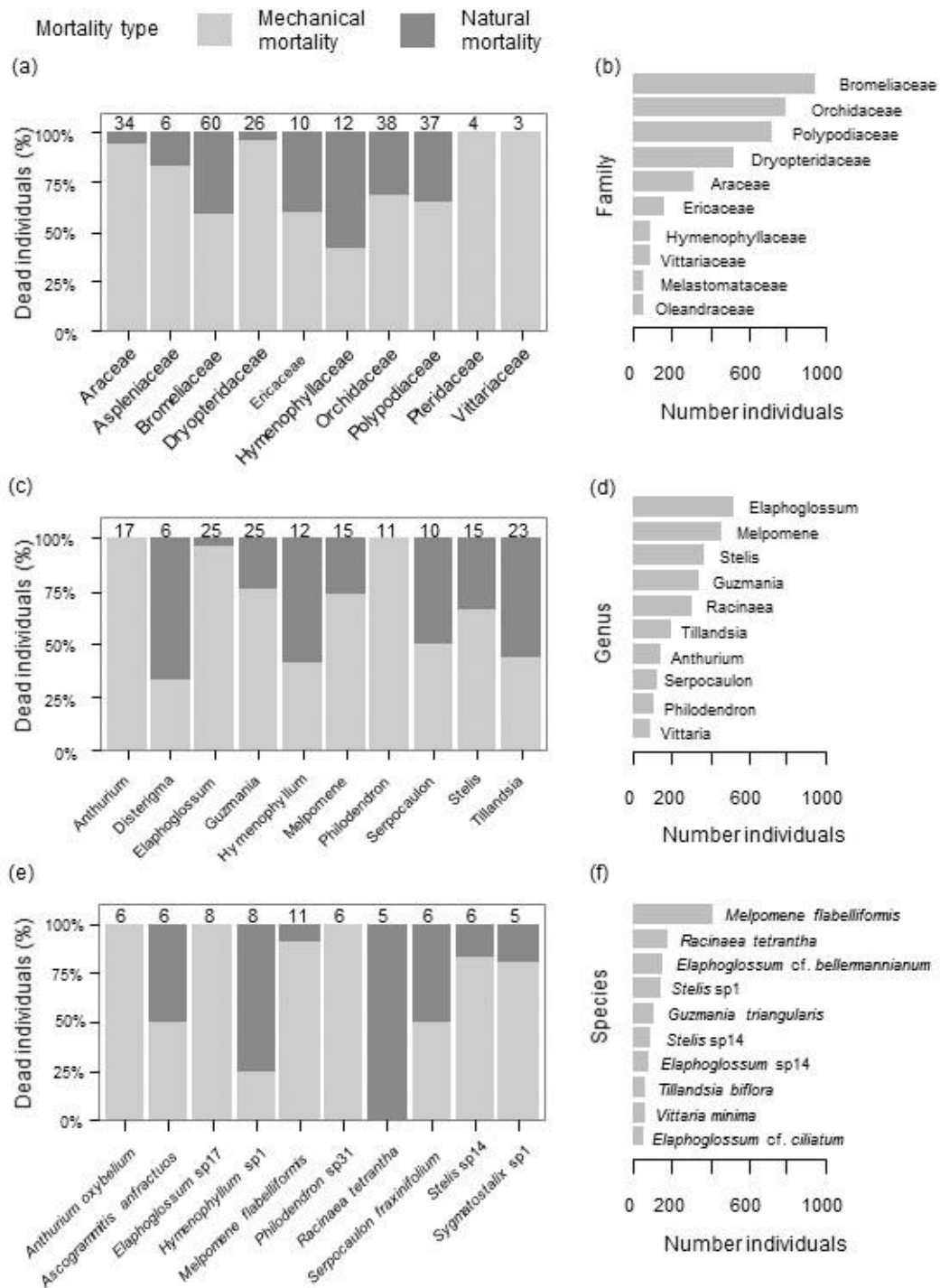
## 3. Results

### 3.1 Types of mortality

Among the 116 surveyed phorophytes, 4,247 epiphytes were located in 654 branches and stem sections. Among all of the phorophytes, we recorded 248 dead epiphytes, which was represented by a regional annual mean mortality rate for all of the surveyed phorophytes of  $7.50 \pm 11.66\% \text{ yr}^{-1}$  (mean  $\pm$  S.D.; Table 2). The mean average mortality rate per phorophyte due to mechanical factors ( $5.58 \pm 11.37\% \text{ yr}^{-1}$ ) was significantly higher (Mann-Whitney: 8711;  $p < 0.001$ ) than that due to natural causes ( $1.91 \pm 3.22\% \text{ yr}^{-1}$ ) (Table 2). At the family and genus level, the epiphyte mortality was highly proportional to the abundance, but this relationship was not observed at the species level (Fig. 2). The 248 dead epiphytes belonged to 23 out of 39 families that were recorded in the first census. Bromeliaceae (24.2%), Orchidaceae (15.3%), Polypodiaceae (14.9%), Araceae (13.7%), and Dryopteridaceae (10.5%) were the families with the highest percentage of dead individuals. *Guzmania* (10.1%, 11 species), *Elaphoglossum* (10.1%, 11 species), *Tillandsia* (9.3%, 7 species), *Anthurium* (6.8%, 8 species), and *Melpomene* (6.0%, 2 species) were the genera with the highest percentage of dead individuals. At the (morpho) species level, the 248 dead individuals belonged to 124 out of the total 389 species found in the first census, 78 of which had a single dead individual. The species with the largest number of dead individuals was *Melpomene flabelliformis* (4.4%), a fern that belongs to the Polypodiaceae family. In all cases, mechanical factors were the overriding cause of mortality (Fig. 2).

**Table 2.** Mean annual mortality rate, natural mortality rate and mechanical factors mortality rate for vascular epiphytes on 116 sampled phorophytes in 9 sites in Colombian Andes. Superscript lower case letters indicate significant differences between the types of mortality ( $p < 0.05$ ).

Site name	Annual mortality rate (% y <sup>-1</sup> )	Natural mortality rate (% y <sup>-1</sup> )	Mechanical factors mortality rate (% y <sup>-1</sup> )	Total number of epiphytes per site	Number of phorophytes with $\geq 10$ epiphytes
Caucasia	3.89 $\pm$ 5.50	3.89 $\pm$ 5.5	0 $\pm$ 0	23	2
El Bagre	9.25 $\pm$ 0	0 $\pm$ 0	9.25 $\pm$ 0	10	1
Segovia	8.84 $\pm$ 8.24	1.36 $\pm$ 3.04	7.48 $\pm$ 9.18	97	5
Amalfi	13.01 $\pm$ 11.71	5.44 $\pm$ 9.42	7.57 $\pm$ 13.12	34	3
Anorí	6.68 $\pm$ 6.77	2.79 $\pm$ 3.56	3.89 $\pm$ 5.24	731	26
Valdivia	8.37 $\pm$ 19.69	0.57 $\pm$ 1.57	7.80 $\pm$ 19.77	645	25
Angelópolis	15.64 $\pm$ 16.63	2.62 $\pm$ 3.88	13.02 $\pm$ 16.31	282	10
Jardín	6.66 $\pm$ 7.15	2.78 $\pm$ 4.19	3.88 $\pm$ 4.64	555	11
Belmira	4.77 $\pm$ 4.05	1.46 $\pm$ 1.96	3.31 $\pm$ 3.77	1870	33
<b>Mean <math>\pm</math> SD</b>	7.50 $\pm$ 11.66	1.91 $\pm$ 3.22 <sup>a</sup>	5.58 $\pm$ 11.37 <sup>b</sup>	472 $\pm$ 596.02	12.89 $\pm$ 12.02



**Figure 2.** Proportion of epiphyte individuals with the highest number of dead individuals either by natural or mechanical factors at family (A), genus (C), and species (E) level. The numbers on top of the bars represent the total number of death individuals. The panels on the right show the ten most abundant families (B), genera (D), and species (F) recorded in the first census.

### **3.2 Determinants of epiphytes mortality**

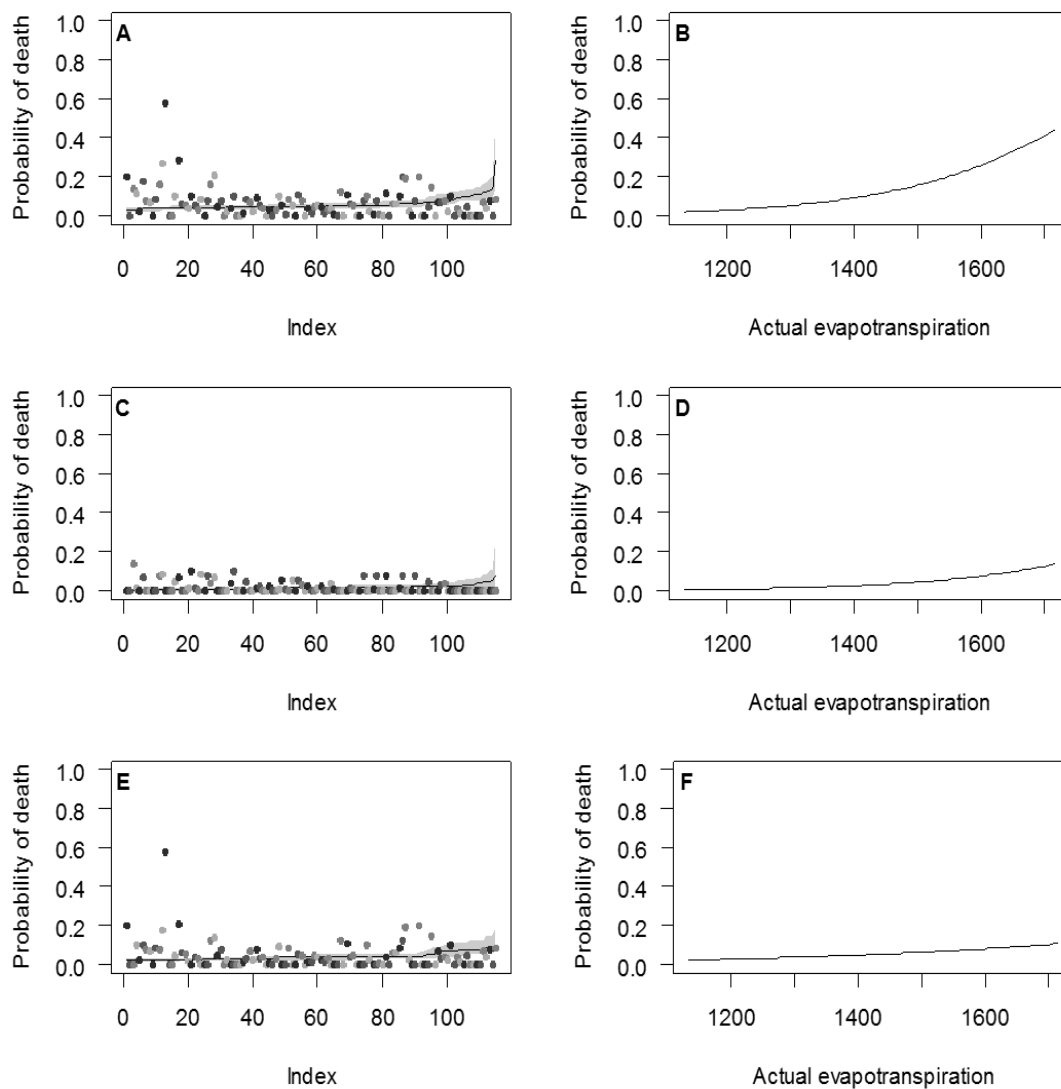
Both local and regional factors were found to play a key role in determining the epiphyte mortality. The actual evapotranspiration (AET) regional factor and the average height of the epiphytes on the phorophyte local factor were both consistently positively associated with the probability of death, independent of the cause of mortality. Overall, a higher AET and height at which the epiphytes were established on the phorophyte correlated with the highest probability of death. This condition remained true for the three cases of mortality analyzed: total, natural, and mechanical mortality. The temperature seasonality (TS) was negatively associated with natural mortality, while the annual temperature range (ATR) was negatively related to mechanical mortality in epiphytes. The height and number of phorophytes branches negatively affected the total and natural probability of death, respectively. Likewise, the fewer the number of individuals with DBH  $\geq$  10 cm, the higher was the probability of epiphyte death as a result of mechanical factors (Table 3). According to the sensitivity analysis, AET was the most important factor in determining the probability of epiphyte death due to either natural or mechanical causes (Fig. 3; see Figs S1, S2, and S3).

**Table 3.** Summary from logistic regression model predicting the probabilities of total natural mortality, mortality and mechanical factors mortality for vascular epiphytes on 115 sampled phorophytes in 9 sites in Colombian Andes. The variables were obtained by mean of backwards stepwise model selection procedure based in the Akaike Information Criterion from the initial model.

	Type of variable	Estimate	SE	z-value	P-value
<b>Total mortality rate</b>					
Intercept	NA	-7.8064	0.8866	-8.805	<0.001 ***
Temperature seasonality	Regional	-0.0061	0.0015	-4.134	<0.001 ***
Actual evapotranspiration	Regional	0.0056	0.0010	5.559	<0.001 ***
Average height of the plants on the phorophyte	Local	0.0515	0.0206	2.495	0.0126 *
Tree height	Local	-0.0287	0.0138	-2.072	0.0383 *
<b>Natural mortality rate</b>					
Intercept	NA	-8.2651	1.6366	-5.050	<0.001 ***
Temperature seasonality	Regional	-0.0079	0.0030	-2.658	0.0079 **
Actual evapotranspiration	Regional	0.0052	0.0019	2.809	0.0050 **
Average height of the plants on the phorophyte	Local	0.0816	0.0395	2.066	0.0388 *
Number of branches of phorophyte	Local	-0.0707	0.0301	-2.346	0.0190 *
<b>Mechanical factors mortality rate</b>					
Intercept	NA	-3.2222	1.2487	-2.58	0.0099 **
Annual temperature range	Regional	-0.0236	0.0071	-3.316	<0.001 ***
Actual evapotranspiration	Regional	0.0025	0.0009	2.867	0.0041 **
Individuals with DBH $\geq$ 10 cm	Local	-0.0011	0.0006	-1.873	0.0610.
Average height of the plants on the phorophyte	Local	0.0376	0.0221	1.699	0.0892.

. P < 0.10, \*P < 0.05; \*\*P < 0.01; \*\*\*P < 0.001.

NA: not applicable.



**Figure 3.** Final model according to the logistic regression analysis for proportional data applied to determine whether the probability of death was related to the selected explanatory variables for total mortality (A), natural mortality (C), and mechanical mortality (E). Pannels on the right shows the sensitivity analysis result for actual evapotranspiration for total mortality (B), natural mortality (D), and mechanical mortality (F), when the other significant variables were fixed in their average.



## 4. Discussion

### 4.1 Pattern and types of epiphyte mortality

The epiphyte mortality rates reported in this study ( $7.5 \pm 11.7\% \text{ yr}^{-1}$ ), which is the first study conducted on a large scale in the neotropics, were within the ranges reported in other long-term studies investigating epiphytes on local scales in the lowlands of Panama ( $\approx 10.8\% \text{ yr}^{-1}$ ; Laube & Zotz 2006). Mortality rates closer to 8% would require a complete community turnover in relatively short time periods ( $\approx 12.5$  years) to ensure the persistence of the species within the epiphyte community. Therefore, epiphyte recruitment, which was not assessed in the present study, should be very high to maintain a steady state in these communities. These findings suggest that, to keep the pace of mortality, natural communities of epiphytes need to be highly dynamic to avoid species loss and extinctions of this particular growth form well known by its high degree of endemism (Duque *et al.* 2014).

High turnover rates along with an expectedly high susceptibility to water availability would suggest that epiphytes are ideal organisms for monitoring the projected effects of global warming. However, an average natural mortality rate of  $1.9 \pm 3.2\% \text{ yr}^{-1}$  does not allow us to reach any conclusions regarding any striking direct effect of climatic factors, which were the only natural cause we were able to identify in the entire survey, as prominent determinants of the recorded natural epiphyte mortality. For example, the average natural mortality rate observed in our study did not differ significantly from the ca. 1% mean mortality rate reported for trees in the tropics (Condit *et al.* 2006). Nonetheless, we must acknowledge that the use of binoculars from the ground to monitor

epiphytes could in some cases hamper the observation of herbivory in some epiphytes. However, although none of the deaths herein were associated with herbivory or pathogens, we must not undervalue these biotic factors. In fact, some studies have shown that herbivory can seriously affect the reproductive organs and meristematic tissues in bromeliads and orchids (Winkler *et al.* 2005), as well as kill the majority of individuals in a population (Schmidt & Zotz 2000).

External and indirect causes of mortality, such as those produced by mechanical factors, were the most important determinants of the epiphyte mortality rates ( $5.6 \pm 11.4\% \text{ yr}^{-1}$ ). The importance of the instability and longevity of the substrate as main drivers of epiphyte mortality has been previously reported (Benzing 1990; Hietz, Ausserer & Schindler 2002; Zotz, Laube & Schmidt 2005; Laube & Zotz 2006; Aguirre *et al.* 2010). Although mechanical factors have also been identified as a key component of the pattern of mortality in epiphytes, the detachment of individuals due to the fallen branches and trunks of neighboring trees has been rarely discussed. The frequency at which this occurred caught our attention and is consistent with the observations of Laube & Zotz (2006) in a lowland forest of Panamá and of Benavides & Gutierrez (2011) in forests of the Colombian Andes. In the same way that seedlings and juvenile trees in the understory are affected by the dynamics of the branches of the largest trees (Clark & Clark 1991; Gillman & Ogden 2005), epiphytes may also be affected by falling branches, palm leaves, and neighboring tree trunks. For example, closeness to large and old trees could increase the probability of death of epiphytes inhabiting the understory. Hence, the increase in forest dynamics can indirectly affect the fate of epiphyte communities through tree mortality induced by drought (Condit, Hubbell & Foster 1995; Phillips *et al.* 2009). Nonetheless, further research focusing on disentangling the internal causes of forest instability (i.e., stand developmental stage, forest functional traits, topography, among others) will help to improve our knowledge regarding the potential causes of epiphyte dynamics, as well as the real extent to which they could be used as indicators of climate change.

Overall, frequent disturbances of the substrate have been proposed as a factor that promotes diversity and the coexistence of various epiphytic species (Benzing 1981). Nonetheless, the recurrence of extreme events (such as drought or strong winds) as a result of climate change (IPCC 2012) also could seriously affect the survival of epiphytes (Foster 2001; Colwell *et al.* 2008). Thus, the net balance of the epiphyte populations would depend on the ability of the species to adapt and recruit other species by mean of short life cycles, an accelerated achievement of reproductive maturity or asexual reproduction through the clonal spread of individuals derived from plant fragments (Hietz *et al.* 2002; Benavides, Wolf & Duivenvoorden 2013). However, most vascular epiphyte species have long life cycles, which can constrain faster recruitment, the capability to colonize new substrates, and the likelihood of adapting to global warming conditions (Benzing 1998). As a result, it is possible that species with long life cycles and slow achievement of reproductive maturity could become extinct on a local scale in a scenario of frequent disruptions and droughts. Negative balances in epiphyte populations have already been shown under natural conditions when the instability of the substrate was taken into account. For example, Hietz (1997) noted that populations of 44 epiphytes species resulted in a higher mortality than recruitment when mortality due to fallen branches was included in the analysis.

## **4.2 Local and regional determinants of epiphytes mortality**

At a regional scale, the actual evapotranspiration (AET) was the main determinant in all of the types of mortality analyzed (Table 3). The AET by itself is a natural factor associated with the water supply that has direct implications on the probability of epiphyte survival (Andrade & Nobel 1996; Nieder *et al.* 2000; Mondragón, Valverde & Hernández-Apolinar 2015). Overall, the higher the AET, the lower was the availability of water, which suggested an augmentation of the probability of death. The great importance of AET in determining the epiphyte mortality highlights the likelihood that future increases in evapotranspiration due to global warming could affect the epiphyte communities (Still *et*

*al.* 1999). However, the response of the epiphytes to the increasing AET rates may differ between forest types. In fact, Zotz *et al.* (2010) noted that some species of bromeliads are more vulnerable to drought in moist montane forests than in seasonal lowland forests, independently of the high rates of evapotranspiration that occur in the latter. Regional differences in drought tolerance are due to morphological and physiological adaptations, such as CAM, that enable epiphyte species to survive in habitats with limited moisture (Zotz & Bader 2009).

Other climatic regional determinants of epiphyte mortality were the temperature seasonality (TS) and the annual temperature range at the sites (ATR; Table 3). The negative relationship between these variables and the types of mortality revealed that the epiphytes that were well adapted to more constant temperatures were more sensitive to unexpected changes in regular climatic conditions. We would expect increases in TS and ATR to have a stronger effect in wetter areas with low seasonality than in warmer areas with high seasonality. In climates with a high annual variation in temperature, the resident species may show a broad climatic tolerance that allows them to survive. Broader climatic tolerance may facilitate the success of epiphytes in the wide range of microclimatic variations observed at different sites (Wagner *et al.* 2015). However, the high proportion of CAM epiphyte species could significantly increase their resistance and tolerance to long periods of poor water availability (Mooney, Bullock & Ehleringer 1989; Winter & Smith 1996; Zotz & Ziegler 1997). This particular condition suggests that additional empirical and experimental studies are still needed to better understand the physiological response of epiphytes to more frequent and severe droughts (Zotz & Bader 2009).

The AET was also significantly associated with the probability of epiphyte death due to mechanical factors. Increases in AET may proportionally promote partial or total desiccation of branches and tree trunks, which were shown to be the main drivers of epiphyte mortality. Because 72.2% of the epiphytes died as a consequence of mechanical factors, we were intuitively tempted to hypothesize that the AET has a direct effect on the forest dynamics and substrate instability and, thus, an indirect effect on epiphyte mortality.

However, many functional characteristics of forests, such as the wood density and growth rates, could be associated with a variety of factors other than AET, such as the soil and the rainfall seasonality (Phillips *et al.* 1994; ter Steege *et al.* 2006). For this reason, the mechanistic approach by which AET influences epiphyte mortality via mechanical factors remains elusive, but the present results shed some light on the expected relationship between the forest dynamics and epiphyte mortality.

The average height of the epiphytes on the phorophytes was a significant local scale factor for explaining all types of mortality (Table 3). The epiphyte settlement height can be assumed to be a surrogate for the microclimatic variation within the forest strata. Our findings show that, on average, epiphytes located in higher strata are at a greater risk of dying than those located in the lower compartments of the forest. As explained previously, the natural mortality of epiphytes inhabiting in the forest canopy could increase due to the presence of high climatic variability, which should promote low humidity and tissue desiccation (Krömer *et al.* 2007). Regarding mechanical factors, a higher location on the trees systematically increases the probability of downed epiphytes and branches as a result of both winds and gravity.

The height of the tree, the number of branches, and the abundance of large individuals (DAP  $\geq$  10 cm) were important local scale factors in our model that also affect the probability of epiphyte death. Tree size has also been positively related to the height and the number of branches per tree, which enhances the three-dimensional conditions that facilitate epiphyte settlement (Benzing 1990; Wolf *et al.* 2009; Benavides *et al.* 2011). Our results suggest that small trees with few branches (i.e., smaller trees) tend to have a higher probability of epiphyte death. Higher sensitivity to changes in the microclimate in the wetter low part of the forest as well as more influence of fallen branches and trunks from the upper canopy can determine the probability of epiphyte death. For example, the variability in microclimate generated in trees that drop their leaves during a part of the year (i.e., deciduous trees) could influence the probability of epiphyte death for those individuals inhabiting beneath the deciduous tree by decreasing the humidity and water availability for plants (Einzmann *et al.* 2014).

### 4.3 Methodological constrains

In the present study, we used phorophytes with a minimum of 10 individuals to obtain a sampling size as large as possible and to test the local hypothesis on the phorophyte scale. Although our original survey took into account all of the epiphytes in 35 trees at each site, the lower abundance and degree of occupation of epiphytes in lowlands compared with highlands resulted in an imbalance of the sample sizes in the final dataset between these two altitudinal categories. Because the demographic analysis was quite sensitive to the sample size, the application of the two filters (reliable branches and 10 individuals) allowed us to improve both the accuracy and precision of the statistical modelling. The most evident constraint, which was associated with the application of the first filter, was the use of binoculars from the ground to tally and monitor the epiphytes. The use of binoculars may have resulted in an underestimation of the total epiphyte species richness of ca. 20% (Flores-Palacios & García-Franco 2001). In our case, the sampling strategy employed should have promoted more significant undersampling in the forest canopy than in the understory, which could have biased the focus of our study to the middle and lower strata of the forests. This assertion is supported by the observed average epiphyte settlement height in phorophytes of  $5.7 \pm 4.4$  m (range of 0.001 m to 20.1 m). This type of sampling bias could have resulted in an underestimation of the probability of epiphyte mortality in relation to the height of the trees. Although we acknowledge the sampling limitations of our study, we do not think that they invalidate the main conclusions of the study. In fact, we think that they should be used as a reference for future studies investigating epiphyte dynamics on a large scale in the tropics.

To conclude, the majority of the long-term epiphyte studies have focused on the dynamics of one or a few populations (Mondragón 2011). To date, in the neotropics, we are only aware of approximately three studies that have evaluated epiphyte dynamics at the community level, and all of them were conducted in lowland forests on a local scale

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(Schmit-Neuerburg 2002; Laube & Zotz 2006, 2007). Although the Andean forests have been shown to be one of the most enriched regions for epiphyte species worldwide, the present study represents the first attempt to record and understand epiphyte dynamics on a regional scale. In the Andean forests, together with global warming, the high rates of deforestation and landscape transformation (Etter & van Wyngaarden 2000; Rodríguez Eraso, Armenteras-Pascual & Alumbroserosa 2013) will increase the threat to and vulnerability of epiphytes (Duque *et al.* 2014). However, the dynamics of non-tree growth forms have been practically ignored in most assessments of plant dynamics, despite the knowledge that they are an important component of the forest diversity (Gentry & Dodson 1987; Kelly *et al.* 2004; Benavides *et al.* 2005). For these reasons, we hope to foster the development and inclusion of new ideas regarding the functional roles epiphytes and other non-tree growth forms play in forests. Concomitantly, we would like to highlight the likely utility of these organisms in monitoring the capability of plant communities to adapt and survive in response to the ongoing global change.

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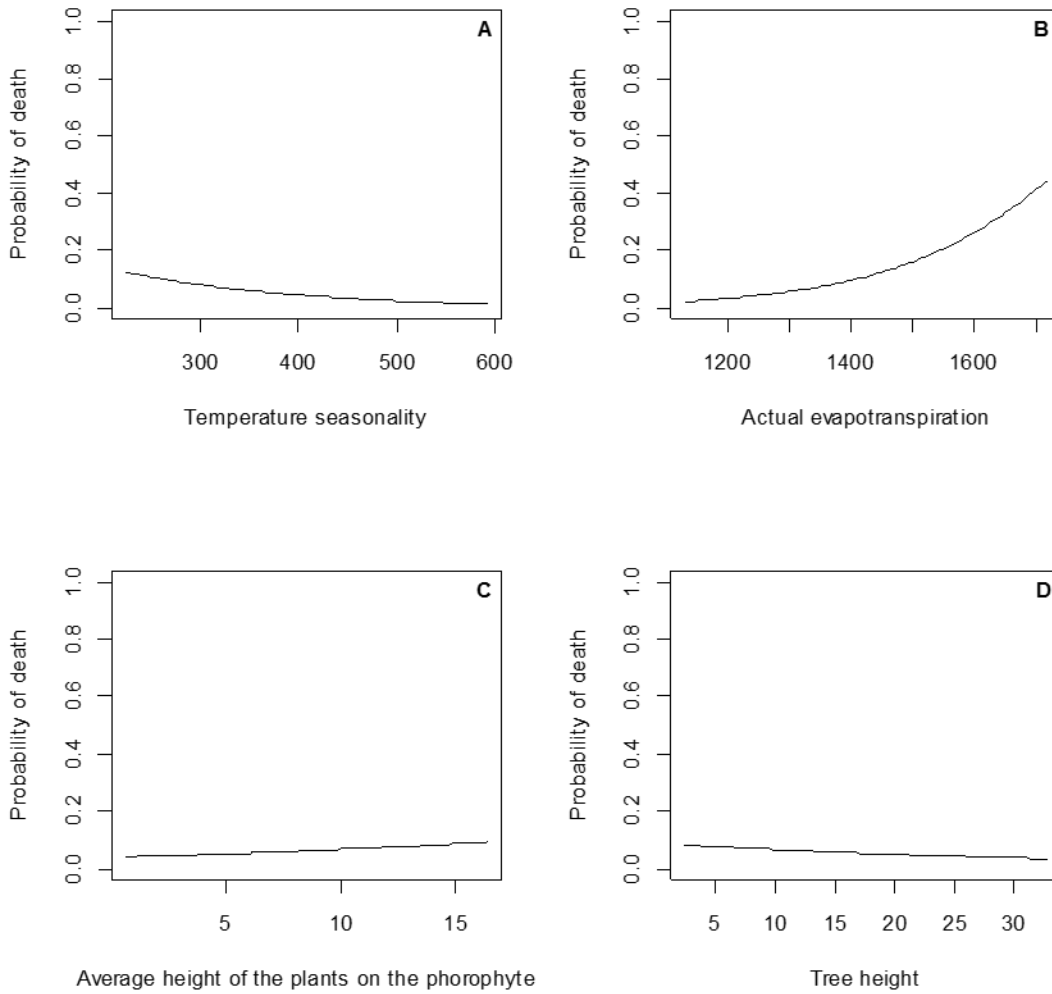
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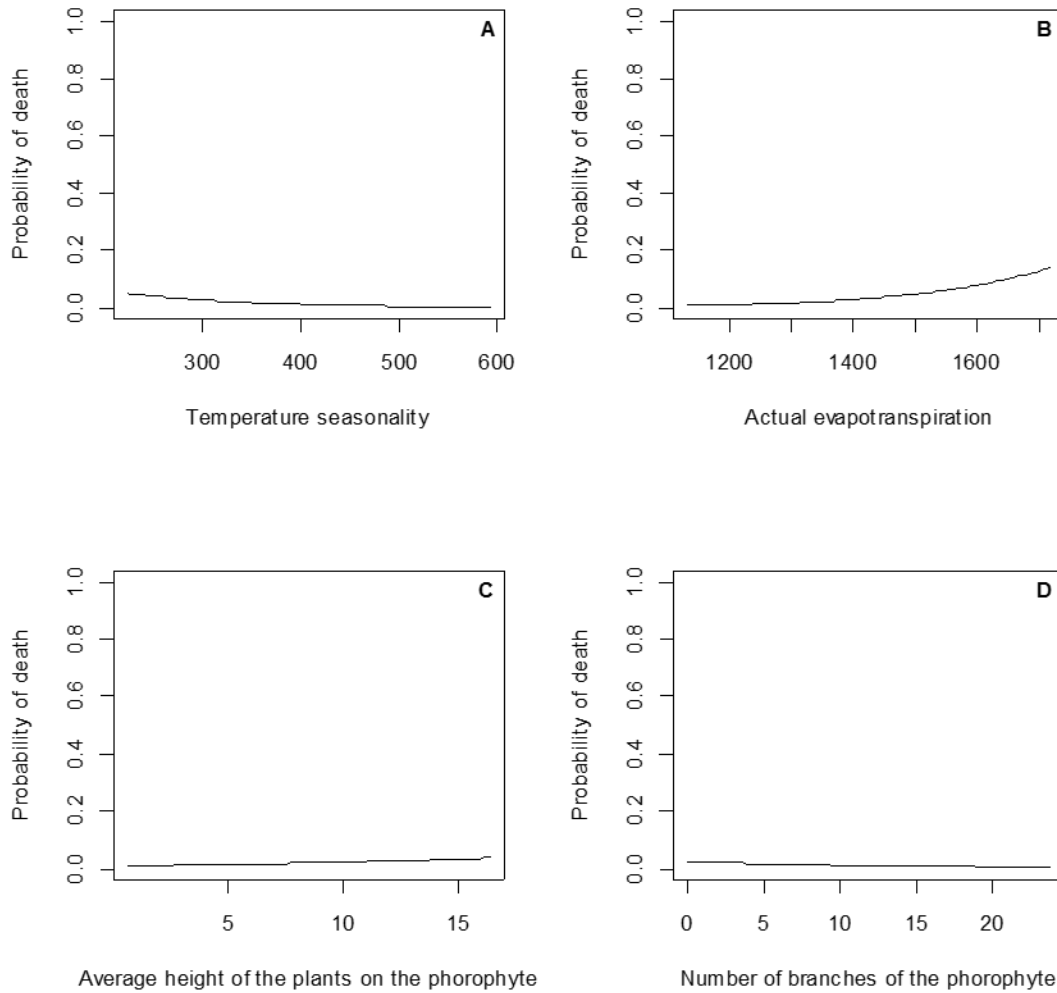


# Appendix 1



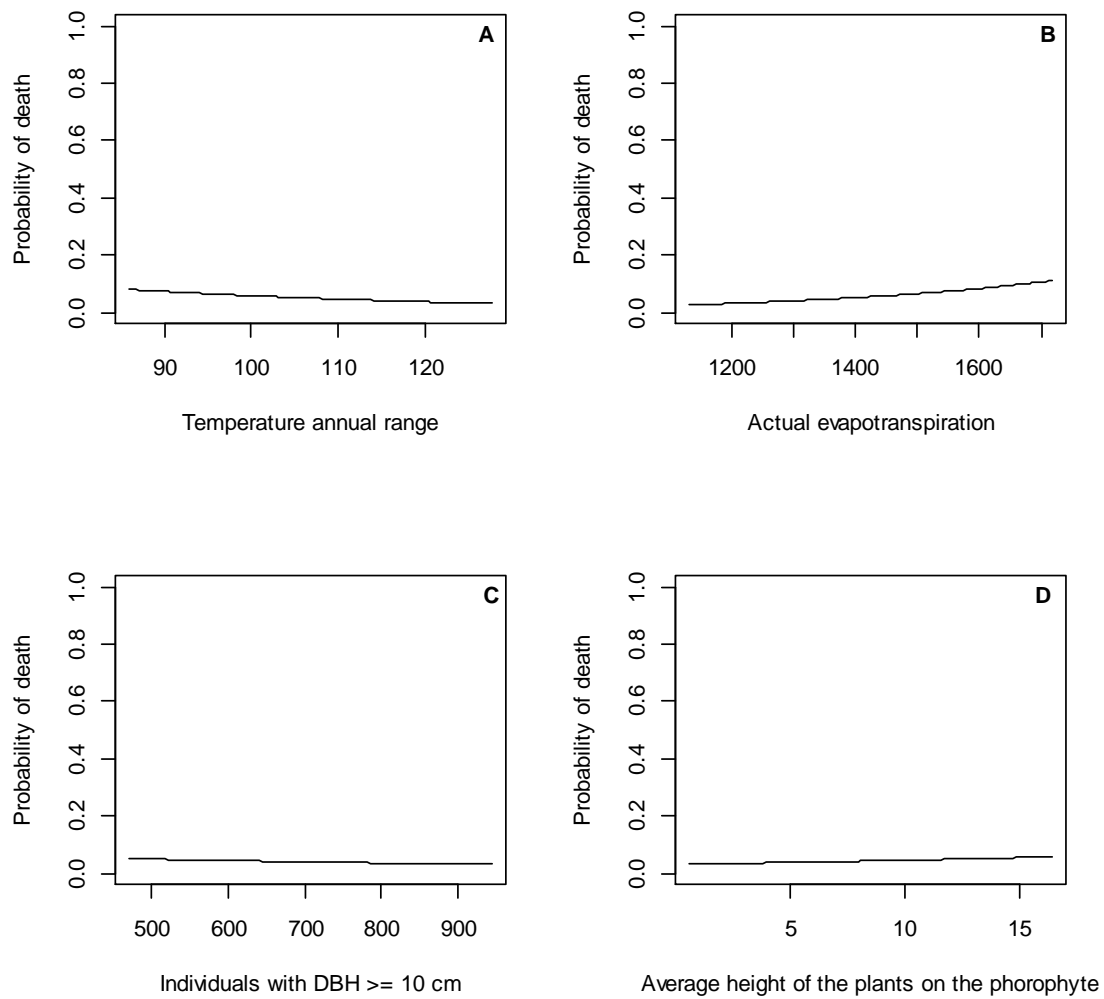
Sensitivity analysis for the determinant variables of the mortality for vascular epiphytes on 115 sampled phorophytes in 9 sites in Colombian Andes. The curves show the effect of each variable in the probability of mortality when the others are left fixed in their average values.

## Appendix 2



Sensitivity analysis for the determinant variables of the natural mortality for vascular epiphytes on 115 sampled phorophytes in 9 sites in Colombian Andes. The curves show the effect of each variable in the probability of mortality when the others are left fixed in their average values.

## Appendix 3



Sensitivity analysis for the determinant variables of the mechanical factors mortality for vascular epiphytes on 115 sampled phorophytes in 9 sites in Colombian Andes. The curves show the effect of each variable in the probability of mortality when the others are left fixed in their average values.