Fine-Scale Plant Richness Mapping of the Andean Páramo According to Macroclimate

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Understanding the main relationships between the current macroclimate and broad spatial patterns of plant diversity is a priority in biogeography, and although there is an important body of studies on the topic worldwide, tropical mountains remain underrepresented. Because understanding primary drivers of diversity patterns in the Andean páramo is still in its infancy, we focused on evaluating the role of the current macroclimate in form of three complementary hypotheses, energy, seasonality and harshness, in explaining local variation of plant species richness. We relied on 1,559 vegetation plots that offered a fine-scale outlook on real species assemblages due to community rules and species' interactions with their surrounding environment, including climate. Generalized Least Squares (GLS) regression models provided insight on the significance of the different hypotheses in explaining local plant richness, but only the energy and seasonality hypotheses received partial support. The best model was then combined with spatial interpolation Kriging modeling techniques to project species richness for a standardized 25 m^2 plot throughout the entire páramo biogeographical province. We highlighted a North-South increase in richness with several species-rich areas, potential local biodiversity hotspots, independent of the general gradient: the Amotape-Huancabamba zone, Sangay and Cotacachi areas, and eastern Venezuelan Andes. Our endeavor to finely map local richness is the first effort predicting macroecological patterns in the emblematic Andean páramo and contributes novel biogeographical knowledge useful to further support in-depth research and conservation focus in the northern Andes.

Keywords: contemporary macroclimate, High Andes, Kriging model, plant diversity, regression model, richness patterns

INTRODUCTION

Understanding spatial patterns of biodiversity across dimensions, scales, and areas of the world remains one of the greatest challenges in biogeography (Lomolino and Heaney, 2004; Kennedy and Norman, 2005). With 15% of the world's total plant richness, the Tropical Andes is a main biodiversity hotspot on earth (Myers et al., 2000; Barthlott et al., 2007), and home to the Andean páramo, a high mountain biogeographical province (Morrone, 2014) known as the most phytodiverse tropical high mountain system worldwide (Sklenár et al., 2014).

The páramo includes all natural and semi-natural ecosystems located above the montane treeline (~3,000–5,000 m) in the northern tropical Andes of Venezuela, Colombia, Ecuador, and northern Peru (Luteyn, 1999) and presents an astonishing phytodiversity of almost 500 genera and 5,000 plant species, 60–80% of which are endemic (Londoño et al., 2014; Rangel-Churio, 2015). It is mostly thanks to the recent orogeny of the northern tropical Andes, geographic proximity to the Amazonian and Chocó-Pacific biomes, and relatively stable climatic conditions though time that the páramo evolved to become the world's coldest and fastest evolving biodiversity hotspot (Madriñan et al., 2013; Anthelme et al., 2014). The páramo, with a spatial distribution over 20 degrees latitude and 2,000 m elevation, constitutes an excellent biogeographical model system to represent tropical mountains worldwide (Anthelme and Peyre, 2019).

Macroecological research on broad-scale spatial patterns of species richness in tropical mountain regions and in the páramo is critically lacking to date. Previous studies have either focused on limited taxonomic groups (e.g., for plants: Izco et al., 2007; Nürk et al., 2013; for animals: Jacobsen, 2003; Sites et al., 2003; Moret, 2009) or reduced geographic areas (Sklenár and Jørgensen, 1999; Sklenář and Ramsay, 2001; but see Cuesta et al., 2017 for a regional approach, although with sparsely distributed data). When focusing on plant species richness, a decreasing tendency has been highlighted along the elevational gradient of certain páramos (Sklenár and Jørgensen, 1999; Sklenář and Ramsay, 2001) and latitudinal gradients remain generally understudied. Several authors have also discussed potential drivers of local species richness and found that human disturbance and several environmental factors, such as annual precipitation and scree, condition plant richness in the high tropical Andes (Sklenář and Ramsay, 2001; Vásquez et al., 2015; Cuesta et al., 2017).

Many hypotheses have been proposed to explain variation in species richness, and the environment, especially the contemporary climate, has held a prevailing place as potential driver (Hawkins et al., 2003; Willig et al., 2003; Field et al., 2009). Other simultaneously-acting hypotheses have also been advanced to play a significant role, among which, other environmental factors such as edaphic conditions, historical climate (Francis and Currie, 2003; Araújo et al., 2008), biome age and area (Rahbek, 1995; Fine, 2015), species diversification rates and historical processes (Ricklefs, 2006; Jetz and Fine, 2012), functional diversity and biotic interactions (Cavieres et al., 2014; Mod et al., 2015). Because of the broad extent of the páramo biogeographical province and the general paucity of fine data to represent potential causal factors associated with richness variation, our exploratory study focused on understanding the role of the contemporary macroclimate, with available data for the entire study area (Karger et al., 2017), as richness driver at the local scale. To do so, three complementary climatic hypotheses were set to represent the overall macroclimate: energy, seasonality, and climatic harshness (Willig et al., 2003; Kreft and Jetz, 2007; Tello and Stevens, 2010; but see Mittelbach et al., 2007).

(1) Energy: Plant species richness is generally found to be conditioned by two forms of environmental energy: kinetic—related to temperature—and potential (or chemical)—the result of photosynthesis constrained by climatic conditions, in form of temperature and water availability (Hawkins et al., 2003; Currie et al., 2004; Allen et al., 2007). Multiple mechanisms have linked both forms of energy to species richness (Currie et al., 2004; Evans et al., 2005). For example, kinetic energy has been proposed to increase biological rates, e.g., mutation, metabolism and generation times, resulting in accelerated speciation processes (Gillooly et al., 2001, 2005). Similarly, high potential energy, hence substantial productivity, can sustain larger population sizes, which can in turn reduce extinction risk and increase speciation probability (Srivastava and Lawton, 1998). In addition, high potential energy has often been correlated to carrying capacity for species, whereby more species can co-exist in highly productive environments under warm and humid climates (Fine, 2015). According to the *energy* hypothesis, areas with high energy concentration would support more plant diversity.
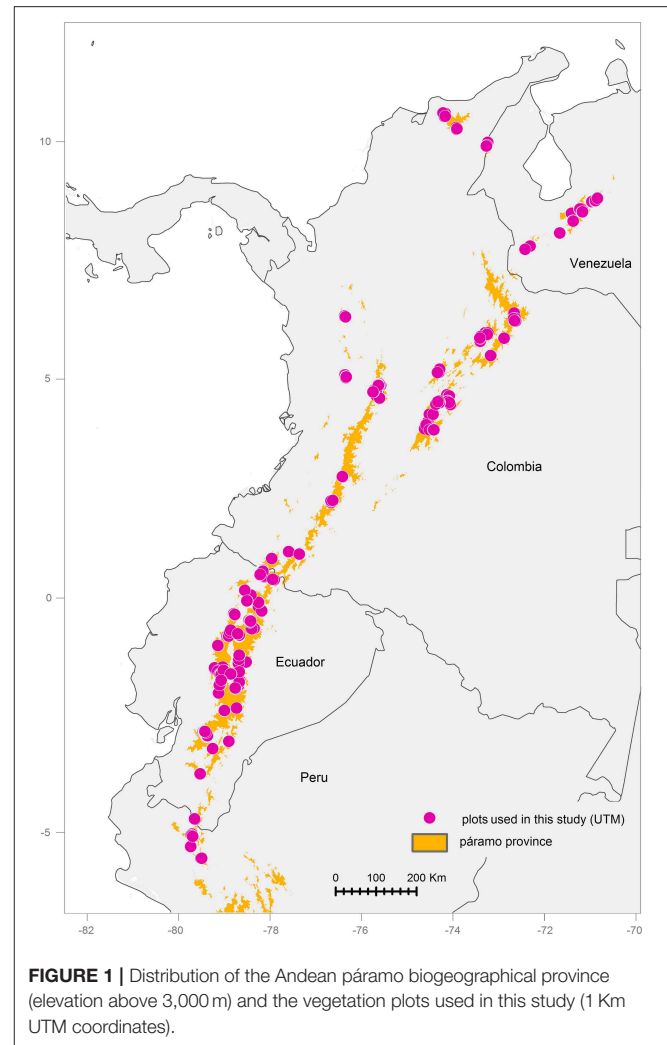
(2) Seasonality: the variation in environmental conditions at multi-temporal scales has been proposed to drive species richness patterns by influencing the co-existence and accumulation of species (Jablonski et al., 2006; Fine, 2015; Pfeifer et al., 2018). For instance, climatic stability over centuries and millennia can decrease the likelihood of extinctions and promote the saturation of niche spaces, resulting in important species richness (Ordonez and Svenning, 2017; Fordham et al., 2018). In contrast, short-term seasonality, i.e., seasonality at the intra-annual and inter-annual scale, has been suggested as a source of climatic instability that can lead to wide population fluctuations and even increase extinction risk during time of low population size (Inchausti and Halley, 2003; Somveille et al., 2015; Rajakaruna and Lewis, 2018). Alternatively, species may adapt to high seasonality by developing broad niches, hence broad geographic distributions with few dispersal and ecological barriers and little population subdivision. This in turn would reduce the likelihood of speciation events and lead to species-poor communities with little fine partitioning of their niche space (Pianka, 1966; MacArthur et al., 1972). Therefore, the *seasonality* hypothesis would state that short-term climatically unstable areas would possess lower species richness than stable ones.

(3) Harshness: the climate extremes might physiologically limit species in their growth and reproduction, hence in their spatial distribution (Francis and Currie, 2003; Currie et al., 2004; Evans et al., 2005; Smith, 2011). While most *hypotheses* about environmental conditions typically use average conditions, the *harshness* hypothesis is correlated to the *energy* hypothesis but suggests that it is the most unsuitable conditions that occur at a site that limit species distributions, hence community composition and diversity (e.g., Knapp et al., 2002; Miriti et al., 2007; Thibault and Brown, 2008). If measures of climatic tolerance are similar for most species, then harsh environments would be tolerated by fewer species and diversity would be lower, as illustrated by the relatively limited species richness at high latitudes due to freezing tolerance (Hawkins et al., 2003). Indeed, although the average annual temperature

can be included in the physiological tolerance range of a species in cold regions, the minimum yearly temperature might limit the species' distribution range and contribute to a diversity decrease at the ecosystem level. A similar mechanism might occur in regions where water availability is limiting during at least part of the year and excludes species that cannot tolerate droughts (Miriti et al., 2007). Although resistance to extreme climatic events is evolution and species-dependent, the combination of cold and dry conditions is generally believed to be harsh for most taxa, as a result, we expected under the *harshness* hypothesis for lower species richness to be found in páramo with harsh climatic conditions.

Mapping fine-scale richness across broad areas has proved very useful guiding conservation and management planning, for example through the identification of local biodiversity hotspots (Myers et al., 2000), however these efforts remain rare to date (Beck et al., 2012; Divíšek and Chytrý, 2018; Večera et al., 2019). Most macroecological studies rely on coarse grain biological data, i.e., grid cell, with correlation analyses and predictions made based on checklist occurrence data or predicted occurrences stacked together (e.g., D'Amen et al., 2015; Ulloa Ulloa et al., 2017). In these cases, local species lists are usually not obtained from real biotic communities responding to ecological assembly rules, but by co-occurrences driven by individualistic observation or probability of presence in a given cell. On the contrary, vegetation data accounts for this issue as it provides fine resolution information on actual species assemblages in direct interaction with the surrounding environment, and as a result, a new body of biogeographical studies is starting to explore predicting spatial richness patterns from this type of data (Divíšek and Chytrý, 2018; Večera et al., 2019). As vegetation databases encompassing tropical mountain areas our flourishing worldwide, including in the páramo (Peyre et al., 2015; Bruelheide et al., 2019), new approaches to macroecological research are becoming accessible for these regions. By correlating local richness with the macroclimate in the páramo, we expected the resulting fine-scale map to highlight a general decrease richness pattern with increasing latitude (Hawkins et al., 2003; Willig et al., 2003), even though it has not yet been confirmed for tropical mountain areas (Bjorholm et al., 2005), as well as decreasing richness with elevation as previously found in Ecuadorian páramos (Sklenář and Ramsay, 2001; McCain and Grytnes, 2010). Finally and related to our climatic hypotheses, we believed local hotspots would be highlighted in climatically clement areas, for example in the western Colombian cordillera and the central eastern Ecuadorian cordillera (Herzog et al., 2011; Rangel-Churio, 2015).

The overarching objective of this study was to understand how the contemporary macroclimate influences local plant richness in the páramo and map fine-scale richness predictions using climatic drivers throughout the biogeographical province. Specifically, the respective roles of energy, seasonality, and harshness were studied as three complementary hypotheses, and local plant richness was mapped to reveal general spatial patterns and biodiversity hotspots in the high northern Andes.

FIGURE 1 | Distribution of the Andean páramo biogeographical province (elevation above 3,000 m) and the vegetation plots used in this study (1 Km UTM coordinates).

METHODS

All statistical analyses were conducted in R 3.3.1 (R Core Team, 2013).

Study Area and Vegetation Data

The study area encompassed the Andean páramo biogeographical province, including the high-elevation northern Andes and the Sierra Nevada de Santa Marta, but excluding other extra-Andean areas with similar altitudinal and/or environmental conditions, such as Amazonian volcanoes or Central American mountains (**Figure 1**). It was therefore delimited in the north by the Sierra Nevada of Santa Marta (11°N, Colombia) and in the south by the Huancabamba depression (6°S, Peru), which is usually considered a main biogeographical barrier for high-elevation plant taxa (Weigend, 2002). The easternmost páramos were located in the Cordillera de Merida (72°W, Venezuela), whereas the westernmost ones were the Piura páramos (80°W, Peru).

For floristic data, all vegetation plots contained in *VegPáramo*, the database for páramo flora and vegetation that compiles data from almost 40 different sources, were downloaded (Peyre et al., 2015). These plots were sampled with the phytosociological method, which involves estimating species cover in a categorical scale (from + to 5) within defined plots of a varying area set for different vegetation physiognomies (Braun-Blanquet, 1951; **Figure 1** and **Figure S1A**). In order to estimate plant richness within each plot, the species relative cover values were transformed into presence-absence data. To standardize the taxonomy across the heterogeneous dataset, synonymy was checked, and updated using the *VegPáramo* taxon list, which contains updated information for about 15,000 northern Andean plant species. For dubious taxa such as orchids, the Plant List (www.plantlist.org) and Tropicos (www.tropicos.org) databases were also consulted. Non-vascular plants were then removed from the dataset, as well as unidentified species. Finally, infra-specific taxa, i.e., subspecies, varieties and forms, were elevated, and combined to the species level. Regarding the plot data, outliers to the study area and plots with a coarse georeferencing precision (>1 km) were removed from the dataset. Because this study focused on spatial patterns of fine-scale species richness over a broad area, plots whose descriptive structure and composition explicitly referred to azonal or ecotone vegetation were eliminated, according to the plot's original authors. Finally, the few plots with unusual areas (< 1 m^2 and > 100 m^2) were removed, for a final dataset containing 1,559 vegetation plots and 1,169 species, spread over the páramo biogeographical province and presenting considerable local-plot richness variation (**Figure S1B** and **Table S1**).

Climatic Data

Disentangling the effects of the three climatic hypotheses is challenging due to the necessary correlation between climatic predictors and consequent overlapping of the hypotheses. For *energy*, we included mean annual temperature (bio1), annual precipitation (bio12), actual evapotranspiration (AET), and mean monthly soil water stress coefficient defined as the fraction (percentage) of soil water content available for evapotranspiration(swcfr). For *seasonality*, we considered mean diurnal temperature range (bio2) for daily variation, temperature seasonality (bio 4) and precipitation seasonality (bio15) for monthly variation, as well as inter-annual temperature variation (bio20) and inter-annual precipitation variation (bio21) for yearly variation. The latter two variables were calculated as the yearly standard deviation of bio1 and bio12, respectively, during the period 1979–2013. Finally to represent *harshness*, we used minimum temperature of the coldest month (bio6), precipitation of the driest month (bio14), and precipitation of the warmest quarter (bio18) that we supposed woud condition richness. The bioclimatic variables (bio), except for bio20 and 21, were downloaded as means for the period 1979–2013, from the (CHELSA Project 1.1, 2017), *Climatologies at High resolution for the Earth's Land Surface Areas* (http://chelsa-climate.org), which is known for enhancing bioclimatic data quality in tropical areas (Karger et al., 2017). Additionally,

the AET and swcfr variables were obtained from the CGIAR-CSI, *Consultative Group on International Agricultural Research Consortium for Spatial Information databases* (www.cgiar-csi.org; Zomer et al., 2008; Trabucco and Zomer, 2010) and all variables were obtained as raster data at a resolution of 30 arc-s (∼1 km). All variables presented a certain amount of multicollinearity, some of them very high as illustrated by high Pearson correlation values (**Figure S2**). Nonetheless, because these variables were used in different models, or altogether but with a robust variable selection process, we considered this approach valid and took the multicollinearity information into account in our discussion.

Drivers of Richness

For these analyses, Generalized Least Squares (GLS) models were used because they efficiently account for the correlation structure in residuals (fitted with the *gls* function of the *nlme* R package; Beale et al., 2010). Through testing several correlation structures, the quadratic spatial correlation with a nugget effect was finally selected and used in all following models, based on its performance given by the AIC and spatial autocorrelation in residuals (function *corRatio* in the *nlme* R package). For each model carried out, all variables were subjected to the forward selection process proposed by Blanchet et al. (2008) to reduce collinearity and identify the most significant predictors. The procedure included successively adding a variable (from 1 to n) to the model and validate it based on variables' p-values (significance level set at 0.05) and model performance (function *ordiR2step* in the R package *vegan*, Oksanen et al., 2012). To compare the performance of the obtained models, a pseudo-R^2 was calculated, based on the squared correlation coefficient between observed and predicted richness. Moreover, models were evaluated according to their AIC and Δ_{AIC} (difference between the selected and the best performing model), considering that any Δ_{AIC} < 2 between models would imply a similar support from the data (Burnham and Anderson, 2002).

Due to the large variation of plot areas in the dataset, characteristic of phytosociological sampling (Braun-Blanquet, 1951; **Figure S1A**), a preliminary analysis was conducted to determine a potential correlation between plot area and local plant richness (Lomolino, 2000). To do so, a regression between plot area in its logarithmic form and richness was conducted, model PlotArea, and showed a significant correlation between the two factors ($pseudoR^2 = 0.128$, p-value< 0.001, **Table 1** and **Figure 2B**). Therefore, plot area was considered a significant predictor of local plant richness and included in its logarithmic form in all the following regression analyses.

Eight regression models using different sets of climatic variables and log(area) were built. Three models included all the predictors associated with only one hypothesis: *energy* (Energy), *seasonality* (Seasonality), and *harshness* (Harshness). Three additional models incorporated all possible combinations of predictors from two hypotheses (models E+S, E+H, or S+H). Finally, a complete climatic model considered all variables representing the three hypotheses (E+S+H).

TABLE 1 | Results for all climatic GLS models.

Model	Component	Predictor	Estimate	P	AIC	$_{Pseudo}R^2$	P_{model}
PlotArea		Intercept	17.307	< 0.001	10,004	0.128	<0.001
	A	Area (log.)	1.961	< 0.001			
Energy		Intercept	16.873	< 0.001	9,973	0.189	<0.001
	A	Area (log.)	1.967	< 0.001			
	E	swcfr	−1.761	< 0.001			
Seasonality		Intercept	17.343	< 0.001	9,987	0.185	<0.001
	A	Area (log.)	1.938	< 0.001			
	S	bio4	1.198	0.001			
	S	bio2	0.778	0.042			
Harshness		Intercept	17.313	< 0.001	10,006	0.131	<0.001
	A	Area (log.)	1.958	< 0.001			
E + S		Intercept	16.956	< 0.001	9,943	0.246	<0.001
	A	Area (log.)	1.897	< 0.001			
	E	swcfr	−1.984	< 0.001			
	E	bio12	−1.837	< 0.001			
	E	bio1	1.000	0.015			
	S	bio15	−2.487	< 0.001			
E + H		Intercept	16.836	< 0.001	9,948	0.225	<0.001
	A	Area (log.)	1.905	< 0.001			
	E	bio12	−3.781	< 0.001			
	E	swcfr	−1.506	< 0.001			
	H	bio14	3.794	< 0.001			
S + H		Intercept	17.317	< 0.001	9,986	0.190	<0.001
	A	Area (log.)	1.933	< 0.001			
	S	bio4	1.123	0.004			
	S	bio15	−1.382	0.010			
	H	bio14	−1.420	0.029			
E + S + H		Intercept	16.936	< 0.001	9,943	0.246	<0.001
	A	Area (log.)	1.894	< 0.001			
	E	swcfr	−1.759	< 0.001			
	E	bio12	−2.925	0.001			
	E	bio1	1.121	0.007			
	S	bio15	−1.403	0.020			
	H	bio14	2.058	0.045			

Considered variables: Energy predictors –bio1, annual mean temperature; bio12, annual precipitation; swcfr, mean monthly soil water stress coefficient; AET, actual evapo-transpiration. Seasonality predictors –bio2, Mean diurnal temperature range; bio4, temperature seasonality; bio15, precipitation seasonality; bio20, inter-annual temperature variation (σ; 1979–2013); bio21, inter-annual precipitation variation (σ; 1979–2013). Harshness predictors –bio6, minimum temperature of coldest month; bio14, precipitation of driest month; bio18, precipitation of warmest quarter.
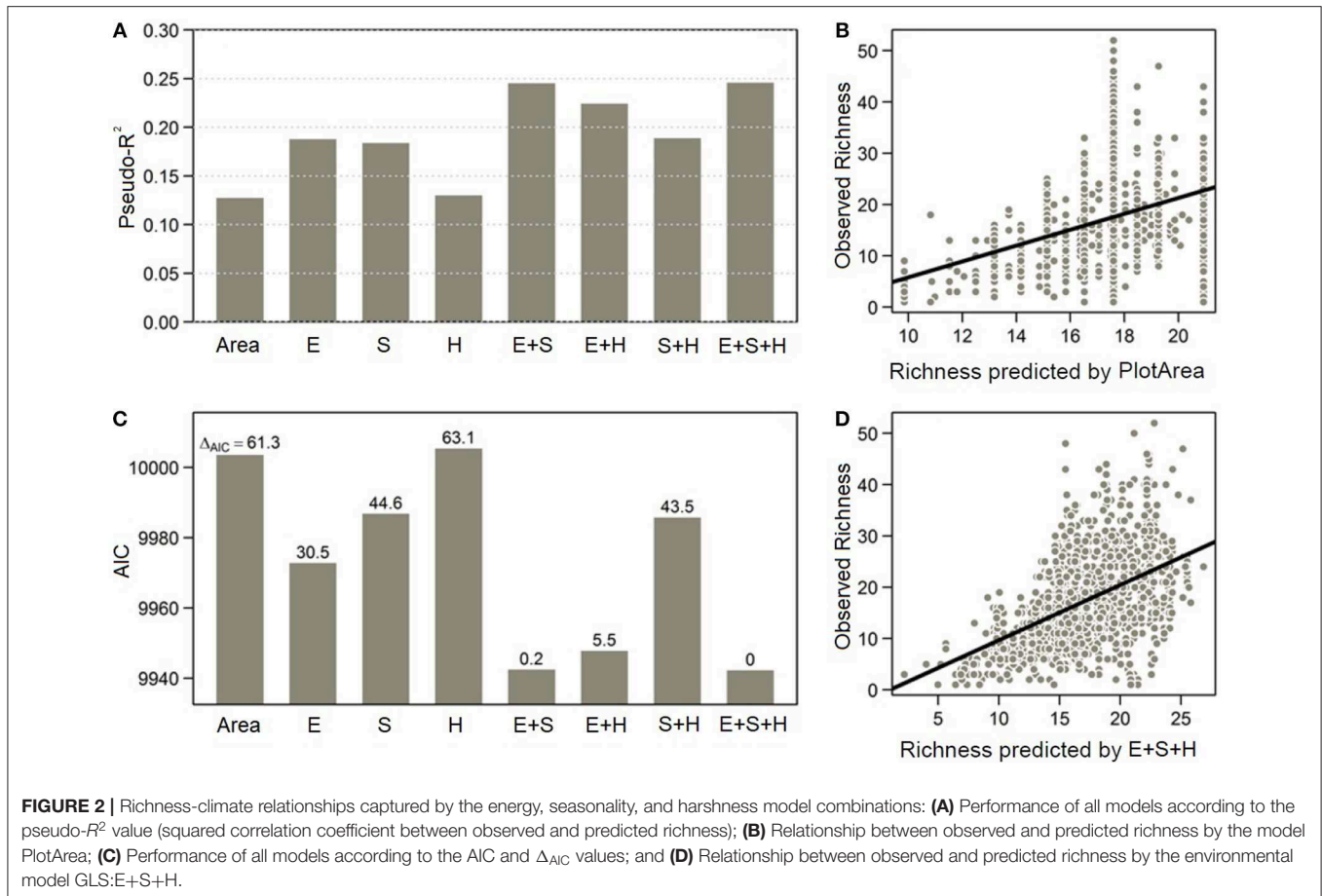
Regional Fine-Scale Richness Patterns

To explore spatial patterns of fine-scale plant richness in the páramo province, three predictive maps were built based on local richness for a standardized by logarithm size plot of 25 m^2 to make predictions comparable despite the varying plot size. The following techniques aimed at optimizing the predictions for under-sampled areas by relying not only on climatic data but also on spatial complexity. The first interpolation technique used was a spatial Ordinary Kriging (OK) model, which estimated local species richness in non-sampled areas based solely on the distance between said area and its nearest sampled points (Banerjee et al., 2003). Second, the best performing GLS model previously obtained was used alone to predict local richness. Last, both the OK and GLS models were combined into a Universal

Kriging (UK) model, which is a commonly used approach to enhance interpolation estimates and account for both climatic gradients and underlying spatial trends (Kreft and Jetz, 2007).

RESULTS

Climatic models varied in their explaining power (**Table 1**). The energy (Energy) and seasonality (Seasonality) models presented a pseudo-R^2 of almost 0.19, corresponding to an explaining power of almost 19 percent of the variation in local richness, while plot area alone showed a pseudo-R^2 around 0.13 only (model PlotArea). On the contrary, the harshness model (Harshness), which only retained the plot area variable of all factors, behaved

FIGURE 2 | Richness-climate relationships captured by the energy, seasonality, and harshness model combinations: **(A)** Performance of all models according to the pseudo-R^2 value (squared correlation coefficient between observed and predicted richness); **(B)** Relationship between observed and predicted richness by the model PlotArea; **(C)** Performance of all models according to the AIC and Δ_{AIC} values; and **(D)** Relationship between observed and predicted richness by the environmental model GLS:E+S+H.
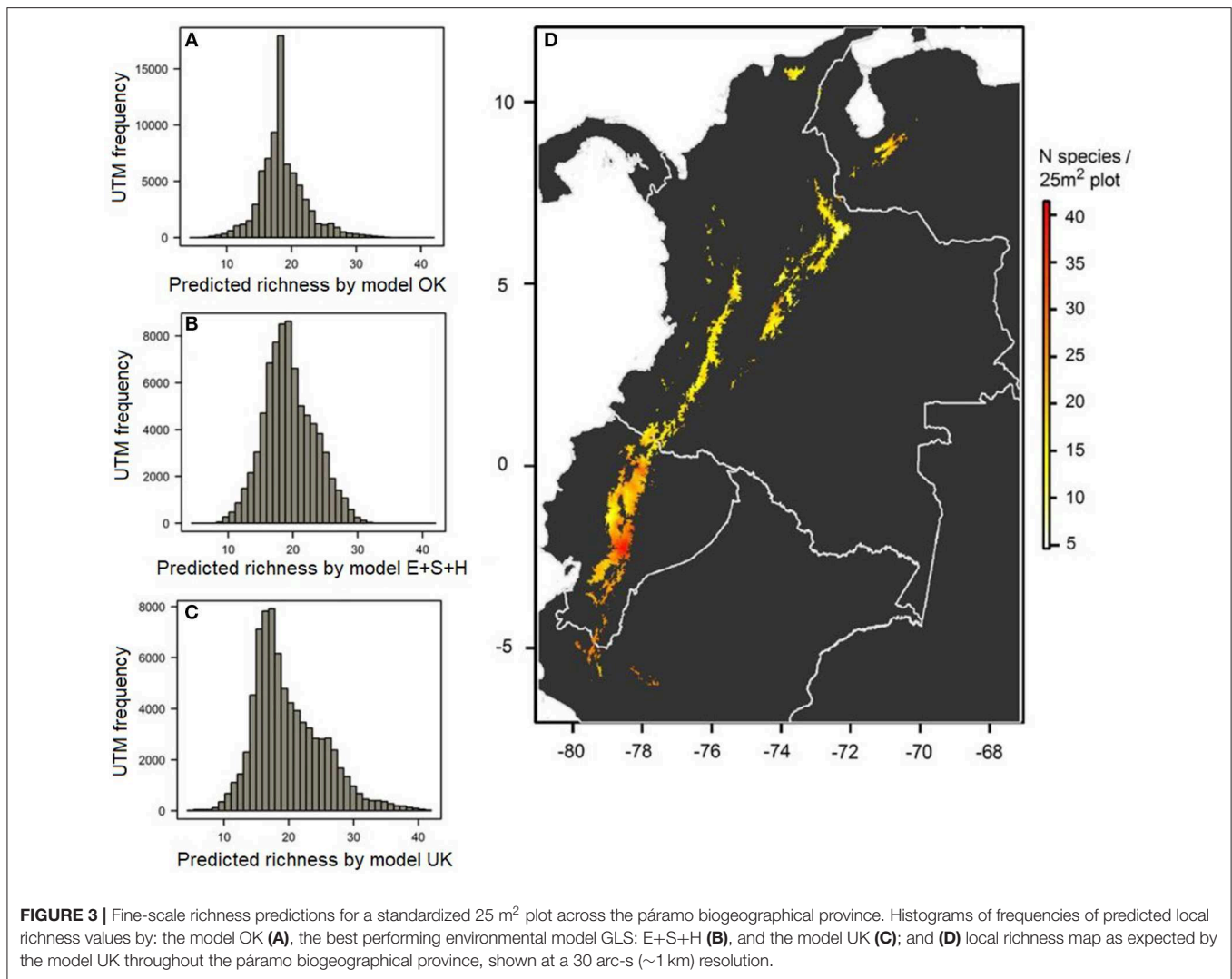
unsurprisingly similarly to model PlotArea. Among all models, the best performing and statistically comparable models with a $\Delta_{AIC} < 2$ were models E+S and E+S+H. These two models presented a pseudo-R^2 close to 0.25, explaining almost 25 percent of local richness variation and showed the lowest AIC value at 9943 (**Figure 2**). Both models included the same significant predictors, except for one variable present only in model E+S+H, which is precipitation of the driest month (bio14), a *harshness* variable strongly correlated with annual precipitation (bio12) (**Figure S2**). They also showed similar tendencies regarding the correlation of predictors with local richness, as detailed below.

First considering the *energy* variables included in models E+S and E+S+H, species richness was correlated positively to annual temperature (bio1) and negatively with soil water stress coefficient (swcfr). Moreover, richness was negatively correlated to annual precipitation (bio12). Other models showed similar results for the correlation between richness and the predictors: swcfr (in models Energy and E+H) and bio12 (in model E+H), whereas bio1 was not included in any other model. Second regarding *seasonality* predictors, models E+S, S+H, and E+S+H retained precipitation seasonality (bio15) and found it negatively correlated to richness. Models Seasonality and S+H both contained temperature seasonality

(bio4), a variable positively correlated to richness, and in the former case, mean diurnal temperature range (bio2) was also retained and positively correlated to richness. Last for *harshness*, precipitation of the driest month (bio14) was the only predictor included in models E+S+H, E+H, and S+H and showed a positive correlation with richness in the first two models and a negative one in the latter. Nonetheless, this variable was not even found significant in the model Harshness. In general, models included more precipitation-related variables, except for model Seasonality, which included a majority of temperature-related predictors.

All models used to create interpolated maps of local plant richness across the páramo province predicted similar spatial patterns (**Figure 3** and **Figure S3**). The best performing GLS model selected to predict richness was model E+S+H because of its good pseudo-R^2 and AIC values and consideration of a *harshness* variable. Both the OK and E+S+H models predicted a variation of 7–35 species per 25 m^2 plot (**Figures 3A,B** and **Figure S3**) and by contrast, the UK model predicted 4–42 species, a fitter value-range to the observed 1–52 species present in the plot data (**Figure 3C** and **Figure S1B**). According to the UK model predictions, a general decrease of species richness was projected from south to north, dividing the locally more diverse páramos south of the equator and the less diverse páramos

FIGURE 3 | Fine-scale richness predictions for a standardized 25 m² plot across the páramo biogeographical province. Histograms of frequencies of predicted local richness values by: the model OK **(A)**, the best performing environmental model GLS: E+S+H **(B)**, and the model UK **(C)**; and **(D)** local richness map as expected by the model UK throughout the páramo biogeographical province, shown at a 30 arc-s (∼1 km) resolution.

in the north (**Figure 3D**). Overall, Colombian páramos were found generally poorer than páramos in other countries. No clear elevational gradient was observed at this scale, assuming high elevations are located in the central part of mountain ranges, while low elevations are located at the borders. Several punctual areas with high local species richness (> 35 species per 25 m² plot) could be observed, for example surrounding the Amotape-Huancabamba zone (∼Lat. 5°S; Long. 79.5°W), the Sangay (∼Lat. 2°S; Long. 78.5°W), and Cotacachi (∼Lat. 0°; Long. 78°W) massifs in Ecuador, as well as the Lara páramos in Venezuela (∼Lat. 9°N; Long. 71°W).

DISCUSSION

Our study is pioneer in studying macroclimatic drivers of plant richness and conducting macroecological analyses over the entire páramo biogeographical province and based on substantial vegetation data. It also represents one of the first few efforts worldwide to propose fine-resolution richness mapping based on vegetation data, hence correlating real species assemblages in

their complexity of interactions and community constraints with macroclimate features. The results obtained shed light on the role of macroclimate in explaining local variation in local richness and provided a richness fine-scale map with potential future uses in research and biodiversity management, for example through the identification of local biodiversity hotspots.

Climatic Drivers of Richness

The macroclimate was found to play a significant but rather small part in explaining variation of local plant richness, 25 percent at best (models E+S and E+S+H) and 13 percent more than plot area alone (PlotArea). Several but not all of the significant correlations found between environmental variables and plant richness agreed with the originally set expectations. Therefore, our findings should be interpreted carefully as potential influences between variables and not as direct cause-consequence relationships.

Regarding *energy*, we observed that local richness increased with annual temperature (bio1), which supports the hypothesis

that high kinetic energy can increase biological rates, hence promoting population differentiation, speciation and therefore greater diversity, although said effects are hardly visible at the plot scale (Gillooly et al., 2001; Hawkins et al., 2003; Evans et al., 2005). Agreeing with this finding was the negative relation found between soil water stress (swcfr) and local richness. This is a commonly encountered correlation in ecology, and unlike temperature that usually enhances net primary productivity, soil water stress tends to reduce it, and therefore influence plant diversity through the ecosystem's productivity (Srivastava and Lawton, 1998; Currie et al., 2004). Nonetheless, our results showed that local richness decreased with annual precipitation (bio12), which in turn contradicts the hypothesis that high potential energy in form of water availability would increase the accumulation of species and saturation of habitats, resulting in higher species richness (Hawkins et al., 2003; McCain and Grytnes, 2010; Fine, 2015). The precipitation-richness relationship is often difficult to isolate from other factors' influence because mixed effects usually occur, for instance winds are important in conditioning local precipitation trends (McCain and Grytnes, 2010). We propose several potential explanations for this unexpected result and recommend further study to evaluate them. First, because most páramos are already humid ecosystems, i.e., receiving between 2,000 and 4,000 mm rain/year (Luteyn, 1999; Rangel-Churio, 2006), we could advance the intermediate-stress hypothesis, which forecasts highest richness at moderate intensities of environmental stress (Grime, 1979). Traditionally, this hypothesis has been more documented along aridity gradients with drought stresses (e.g., Armas et al., 2011; Butterfield et al., 2016), however, humidity gradients with wet stresses are being increasingly studied (e.g., Kramer and Boyer, 1995; Knapp et al., 2008). Most páramos receive sufficient water to function adequately, and only a few endure temporal droughts, for example the rain-shadow deserts of Mount Chimborazo (~Lat. 1.5°S; Long. 78.8°W) and Piedras blancas (~Lat. 8.8°N; Long. 70.8°W) (Sklen and Lægaard, 2003; Stansell et al., 2005). Nonetheless, many páramos face a very important up to extreme water intake, which could result in a temporal or permanent wet stress, for example in the pluvial páramos of the Western Colombian Cordillera that receive more than 6,000 mm/year (Rangel-Churio, 2006). This situation could result in less species able to tolerate the very humid environmental conditions and anoxic soils, and limit the overall species saturation of páramo ecosystems (Kammer and Möhl, 2002). Second, important precipitation could indirectly imply denser fog and cloud cover, known as horizontal precipitation, which constitutes the main water intake in most páramos (Buytaert et al., 2006; Sklenár et al., 2008) but which is very difficult to account for in models. Fog and cloud cover benefit ecosystems by providing substantial amounts of humidity for plants, protecting organisms from the damaging solar radiation and buffering extreme temperatures (Luteyn, 1999; Sklenár et al., 2008). Nonetheless, too much intercepted water around the leaves could also limit evapotranspiration and photosynthetic processes (Smith and McClean, 1989; Asbjornsen et al., 2011), resulting in less productivity and as a result lower richness.

Last, precipitation might be correlated to the abundance of growth forms in a plot, which by occupying different fractions of the available space might allow more or less functional hence taxonomic diversity to co-occur locally (Wilson et al., 2012). An extreme example would be how in very humid páramos are usually associated with vegetation dominated by bamboos of the genus *Chusquea*, which tend to prevail and leave little space for other plant species to grow, resulting in turn in relatively low richness (Luteyn, 1999; Cleef et al., 2005; Cuello and Cleef, 2009). Downscaling our results to the páramo vegetation type or phytogeographical unit (e.g., Peyre et al., 2018) might provide clearer insight on the validity of these hypotheses (Divíšek and Chytrý, 2018).

For the *seasonality* hypothesis, our main results highlighted the negative correlation between richness and precipitation seasonality (bio15). This finding agrees with our original hypothesis stating that in climatically stable páramos, where seasonality is limited, species would tend to accumulate and narrow-niche species would be favored. Previous studies have agreed with this hypothesis for animals (Somveille et al., 2015; Pfeifer et al., 2018) and also plants (Morueta-Holme et al., 2013), because short-term climatic stability means less migrations and important adaptations, i.e., broad-niche species, resulting in relatively species-poor ecosystems (Pianka, 1966; MacArthur et al., 1972). However, in lesser means, our results contradict the *seasonality* hypothesis. The positive correlation between richness and temperature seasonality (bio4) and mean diurnal temperature range (bio2), observed in all models except the best performing E+S and E+S+H, suggest that short-term temperature variability at the day and season levels increase richness. In light of these unexpected results, we recommend further studies to focus on the effect of temperature seasonality on richness in more local conditions, for example looking at how temperature variability affects specific phenological plant responses (e.g., Pfitsch, 1988; Fagua and Gonzalez, 2007), which in turn could condition communities' composition and diversity. Finally, our study gave little support to the *harshness* hypothesis, with precipitation of the driest month (bio14) the only harshness variable retained in our models, moreover strongly correlated with bio12. This predictor showed a mostly positive relationship with richness, which was expected given that precipitation under extreme stress could be an important conditioner of plant survival and growth, hence of community diversity (Sklenár and Jørgensen, 1999; Sklenár and Balslev, 2005). However, this correlation was inconclusive because it was found negative in model S+H.

To conclude, our results did not support completely any of our original hypotheses on the roles of the contemporary macroclimate in form of *energy*, *seasonality* and *harshness* in conditioning local plant richness in the páramo. We found that the highest plant richness could exist under relatively warm conditions, with little soil water stress, where humidity was not too important, i.e., in our opinion in semi-dry climates, and under stable humidity conditions but varying temperatures. Therefore, our energy and climatic seasonality hypotheses were

partly sustained, whereas harshness was not, at least at this study scale, this perhaps due to the strong overlap between the energy and harshness predictors. As a result, we suppose that including more specific bioclimatic factors representative of harshness and less correlated to energy factors, e.g., number of freezing days, could have better disentangled the harshness effects on local plant richness, however this information remains unavailable for the extent of our study.

Regional Fine-Scale Richness Patterns

Our predicted map of fine-scale richness for a standardized 25 m² páramo plot showed important variation throughout the biogeographical province. The results forecasted a general south-north richness decrease with a marked contrast between northern and southern latitudes, which was unexpected in our original hypothesis expecting a double-ended decreasing richness gradient with latitude (Hawkins et al., 2003; Willig et al., 2003). Another unexpected finding was the overall low richness predicted for Colombia at the plot level, whereas the country is usually considered the most diverse páramo country in terms of national richness (Rangel-Churio, 2006, 2015). One potential explanation for these results might be the heterogeneity in phytosociological sampling approaches between vegetations schools in the different countries, a problem commonly encountered when using multi-sources vegetation databases (Michalcová et al., 2011). Because it is difficult to correctly evaluate, we recommend considering this potential bias carefully. Our results also predicted no-clear patterns of richness with elevation at this scale, and highlighted particularly rich páramo areas, i.e., > 35 species (per 25 m² plot), and poor ones, i.e., < 10 species, independent of latitude and elevation.

Among the species rich areas identified were the Amotape-Huancabamba zone (~Lat. 5°S; Long. 79.5°W), the Sangay (~Lat. 2°S; Long. 78.5°W) and Cotacachi (~Lat. 0°; Long. 78°W) massifs in Ecuador, as well as the Lara páramos (~Lat. 9°N; Long. 71°W). This can be due to the geographic location of these mountain ranges, either (i) near lowland renown hotspots such as Amazonian and Chocó-Pacific biomes, in the case of Sangay and Cotacachi, respectively (Barthlott et al., 2007), or (ii) at geographic extremities of the páramo province, which promotes interchanging species with the immediate adjacent regions, such as the Llanos Occidentales in Lara and the Puna in the Amotape-Huancabamba zone (Weigend, 2002). Following that pattern, we expected the Colombian western cordillera to show high local biodiversity, but found the opposite. This might be explained by our previous interpretations on the extreme precipitation-richness relationship or by a sampling bias affecting the richness-precipitation relationship found. Previous studies had already mentioned the ecological importance of the Amotape-Huancabamba zone or easternmost Venezuelan páramos and emphasized their species richness, ecosystem diversity, endemism, and good conservation state (Lozano et al., 2009; Cuello et al., 2010). These areas remain relatively pristine thanks to direct conservation measures, for example representation in the Podocarpus and Guaramacal National Parks, as well as indirect ones, such as difficult access. Even though management efforts are in place, we believe there is a need for further research on the páramo's biogeography and global threats to reinforce preservation strategies, for example anticipating climate change (Mace et al., 2000). Although our study is exploratory and focused on the local scale, we encourage further studies to focus on these predicted species-rich areas with potential for revealing biodiversity hotspots at a broader-scale within the páramo biogeographical province. When doing so, it would be important to focus on species richness at a larger scale but also quantify ecological value in complementary ways, for example correlating richness patterns with patterns of endemism (Sklenár and Jørgensen, 1999).

Study Limitations and Future Recommendations

Our study has certain drawbacks that should be considered when interpreting the obtained results. First, the 1 km resolution of our climatic data might be considered coarse and it is possible that we did not detect valuable information due to the fine Andean topographic heterogeneity. Although we acknowledge that the fine micro- and meso-climate might play a crucial part in driving local species richness, perhaps more than the macroclimate (Anthelme and Lavergne, 2018; Graae et al., 2018), obtaining the corresponding data for the extent of our study remains considerably challenging. Second, some areas were rather under-sampled, such as the Colombian western cordillera, and it is possible that because of the resulting under-representation, their specific trends might have been overlooked in our results, making spatial interpolations from the closest sampled areas, even though useful, potentially dubious (Divíšek and Chytrý, 2018; Večera et al., 2019). We recommend additional sampling in these areas that are now more easily accessible thanks to the ended armed conflict in Colombia and in urgent need of further data exploration and associated environmental legislation (Negret et al., 2017). Last, our best performing regression models, E+S and E+S+H, only accounted for 25 percent of local species richness variation. As a result, while our results are bringing novel insight on the significant predictors of páramo plant richness, their explaining power remains relatively low and therefore, our interpretations should be handled accordingly. We believe important to focus future endeavors on additional potential richness drivers in the páramo such as the broad contemporary environment, past climate variations, disturbance variables, biome area, and biotic interactions for example (Sklenář and Ramsay, 2001; Cavieres et al., 2014; Vásquez et al., 2015). Finally, we consider that our results, despite the previously established drawbacks, advance important theories on páramo biogeography and the relevant but weak relationship between local plant richness and the macroclimate. They are also meaningful and able to guide further research and management focus on specific páramo areas identified as local biodiversity hotspots, and we believe it would be useful as a future perspective to downscale the results and focus on the specific vegetation type of phytogeographical units to identify not only geographic hotspots but habitat hotspots (Divíšek and Chytrý,

2018) with direct implications in ecosystem and biodiversity management planning.

DATA AVAILABILITY STATEMENT

The data used in this study are archived and freely available on the open-access VegPáramo database webpage (www.vegparamo.com) and in **Table S1**.

AUTHOR CONTRIBUTIONS

GP, HB, XF, and JT study conception and design and critical revision. GP and JT acquisition of data, analysis interpretation of data, and drafting of manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo. 2019.00377/full#supplementary-material

Table S1 | Final vegetation dataset used for the analyses and containing plot geographic information and species contents.

Figure S1 | Variation in area and richness across the páramo vegetation plot data: **(A)** Histogram of frequencies of plot area; **(B)** Histogram of frequencies of local species richness at plot level.

Figure S2 | Correlation matrix showing the univariate relationships among each environmental predictor for variable selection in the GLS environmental models. The color scale reflects Pearson's correlation coefficients and the "X" marks correlations that were not statistically significant. Variables for hypotheses: Energy –*bio1,* annual mean temperature; *bio 12,* annual precipitation; *swcfr,* mean monthly soil water stress coefficient; *AET,* actual evapo-transpiration; Seasonality–*bio2,* Mean diurnal temperature range; *bio4,* temperature seasonality; *bio15,* precipitation seasonality; *bio20,* inter-annual temperature variation (σ; 1979–2013); *bio21,* inter-annual precipitation variation (σ; 1979–2013); Harshness–*bio6,* minimum temperature of coldest month; *bio14,* precipitation of driest month; *bio18,* precipitation of warmest quarter.

Figure S3 | Geographic patterns of local species richness values (for a 25 m² plot) throughout the páramo biogeographical province as predicted by the models OK **(A)** and E+S+H **(B)**.

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