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Environmental drivers of tree species richness in the southernmost portion of the Paranaense forests

Carolina Toranza^{1,2*} , Juan Andrés Martínez-Lanfranco³, Federico Haretche² and Alejandro Brazeiro²

Abstract

Background The Rio de la Plata grassland region is dominated by temperate grasslands, with the scarce natural forests, influenced floristically by adjacent biogeographical provinces. Uruguay represents the southern limit for many tree species of the Paranaense Province, several of which inhabit the hillside forests. With many species shifting poleward due to climate change, we do not yet know how current environmental factors, particularly climatic ones, are linked to the tree diversity of this flora nowadays. The aim of this study is to understand the geographic pattern of tree richness in the hillside forests of Uruguay, evaluating the water–energy and the environmental heterogeneity hypotheses. The distribution of the hillside forest trees was obtained by compiling and updating the herbaria database and distribution maps of woody plants of Uruguay. The presence/absence of each species, and then the species richness, were georeferenced over a grid that covers Uruguay with 302 cells (660 km²). Over the same grid were compiled environmental variables associated with climate and environmental heterogeneity. The relationship between richness and environmental variables was studied by applying general linear models (GLM). As a strong autocorrelation was detected, a residuals auto-covariate term was incorporated into the GLM, to take into account the species richness spatial structure.

Results The tree flora of the hillside forest was composed mainly by Paranaense species that show a latitudinal gradient, with two high richness cores, in the east and northeast of Uruguay. The final model including the environmental variables and the spatial term explained 84% of the variability of tree richness. Species richness showed a positive relationship with precipitation, forest cover, potential evapotranspiration and productivity, while a negative effect of temperature variation was found. The spatial component was the primary predictor, accounting for a 30% of spatial pattern of tree richness.

Conclusions This study accounts for a large proportion of the environmental and spatial variations of the tree richness pattern of the Paranaense flora in its southernmost portion. It brings support to both water–energy and environmental heterogeneity hypotheses, emphasizing the role of climate and its variation and the habitat availability on the hillside forest diversity.

Keywords Hillside forest, Climate, Spatial pattern, Modeling

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Background

Understanding the diversity patterns is essential for its theoretical aspects to ensure effective conservation and management of ecosystems (Lomolino et al. 2010). Climate, environmental heterogeneity, biotic interactions, historical processes and randomness have been pointed out as drivers of the diversity patterns, varying its influence at different scales (Ricklefs 1990; Hubbell 2001). One of the most supported hypotheses to explain the geographical patterns of species richness is the ‘water–energy hypothesis’ (O’Brien 1998; Francis and Currie 2003). This hypothesis proposes that areas with greater availability of water and energy will be able to support larger population and a greater number of species, and predicts a positive relationship between species richness and water-energy availability (O’Brien 1998). The strength of this relationship varies with spatial scale, being more relevant at the macro and mesoscale (O’Brien 1993; Gaston 2000). In the case of vascular plants there is wide evidence on the role of energy and the interaction between energy and water on the richness patterns, regardless of the indicators used in the models (Hawkins et al. 2003). Among the studies that address this hypothesis, there is a series of works carried out at the end of the 20th century on African woody plants, where the strong relationship between woody plant richness and water–energy balance is evident (O’Brien 1993, 1998; O’Brien et al. 2000). On the other hand, several studies evaluating the role of different explanatory hypotheses for diversity patterns (e.g., climate/productivity, environmental heterogeneity, edaphic nutrients, area, biotic interactions, and dispersal/history), in different taxonomic groups, and at multiple spatial scales, found that the hypothesis related to climate (water–energy) and productivity variables had the highest overall primacy in relation to the other ones (Hawkins et al. 2003; Field et al. 2009; Toszogyova and Storch 2019).

In addition to the effect of climate, numerous studies point to the environmental heterogeneity as a determinant of terrestrial biodiversity (Shmida and Wilson 1985; Bailey et al. 2017). Heterogeneous environments have a greater availability of niches, which promotes coexistence among species, decreases competitive exclusion and thus promotes species richness (Whittaker 1998; Palmer 2007). Environmental heterogeneity accounts for the variation in diversity not explained climatically (Kerr and Packer 1997), and its effect would occur mainly through increased habitat availability and greater segregation of limiting resources (Ricklefs 1990). In terrestrial ecosystems, habitat availability and geodiversity (e.g., soils, topography, elevation) are often used as indicators of environmental heterogeneity. In a recent global-scale study of the diversity pattern of species listed by the

International Union for Conservation of Nature (IUCN), the authors found that niche partitioning is fundamental to understanding the positive relationship between species richness and habitat diversity (Udy et al. 2021), bringing support to the environmental heterogeneity hypothesis. In this sense, natural communities are strongly structured by niche partitioning among species (Kadmon and Allouche 2007). Heterogeneous environments provide more niches and promote niche partitioning; therefore, increased coexistence and species richness is expected in areas of higher environmental heterogeneity (Potts et al. 2004; Johnson et al. 2017; Udy et al. 2021). On a smaller scale, geodiversity was found to explain a portion of the pattern of threatened species richness in Finland’s national parks (Tukiainen et al. 2016). While temperature is the main predictor of species richness, the geodiversity indicator variables (e.g., rock type and soil type richness, geomorphological and hydrological diversity) increase the explanatory power of the models (Tukiainen et al. 2016).

The relative contribution of the climate and environmental heterogeneity to richness patterns varies with the spatial scale of the study, with climate being the most important determinant at large scales and environmental heterogeneity at the landscape or local scale (Tello and Stevens 2010). In this sense, various studies indicate that climate and environmental heterogeneity play a complementary role in generating geographic patterns of terrestrial diversity (Jiménez et al. 2009; Cramer and Verboom 2016). The Río de la Plata grasslands (RPG) region, encompasses southern Brazil, eastern Argentina and Uruguay and is one of the most important grassland regions in the world, as well as one of the most transformed by the change in land use (Brazeiro et al. 2020). This region is dominated by grassland and shrubby grassland ecosystems, with scarce areas of forests and savannas (Overbeck et al. 2007). The forests of the RPG show a patchy distribution in the landscapes, usually associated with special conditions such as watercourses, hills and ravines, or certain soil types (Brussa and Grela 2007; Toranza et al. 2019; Betancourt 2021). In contrast with others South American subtropical forests, the forests at the RPG region occur in an area with water deficit and wide temperature range. According to our knowledge, only a few recent studies have focused on understanding the environmental determinants of the diversity gradient of Atlantic and Pampa forests as a whole (Oliveira-Filho et al. 2013; Rezende et al. 2018). Both of which detected a strong latitudinal gradient in tree richness, with a marked decrease in species numbers towards the south of Uruguay (Haretche et al. 2012; Oliveira-Filho et al. 2013).

Uruguay constitutes the southern distribution limit for many tree species of Atlantic and Paranaense origins

that enter its territory (Cabrera and Willink 1973; Grela 2004). The transitional nature of the Uruguayan tree flora has been pointed out since the early 20th century (Chebataroff 1942; Grela 2004; Haretche et al. 2012). This flora enters into Uruguay through biological corridors such as the Río Uruguay in the west, and the Sierras del Este and Quebradas del Norte in the east of the country (Grela 2004; Nores et al. 2005). In the context of climate change, with many species shifting poleward, an increase in forest coverage is projected in Uruguay (Salazar et al. 2007; Anadón et al. 2014). Moreover, an expansion of forest area in the last decades has been reported in the east of Uruguay (Bernardi et al. 2019), mainly linked to climate and decreased grazing pressure (Brazeiro et al. 2018; Bernardi et al. 2019). However, we know very little about how current environmental factors, particularly climatic ones, explain the diversity of tree species in Uruguay. In order to advance the comprehension of the processes that generate and maintain the diversity of these forests, the aim of this study is to understand the geographic pattern of tree species richness in the southernmost portion of the Paranaense forests and its environmental drivers, evaluating the water–energy and the environmental heterogeneity hypotheses.

Methods

Study area

Uruguay is located in southeast South America (– 30,0856–– 34,9742 SL, 53,1828–58,4336 WL) and has a continental area of 176,215 km². The country has a warm temperate climate characterized by hot and humid summers, and cool to mild winters (Cfa, sensu Köppen-Geiger), with mean annual temperature ranging between 16 °C and 20 °C and mean annual rainfall between 1100 and 1400 mm yr⁻¹. The temperature is strongly seasonal, and rainfall is evenly distributed during the year, but strongly variable among years (www.inumet.gub.uy/clima/climatologia-estacional).

Uruguay has seven natural ecoregions which has been established based on geomorphology, soils, physiography, and its biota (Brazeiro 2015). Grasslands, the main natural ecosystem, currently occupies 65.9% of the territory (Baeza et al. 2014), meanwhile natural forests cover only 5.2% of the country (MGAP 2018). The main land uses are livestock, cropping, and exotic forest plantations covering about 25.0% of the territory (Baeza et al. 2014; MGAP 2016). The woody flora of Uruguay includes 301 species, a high diversity in the context of the RPG region (Haretche et al. 2012). Although Uruguay is fully included in the Pampa region (Cabrera and Willink 1973), the woody flora is highly linked to the adjacent biogeographic provinces, e.g. Paranaense and Chaco (Grela 2004; Haretche et al. 2012).

Biological and environmental databases

In this study we used the woody plants database of the Biodiversidad y Ecología de la Conservación, Instituto de Ecología y Ciencias Ambientales, Facultad de Ciencias, Universidad de la República, Uruguay (Brazeiro 2015; www.fcien.edu.uy/institucional/academic-structure/institutes/ecology-and-environmental-sciences).

The species distributions of the database were generated based on 7,381 specimens from the National Herbaria, including: 4504 specimens from Herbario Bernardo Rosengurtt (MVFA), 2145 specimens from Herbario del Museo Jardín Botánico Prof. Atilio Lombardo (MVJB), and 732 specimens from Colección botánica del Museo Nacional de Historia Natural (MVM). The database additionally includes 1400 field records and 265 additional records obtained from thesis and technical reports. These data were georeferenced on a grid of 302 cells of about 22×30 km (resolution of 660 km²) covering the whole country. This grid belonging to Servicio Geográfico Militar of Uruguay has been widely used in previous studies on species distribution and diversity (Haretche et al. 2012; Pérez-Quesada and Brazeiro 2013; Brazeiro et al. 2020). Relying on this database, the Brussa and Grela (2007) potential distribution maps of woody plants were updated by botanists, adding species not considered previously. The woody species were categorized according to their lifeform as: shrubs, tree ferns, and trees. After that, the trees of hillside forests were selected, with a total of 73 species. Finally, on the basis of a bibliographic and regional database search, carried out by a botanist from our group, each tree species from the hillside forest was classified according to its biogeographic origin according to its distribution range as follows: P=Paranaense, C: Chaco, C-P: Chaco-paranaense, Pa: Pampa, Pan: Pantropical. On the same grid, the environmental variables that represented the main theoretical hypotheses evaluated in this study were compiled: water–energy hypothesis and the environmental heterogeneity hypothesis (Table 1). Finally, from the grid of 302 cells of Uruguay, we worked only with the 137 cells where hillside forests are distributed.

Modeling of tree richness of hillside forests

To avoid the inclusion of highly collinear variables in the models, an exploration of pairwise correlations between variables and variance inflation factor (VIF) estimates was performed. For this, the environmental variables were grouped into climatic and non-climatic and then they were evaluated together. Finally, a group of variables without high correlations among them ($r^2 < 0.70$) and VIF < 2, was retained (Dormann et al. 2013). Among highly correlated variables, we retained those having

Table 1 Environmental variables compiled on the grid covering Uruguay (resolution: 660 km²), grouped according to the explanatory hypotheses

	Definition	Type	Source
WEH			
T _{mean}	Annual mean temperature and its CV	C	Hijmans et al. (2005)
T _{max}	Annual maximum average temperature and its CV	C	Hijmans et al. (2005)
T _{max1}	Maximum temperature of the hottest month (January)	C	Hijmans et al. (2005)
T _{min}	Annual minimum average temperature and its CV	C	Hijmans et al. (2005)
T _{min7}	Minimum temperature of the coldest month (July)	C	Hijmans et al. (2005)
MAP	Mean annual precipitation and its CV	C	Hijmans et al. (2005)
Prec ₆	Mean precipitation of the rainiest month (June)	C	Hijmans et al. (2005)
P _{warmest}	Mean precipitation of the warmest quarter (Jan-Feb-March)	C	INUMET (2022)
P _{coldest}	Mean precipitation of the warmest quarter (Jan-Feb-March)	C	INUMET (2022)
P _{annual}	Cumulative annual precipitation	C	INUMET (2022)
SWB	Surface water balance	C	INUMET (2022)
PET	Potential evapotranspiration	C	INUMET (2022)
AET	Actual evapotranspiration	C	Brazeiro (2015)
NDVI	Normalized Difference Vegetation Index	C	Ceroni et al. (2015)
IVN-I	Annual integral of the NDVI	C	Baeza et al. (2006)
EHH			
Geoformas	Dominant landform (11)	D	Panario (1988)
Suelos	Dominant soil (14)	D	Altamirano et al. (1976)
Hsuelos	Soil diversity (Shannon)	C	Altamirano et al. (1976)
Rsuelos	Soil richness	C	Altamirano et al. (1976)
Altmax	Maximum altitude	C	IdeMTOP (2020)
R _{alt}	Altitudinal range	C	IdeMTOP (2020)
Altmed	Mean altitude	C	IdeMTOP (2020)
AreaHF	Hillside forest area per cell	C	Toranza et al. (2019)

WEH: Water–energy hypothesis' variables and EHH: Environmental heterogeneity hypothesis' variables, which were used in the modeling of richness pattern of hillside forest trees. The type of each variable, continuous (C) or discrete (D), as well as the source from which they were obtained are indicated. In the case of discrete variables, the number of categories is indicated in parentheses

clearer connection with diversity hypotheses evaluated in this study. We parametrized a full model with the hypothesized predictors and their quadratic terms and based the interpretation on the effect sizes and significance testing (e.g., we did not implement variable selection routines).

To model the relationship between tree species richness and hypothesized predictor variables, we used Generalized Linear Models (GLM) (Guisan et al. 2002). Firstly, we used Poisson and Negative Binomial distributions and a log-link function, yet, upon inspection of model residuals, we detected deviations of model distributional assumptions (data not shown). We ultimately used a Gaussian model that represented a good fit to the data and fulfilled model assumptions (Additional file 2: Fig. S1). We assessed the relative importance of model predictors in explaining tree species richness by decomposing the total GLM-explained variance (R^2) into the individual and unique contribution of each predictor using R package 'glmm.hp' (Lai et al. 2022).

On the other hand, the challenge of analyzing spatial data is widely recognized among ecologists, since they generally show spatial dependence (Dormann et al. 2007). The autocorrelation affects the data independence assumption and can increase the Type I errors in the models (Legendre 1993), altering the regression coefficients (Bini et al. 2009), and in consequence conditions our ability to make ecological inferences and predictions (Miller et al. 2007). A series of methods have been developed to account for the spatial dependency of data in the modeling of ecological phenomena (Dormann et al. 2007; Miller et al. 2007; Flecher and Fortin 2018). In this study, after confirming strong autocorrelation in the residuals of the environmental model through correlograms and semi-variograms, we apply auto-covariate models (Augustin et al. 1996). This is a relatively straightforward approach, similar to non-spatial regression, which incorporates an auto-covariate term to model neighborhood effects (Flecher and Fortin 2018). Given that the inclusion of an auto-covariate in the model may mask the effect

of other environmental predictors, in this study we followed the auto-covariate residuals method proposed by Crase et al. (2012). On this approach, the spatial term is constructed based on the residuals of the environmental model and then incorporated into the regression model (Crase et al. 2012).

GLM with the environmental variables emerge as a good approach, capturing a significant portion of the geographic variation in the tree richness of the hillside forests. However, since this model was not able to control spatial dependence in the residuals, a new GLM was performed incorporating environmental variables plus an auto-covariate residuals term (autocov). We evaluated model fit and assumptions using normalized quantile scaled residuals implemented in the R package 'DHARMA' (Hartig 2022). Further, we diagnosed spatial autocorrelation of model estimating the degree of spatial dependence as a function of geographical distance using spline cross-correlograms with R package 'ncf' (Bjornstad 2022). The performance of the models was evaluated through the adjusted R^2 . The incorporation of the autocov successfully accounted for autocorrelation in the model residuals.

Results

The trees of the hillside forests are grouped into 31 families, of which 55% are represented by a single species. The most important families were Myrtaceae, Anacardiaceae and Salicaceae, and more than 90% of the tree species have a Paranaense forest origin (Additional file 1: Table S1). The tree richness of hillside forests varied between 22 to 71 species per cell in Uruguay, showing a clear latitudinal gradient, with richness decreasing from northeast to south and southwest. The tree richness pattern of hillside forests exhibit pattern with two high-richness cores, one in the Quebradas del Norte at the northeast and another in the Sierras del Este at the east of the country (Fig. 1).

The Gaussian GLM parametrized with the environmental variables and the spatial auto-covariate explained 84% of the variation in tree species richness (Table 2). The final Gaussian GLM showed no evidence for model misspecifications; quantile residual QQ-plots and associated indicated no deviations from underlying assumptions regarding parametric distribution (e.g., normality of scaled residuals), and no traces of overdispersion or influential data points (Additional file 2: Fig. S1). Furthermore, the model showed no spatial autocorrelation, as the estimated spatial cross-correlation function remained within the 95% confidence envelope (Additional file 2: Fig. S2).

A clear relationship was found between tree richness and precipitation surrogates, particularly mean annual

precipitation (MAP) and the precipitation of coldest months (Table 2, Fig. 2). Likewise, a linear positive effect of habitat availability, specifically of the hillside forest area, on tree richness was detected (Fig. 2).

Potential evapotranspiration, a proxy for energy availability, was positively associated with tree richness, while a negative relationship was found with the variation of the maximum temperature (Table 2, Fig. 2). Finally, the models detected a positive relationship between tree richness and hillside forest productivity (Table 2). It is noteworthy the role played by the spatial component in the hillside forest tree richness geographic variation, with auto-covariate being the predictor with the strongest individual effect on it (Table 2, Fig. 3).

Discussion

Spatial pattern of hillside forest tree richness in Uruguay

The tree richness of hillside forests exhibited an important geographic variability, with high-richness cores in the eastern and northeastern region and low diversity areas in the forests of southern and western Uruguay, located outside the Sierras del Este and Quebradas del Norte corridors. The detected latitudinal gradient in tree richness is consistent with previous reports for forests in the Pampas region (Oliveira-Filho et al. 2013; Rezende et al. 2018). The hillside forests of Uruguay host the southernmost portion of the Paranaense flora, and the dominant presence of the Myrtaceae family emphasizes its relationship with the forests of southern Brazil and its continuity with the flora of the Serra do Sudeste (Jarenkow and Waechter 2001; Junitz and Jarenkow 2003). Additionally, the low number of species per genus and the large number of families represented by a single species highlight the transitional nature of the hillside forests flora of Uruguay (Haretche et al. 2012). This indicates the presence of interdigitations of the Atlantic forest biome in the Pampa biome, beyond the previous proposed limits for the transition zone (Gonçalves and Souza 2014).

Numerous studies document the relationship between tree richness patterns and environmental variability at different spatial scales (Cramer and Verboom 2016; Chu et al. 2019). The models applied here showed that 84% of the tree richness pattern in hillside forests is explained by environmental conditions and spatial structure, and are consistent with previous studies conducted at mesoscale (Jiménez et al. 2009). Moreover, the greatest proportion of the variation in tree richness was explained by climate and environmental heterogeneity. Climate plays a central role, with a consistent effect of water and energy availability on tree richness. These results bring support to the 'water-energy' hypothesis and are consistent with findings across

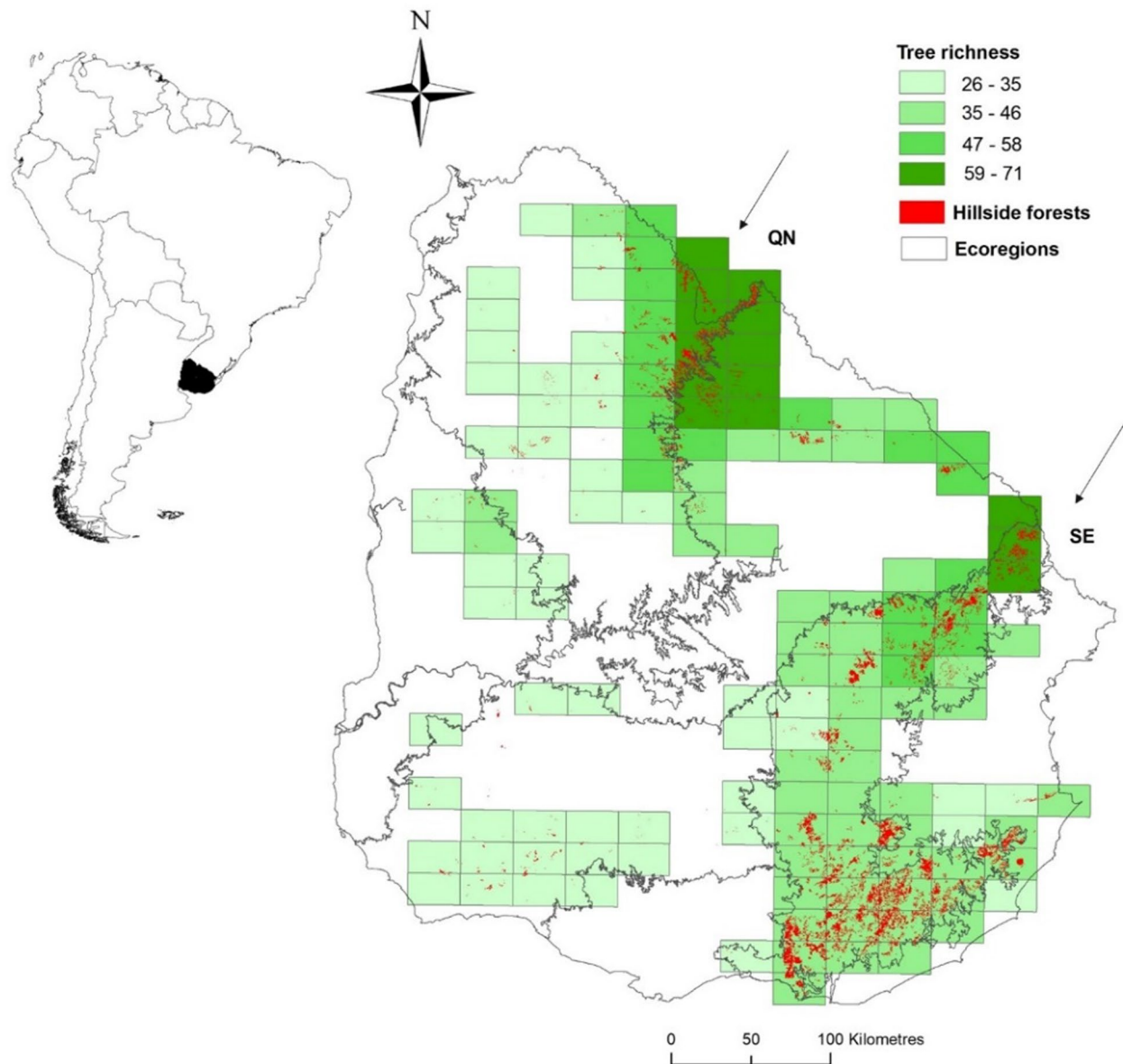


Fig. 1 Spatial pattern of tree species richness in the hillside forests of Uruguay (scale 1:50,000). The distribution of the hillside forest (in red), the Uruguayan Ecoregions, and the location of the Quebradas del Norte (QN) and Sierras del Este in Uruguay are shown

multiple taxa and regions (Khine et al. 2019; Alahuhta et al. 2020; Liang et al. 2020). On the other hand, a clear association was detected between tree richness and habitat availability, a surrogate of the environmental heterogeneity. Finally, it is remarkable that the variable with the strongest individual effect on hillside forest tree richness was linked to spatial variation. This result could be associated with the dispersion of species through biological corridors and a biogeographical

effect of floristic connectivity with neighboring provinces, among others (Ricklefs and Shluter 1993).

Water–energy hypothesis and tree richness of the hillside forests

Different mechanisms underlie the effect of climate and the observed relationship between energy and species richness (Hawkins et al. 2003). In the case of plants, the energy associated with photosynthetically active radiation has been identified as the key factor in

Table 2 Results of the GLM including environmental predictors and the spatial term (autocov)

Variables	GLM (estimates)	Std. Error	t value	P value
Log(areaHF)	28.6	6.7	4.3	<0.001
Log(areaBS) ²	2.9	5.4	0.6	0.58
MAP	17.7	12.9	1.4	0.17
MAP ²	17.8	17.8	2.7	<0.01
Pcoldest	61.1	9.7	6.3	<0.001
Pcoldest ²	6.8	6.3	1.1	0.28
CV_Tmax	-12.2	7.3	-1.7	0.09
CV_Tmax ²	-10.6	6.9	-1.5	0.13
NDVI	2.1	5.7	0.4	0.71
NDVI ²	-2.5	5.8	-0.4	0.66
PET	36.8	12.8	2.8	<0.01
PET ²	-6.2	6.9	-0.9	0.37
autocov	65.4	7.1	9.2	<0.001
autocov ²	17.7	5.7	3.1	<0.01
R ² adj	0.84			

The R²adj the model is shown. *Log(areaHF)* hillside forest area; *MAP* mean annual precipitation, *Pcoldest* precipitation in the coldest month (June, July and August), *CV_Tmax* coefficient of variation of maximum temperature, *NDVI* normalized difference vegetation index, *PET* potential evapotranspiration

understanding the spatial patterns of richness (Clarke and Gaston 2006). In turn, since the energy uptake by plants is linked to water availability, one of the leading energy hypotheses contributing to explaining spatial patterns of plant richness is associated with variation in water availability (Currie 1991; O'Brien 1993, 1998; Kreft and Jetz 2007). The present study provides evidence that supports the 'water-energy' hypothesis, as the tree richness of the hillside forests was positively associated with different predictors related to energy, water and water/energy interaction factors.

The MAP and the precipitation of the coldest months promoted species richness in the hillside forests of Uruguay. Furthermore, this finding is consistent with recent studies on species richness patterns in Atlantic forest trees, particularly in the southern portion of the biome (Zwiener et al. 2020). This dependence on precipitation, strongly detected towards the southern portion of this flora, emphasizes the role of water availability in the energy–richness relationship in plants (Clarke and Gaston 2006). In addition, a positive effect of potential evapotranspiration on species richness was detected. This variable, which measures the rate at which a saturated surface loses water to the atmosphere, is one of the energy proxies most strongly linked to tree species richness patterns (Currie 1991; Hawkins et al. 2003). In fact, the groundbreaking work by O'Brien (1993, 1998) argues that potential evapotranspiration, along with precipitation, is the best predictor of terrestrial plant richness.

Hillside forest tree richness was negatively correlated with the annual temperature variation. This result supports the hypothesis of environmental variability, which suggests that fewer species can tolerate variable environmental conditions, leading to a decline from the tropics to temperate zones (Whittaker et al. 2001; Ruggiero and Kitzberger 2004). The effect of climate variability or seasonality on species richness has been less studied than the absolute effect of variables such as temperature. However, the role of climate variability or seasonality has been documented in multiple studies as a limiting factor for the dispersion of tropical clades towards temperate regions and in richness gradients (O'Brien 1993; Wiens et al. 2006; Wang et al. 2010).

In this study, the minimum temperature was not selected as a predictor of tree richness in any of the models. This result differs from the ones previously reported for the tree flora of this region (Giehl and Jarenkow 2012; Oliveira-Filho et al. 2013; Zwiener et al. 2020). In this regard, part of the explanation may be associated with the narrow latitudinal range of the present study (30° to 35° SL), or with the fact that the tropical species reaching Uruguay correspond to a subset of the Atlantic biome, which has already been filtered by temperature.

Environmental heterogeneity hypothesis and tree richness of the hillside forest

Several studies have proposed that environmental heterogeneity complements the effect of climate in determining species richness gradients, particularly at intermediate or small spatial scales (Shmida and Wilson 1985; Bailey et al. 2017). Although we did not find a relationship between tree richness and the direct proxies of environmental heterogeneity (e.g., soil diversity, landforms, altitudinal range), we found a strong effect of habitat availability (e.g., forest cover) on the richness of hillside tree species. In this sense, habitat availability has been previously identified as an indirect surrogate for environmental heterogeneity, given the relationship between the increase in available habitat and environmental diversity, which ultimately results in greater niche segregation and an increase in species richness (Shmida and Wilson 1985; Ricklefs 1990; Trevail et al. 2021).

The effect of habitat on species richness has been demonstrated through various indicators (Menéndez et al. 2007; Liira et al. 2008; Gao et al. 2018), including habitat area (Krauss et al. 2004). In this study, hillside forest cover was used as a proxy of habitat availability, verifying a positive linear relationship with hillside tree richness. The relationship between richness and habitat area is one of the most well-known and documented ecological phenomena (Lomolino 2001). Furthermore, this relationship is particularly relevant in the current context, because

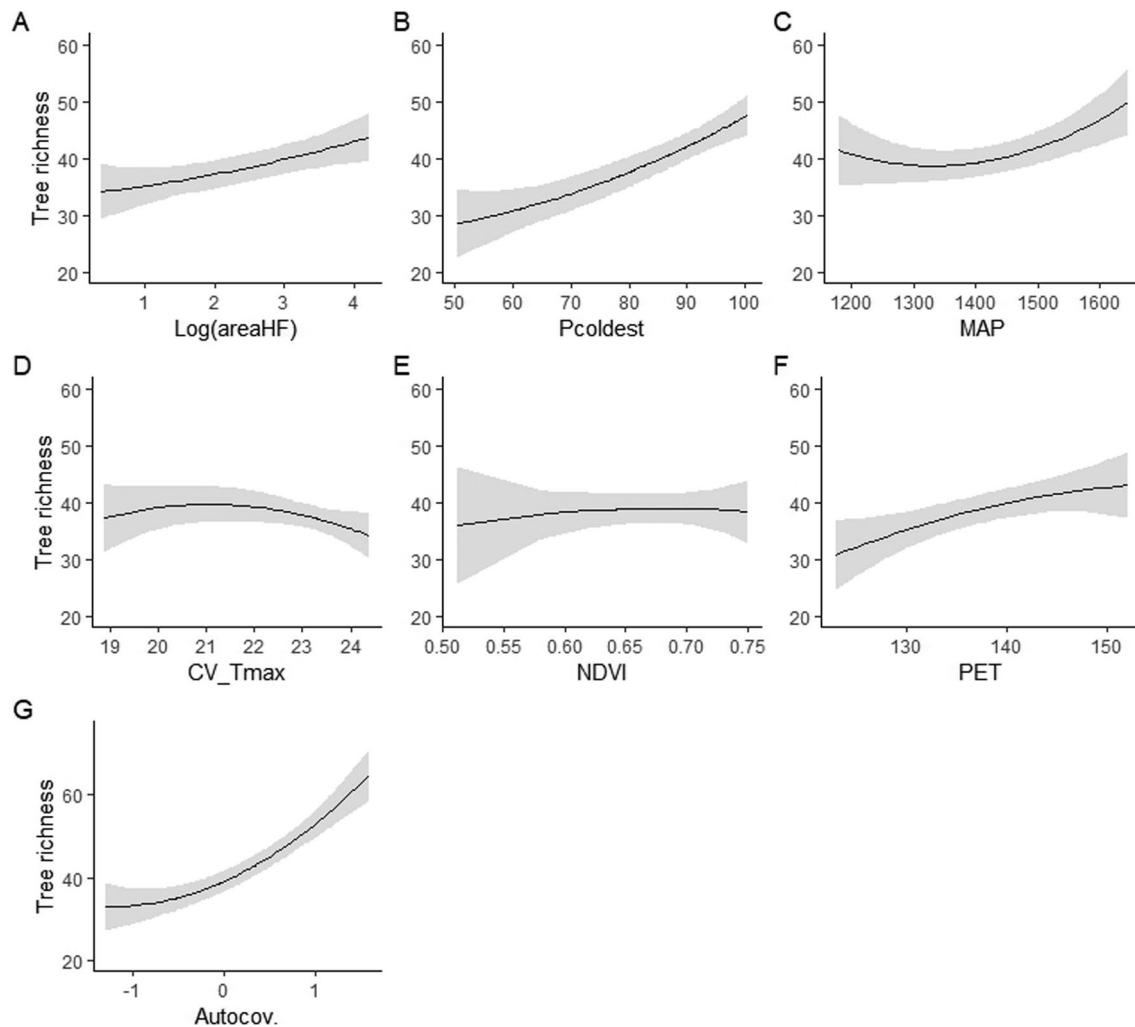


Fig. 2 Marginal predictions and 95% CI for final tree species richness Gaussian GLM of hillside forest. Predictors: Log(areaHF): hillside forest area; MAP mean annual precipitation, Pcoldest precipitation in the coldest month (June, July, and August), CV_Tmax coefficient of variation of maximum temperature, NDVI normalized difference vegetation index, PET potential evapotranspiration

habitat availability has been identified as one of the key explanatory factors for climate-driven changes in species distribution across multiple taxonomic groups (Platts et al. 2019).

Tree richness and spatial processes

The richness of hillside trees was associated with a spatial variation, which is not related to the environmental variables included in the model according to the theoretical hypotheses evaluated here. In this study we have accounted for this spatial variation by including the residual auto-covariate in the final model. This variable represents the presence of other spatially explicit phenomena, and can represent either purely spatial processes, historical phenomena, such as the dispersal of

organisms across biogeographic corridors, or current environmental variation not considered in the study (Currie 2007). Climatic changes during the Quaternary period, led to the southward expansion of tropical and subtropical forest flora during interglacial periods and their retraction during glaciations, which in our region resulted in temperature cooling and increased aridity (Rambo 1954). According to the Pleistocene refugia theory, there were specific areas (refugia) where this tropical flora managed to persist under unfavorable climatic conditions. Recent studies on the geographic structure of genetic variability in different plants indicate that the Quebradas del Norte and the Sierras del Este acted as Pleistocene refuges in the eastern region of Uruguay allowing the persistence of a relict tropical

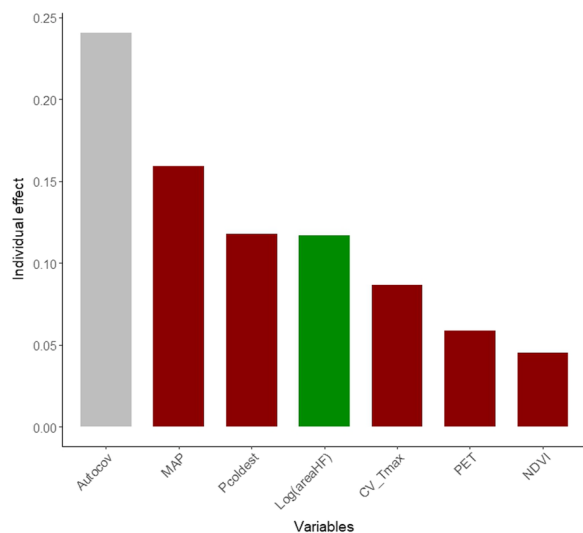


Fig. 3 Variable importance from final tree species richness as the unique contribution of each predictor to model explained variance (summing up to the total R^2) from hierarchical variance partitioning. Predictors ranked by decreasing individual contributions. Variables in red are related to the water–energy hypothesis (MAP: mean annual precipitation, *Pcoldest* precipitation in the coldest month (June, July and August); *CV_Tmax* coefficient of variation of maximum temperature, *PET* potential evapotranspiration and *NDVI* normalized difference vegetation index), green to the environmental heterogeneity hypothesis (Log(areaHF): hillside forest area), and gray to the residual spatial auto-covariate (autocov)

flora (Speranza et al. 2007; Turchetto-Zolet et al. 2016; Moreno et al. 2018; Hernández 2019). This would contribute to understanding why in these areas the tree richness is higher than expected due to the current climate and environmental heterogeneity, and coincides with what has been found in areas of high plant diversity in other regions (Médail and Diadema 2009). Currently, the favorability of climatic conditions and the decrease in grazing pressure in eastern Uruguay would promote the expansion of woodland flora through hill corridors once again (Anadón et al. 2014; Bernardi et al. 2019), which could explain a portion of the spatial structure in tree species richness.

An alternative hypothesis proposes a mass effect to explain the high-richness cores in the east and northeast of Uruguay (Shmida and Wilson 1985). This effect would be associated with the dispersion of propagules through geomorphological continuity and habitat connectivity between Sierras del Este and the Quebradas del Norte with the Serra do Sudeste and Cuesta de Haedo in southern Brazil respectively (Pérez-Quesada and Brazeiro 2013). According to the authors, the high-richness cores can be accounted by the presence of specific and spatially localized habitat types (e.g., scarps and ravines) that allow the occurrence of species with restricted distribution in

Uruguay, thus increasing the richness of woody plants in these areas (Pérez-Quesada and Brazeiro 2013).

Conclusions

The tree richness pattern of hillside forests of Uruguay displays a latitudinal gradient with two high-richness cores in the eastern and northeastern regions of the country. A significant portion of the geographical variation in species richness is associated with the climate, increasing with the availability of water (MAP) and energy (evapotranspiration). While the richness of tree species was not associated with direct measures of environmental heterogeneity, tree richness was related to habitat availability, an indirect proxy of the environmental heterogeneity. But, in this work we detected that about a quarter of the variation of tree richness was explained by space. In this vein, the pattern of tree richness of the hillside forest is mainly explained by the combination of the climate, environmental heterogeneity and spatial processes. The effect of the latter on the spatial pattern of tree richness could be linked to the biological corridors of ravines and eastern mountain ranges, but it may also be a result of other regional and historical processes not explored here and not yet understood in this flora.

Abbreviations

IUCN	International Union for Conservation of Nature
RPG	Río de la Plata grasslands
MVFA	Herbario de la Facultad de Agronomía
MVJB	Herbario del Museo Jardín Botánico Prof. Atilio Lombardo
MVM	Colección botánica del Museo Nacional de Historia Natural
VIF	Variance inflation factor
GLM	Generalized linear models
MAP	Mean annual precipitation

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s13717-024-00517-5>.

Additional file 1: Table S1. List of the tree species of the hillside forest of Uruguay. The biogeographic affinity of each species (Biog. affinity) is indicated according to their distribution.

Additional file 2: Fig. S1. Analysis of the GLM residuals including both the environmental predictors and the spatial term (autocov). **Fig. S2.** Correlogram showing no spatial correlation (Moran's I) in the residuals of the GLM including both environmental predictors and the spatial term (autocov). **Fig. S3.** Graph showing the standardized coefficients of the environmental predictors included in the GLM.

Acknowledgements

We would like to thank all the botanists whose work over the years generated the information that made this study possible.

Author contributions

CT and AB designed the study. CT got grants from the CAP, PEDECIBA and edited the manuscript. FH compiled the botanical database and updated the distributions of tree species. CT and JAM-L did the data analysis. CT, JAM-L and AB contributed to the whole manuscript preparation and design and wrote the main manuscript text. CT and JAM-L prepared all figures. All authors read and approved the final manuscript.

Funding

This work was supported by the Comisión Académica de Posgrado de la Universidad de la República de Uruguay and PEDECIBA.

Availability of data and materials

Data are available from the corresponding author upon reasonable request.

Declarations**Ethics approval and consent to participate**

Not applicable.

Consent for publication

All authors consent to the publication of the manuscript and supplementary material.

Competing interests

The authors declare that they have no conflict of interest.

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Received: 25 October 2023 Accepted: 22 April 2024

Published online: 22 May 2024

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