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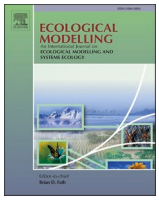

Insights on biodiversity drivers to predict species richness in tropical forests at the local scale

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ABSTRACT

Disentangling the relative importance of different biodiversity drivers (i.e., climate, edaphic, historical factors, or human impact) to predict plant species richness at the local scale is one of the most important challenges in ecology. Biodiversity modelling is a key tool for the integration of these drivers and the predictions generated are essential, for example, for climate change forecast and conservation planning. However, the reliability of biodiversity models at the local scale remains poorly understood, especially in tropical species-rich areas, where they are required. We inventoried all woody plants with stems $\geq$ 2.5 cm in 397 plots across the Andes-Amazon gradient. We generated and mapped 19 uncorrelated biodiversity drivers at 90 m resolution, grouped into four categories: microclimatic, microtopographic, anthropic, and edaphic. In order to evaluate the importance of the different categories, we grouped biodiversity drivers into four different clusters by categories. For each of the four clusters of biodiversity drivers, we modelled the observed species richness using two statistical techniques (random forest and Bayesian inference) and two modelling procedures (including or excluding a spatial component). All the biodiversity models produced were evaluated by cross-validation. Species richness was accurately predicted by random forest (Spearman correlation up to 0.85 and explained variance up to 67%). The results suggest that precipitation and temperature are important driving forces of species richness in the region. Nonetheless, a spatial component should be considered to properly predict biodiversity. This could reflect macroevolutionary underlying forces not considered here, such as colonization time, dispersal capacities, or speciation rates. However, the proposed biodiversity modelling approach can predict accurately species richness at the local scale and detailed resolution (90 m) in tropical areas, something that previous works had found extremely challenging. The innovative methodology presented here could be employed in other areas with conservation needs.

1. Introduction

Biological communities are threatened by intensifying human impact on ecosystems (Sheldon et al., 2011). A crucial challenge for the immediate future will be to conserve biodiversity under the current climate change scenario (Fadrique et al., 2018). To shed light on this global issue, biodiversity modelling is broadly employed in numerous fields (D'Amen et al., 2017). Biodiversity models can be used to support conservation planning (Guisan et al., 2013), or assessments of climate change effects on biodiversity (Randin et al., 2009; Urban et al., 2016).

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Although biodiversity modelling has undergone substantial developments, our ability to predict biodiversity at local scales remains limited (Urban et al., 2016; Yates et al., 2018). This is particularly true in tropical areas due to high species diversity/complexity (Jetz et al., 2012) and problems with data quality and availability (Cayuela et al., 2009; Loiselle et al., 2008). The tropical Andes is one of the most species-rich areas on the planet, as well as one of the most relevant regions for the conservation of biodiversity (Brooks et al., 2006; Myers et al., 2000). Significant climate change effects have been already noticed in the tropical Andes, reshaping the spatial distribution of tree species among other things (Fadrique et al., 2018). In this context, accurate predictions of local biodiversity would allow to build more realistic conservation plans (Mateo et al., 2019b).

Models to predict biodiversity patterns vary (D'Amen et al. 2017, Guisan et al. 2017) from purely correlative (e.g., Gotelli et al., 2009; Guisan and Rahbek, 2011) to mechanistic (e.g., Mokany and Ferrier, 2011). The different approaches try to predict various aspects of taxonomic diversity such as species composition (e.g., Mateo et al., 2012), species richness (e.g., Di Febbraro et al., 2018), and beta-diversity (e.g., Mokany et al., 2011), or even other dimensions of biodiversity such as functional or phylogenetic diversities (e.g., D'Amen et al., 2018). Regarding the modelling of local species richness (SR), the two most recurrent options are: 1) direct modelling of species numbers, a technique named 'macroecological modelling' (MEM, Gotelli et al., 2009); and 2) stacking of species distribution models for individual species (S-SDMs; Dubuis et al., 2011; Mateo et al., 2012). These approaches have complementary difficulties (Guisan and Rahbek, 2011). MEM cannot derive any information about species composition, while S-SDMs can predict species composition, but it does not include environmental controls (biodiversity drivers) on SR that are hypothesized by MEMs, frequently resulting in an overestimation of SR (Dubuis et al., 2011; Mateo et al., 2012).

The importance of different biodiversity drivers, such as climate, historical factors, or human impact, is another important challenge for biodiversity modelling (Mateo et al., 2017; Thuiller et al., 2013). In addition, these drivers vary from local scale environmental conditions to historical or biogeographical factors operating at larger regional levels (Mateo et al., 2017; Willis and Whittaker, 2002).

In the near past, SR was postulated to be largely limited by the available energy (Wright, 1983), and it was commonly hypothesized that SR could be predicted through a measure of the available environmental energy, basically (precipitation and temperature; Currie, 1991). Our current understanding of SR embraces supplementary hypotheses (Cornell and Harrison, 2014; Harmon and Harrison, 2015), implying that our understanding of biodiversity patterns at the local scale requires additional information such as evolutionary or historical drivers (i.e., processes that take place at larger regional scales, Godfray and Lawton, 2001). At the local scale SR is shaped by the properties of regional species pools, which in turn are the result of speciation, immigration, range extension, diversification rates, regional area and geological age (Cornell, 2013; Cornell and Harrison, 2014). Consequently, zones with larger inputs of energy or constant climates (tropical areas) show greater species numbers, not only as a consequence of higher energy availability (Brown, 2014), but also due to higher sustained diversification rates and, subsequently, larger regional species pools (Cornell, 2013). Even for these hypotheses, and as a preliminary approximation, temperature, precipitation, and climate seasonality could be worthy SR predictors, although other drivers should be considered when possible (Guisan and Rahbek, 2011; Mateo et al., 2017). Regional SR drivers, such as broad-scale environmental gradients (i.e., climate), could determine SR at broader scales; within that regional SR, local SR spatial patterns would be shaped by other environmental and stochastic factors, or niche and dispersal assembly rules (Guisan and Rahbek, 2011; Hubbell, 2001; Laliberté et al., 2009). Therefore, macroevolutionary dynamics (i.e., colonization time, differences in speciation rates, or dispersal limitation) would generate the difference in community assembly process (Benício et al., 2021) that could be reflected in spatial richness patterns.

Our first objective was to achieve a better understanding of the drivers that influence the spatial organization of plant assemblages in tropical forests at the landscape scale. Within this objective, we studied the well-sampled forests of the Madidi region along a ca. 4000 m altitudinal gradient in the eastern slopes of the Bolivian Andes (Friedman-Rudovsky, 2012). Climate shifts occur dramatically across this altitudinal gradient. Therefore, our first hypothesis was that temperature and precipitation should be the primary SR predictors, even though other factors could contribute to explain additional variation. To test this hypothesis, we evaluated models with or without spatial patterns. The idea was to generate spatial predictors that allow the model to consider the spatial structure of the training data (i.e., woody plant communities; see Dray et al, 2006, Peres-Neto et al, 2010). If macroevolutionary dynamics (or other biodiversity drivers not considered here) are important in species richness assembly process at local scale in these tropical areas (Benício et al., 2021), improved results would be obtained with biodiversity models that consider a spatial pattern.

Our second objective was to generate accurate predictions of SR at the local scale and fine resolution (90 m). Our second hypothesis was that if the biodiversity drivers were precisely generated in the previous step, reasonably accurate biodiversity models could be generated at the local scale. In the literature, multiple examples for predicting biodiversity at coarse resolution (1-50 km) are available at the country level (Lessmann et al., 2014; Mateo et al., 2012) or regional extents in tropical areas (de la Estrella et al., 2012), but only a few examples attempt predicting biodiversity in tropical areas at the local scale and fine resolution (e.g., Pouteau et al., 2015; Pouteau et al., 2019). In these works, the variables employed as predictors are mostly derived from remote sensing (Pouteau et al., 2018), as the normalized-difference vegetation index (Gillespie, 2005) or canopy structure (Fricker et al., 2015). To our knowledge, potential biodiversity drivers (i.e., climate, topographic heterogeneity, human impact) have not been employed as predictors during the modelling process at the local scale.

Our aim was to implement various biodiversity models to better understand the processes that generate plant biodiversity in the Andes-Amazon gradient. The reliable model developed could be integrated into a conservation management strategy for the study area (Guisan et al., 2013; Mateo et al., 2019b), and the proposed methodology may possibly be implemented to better understand and predict biodiversity patterns in other tropical megadiverse areas worldwide.

2. Material and methods

2.1. Study area and vegetation plots

We studied mature forests of the Madidi National Park and surrounding areas in north-western Bolivia using inventories of temporary 0.1-ha plots (20 × 50 m) across the Andes-Amazon gradient (latitudes –12.43° to –15.72°, longitudes –69.48° to–66.66°). A total of 397 plots were established from 250 to c. 4000 m elevation, including plots in dry tropical forests. Plots were located in forests with no signs of recent human disturbance, avoiding big canopy gaps or evident heterogeneity in soils or tree physiognomy within a plot. All woody plant stems $\geq$ 2.5 cm dbh (diameter at breast height, measured at 130 cm from the ground) were inventoried following a standard protocol (Arellano et al., 2016). The floristic database is maintained by the Missouri Botanical Garden and the dataset can be requested from the Madidi Project (https://madidiproject.weebly.com/). Superficial soil samples (0–15 cm below the litter layer) were collected, air-dried, and sieved through a 2 mm sieve to analyse their main physico-chemical properties.

2.2. Biodiversity drivers (predictors)

In order to understand the processes that generate and maintain

diversity, we considered potential plant biodiversity drivers in four main categories: climate, topography, anthropic, and edaphic. These drivers are expected to capture important factors for plant biodiversity at the local scale.

Reliable estimation of microclimatic environments (i.e., derived from precise topography layers, resolution lower than 100 m) is crucial to comprehend how species interact with the environment, and it is progressively recognised as essential for predicting species distributions (Maclean et al., 2021). Here, a set of eight microclimatic variables were generated in the form of accurate (~90 m resolution) raster layers through a downscaling procedure (Mateo et al., 2019b) from variables available at a resolution of 30 arc-seconds (~1 km^2 at the equator) in CHELSA 1.2 (Karger et al., 2017). First, to avoid multicollinearity, we implemented a pairwise correlation evaluation on all the accessible variables (monthly precipitation, and monthly minimum, maximum, and mean temperatures). In each pair with a correlation value greater than 0.7 (Dormann et al., 2013), we removed one climate variable. We obtained a final set of six representative climate variables: precipitation of the driest month (January), precipitation of the wettest month (July), mean temperature of the hottest month (October), mean temperature of the coldest month (July), maximum temperature of the hottest month (October), minimum temperature of the coldest month (July). Second, variables were downscaled from 1 km to 30 m resolution. For temperature variables, this was accomplished in R using local linear regressions (Mateo et al., 2019b) through a relationship of temperature with a 30 m resolution digital elevation model (DEM, https://www.usgs.gov/centers/eros). For precipitation variables, downscaling was accomplished by means of a bilinear approach using the resample function in R package raster. Third, after downscaling was completed, we generated three other climate variables: precipitation seasonality (July precipitation minus January precipitation), temperature seasonality (October mean temperature minus July mean temperature), and temperature spatial heterogeneity (standard deviation of mean July temperature in a window of nine 30 × 30 m pixels). Finally, climate variables were generated at 90 m resolution by averaging values across nine 30 × 30 m pixels (except for temperature heterogeneity, which was already estimated at this resolution).

Microtopography predictors (heterogeneity and moisture) were derived from a 30 m resolution digital elevation model as follows. First, we calculated linear aspect, slope (slope tool in ArcGIS 10.7), and accumulated flow into each down-slope cell towards the shortest surface distance to any stream (hydrology toolset in ArcGIS 10.7). Second, we calculated heterogeneity predictors (90 m resolution) by the calculation of the standard deviation in a window of nine 30 × 30 m pixels for altitude, linear aspect, and slope. The final accumulated flow variable was calculated at 90 m resolution as the mean of nine 30 × 30 m pixels.

We obtained information on edaphic variables at each of the 397 plots. Soil texture (percentages of sand, silt, and clay) was determined by Bouyoucos' hydrometer method (Bouyoucos, 1962). Soil pH was determined in a 1:2.5 (w/v) soil-deionized water suspension. Organic carbon (C) content was determined by wet digestion (Walkley, 1947). Total nitrogen (N) was obtained with the semi-micro Kjeldahl method (van Reeuwijk, 2002). We used two extractive methods for Ca, Mg and K, applied to different sets of samples: (1) extraction using 1 M ammonium acetate solution, and (2) extraction using the Mehlich-3 solution (Mehlich, 1984). The results from both methods were standardized since both are linearly correlated according to Arellano et al. (2016). We also calculated the C:N ratio as this variable is considered an important indicator of soil fertility in forest soil quality assessments (Schoenholtz et al., 2000).

Finally, the human impact at each plot was obtained from the ''human footprint'' layer (~900 m resolution) created by Sanderson et al. (2009). These data represent the relative human influence in every biome as a percentage. As this variable was not correlated with altitude, a meaningful downscaling was not possible.

To avoid multicollinearity across all sets of predictors, we excluded highly correlated predictors (Pearson's r > 0.70, Dormann et al., 2013), keeping 19 of them (see Table 1).

In order to evaluate our first hypothesis, the predictors (Table 1) were grouped in four clusters by considering biodiversity driver categories (i.e., climate, topography, anthropic and edaphic). The four clusters were generated by the consecutive inclusion of a category: 1) climate (C); 2) climate, and topography (CT); 3) climate, topography, and anthropic (CTA); and 4) climate, topography, anthropic, and edaphic (CTAE). After this process, we obtained four clusters of predictors each to compare the importance of biodiversity drivers by categories to explain and predict woody plant SR patterns. The aim was to improve the understanding of ecological processes (Houlahan et al., 2017), answering questions such as: (1) How essential are climate variables to predict SR in tropical areas at local scale? Because of the extensive elevational gradient considered, our hypothesis is that climate will be the main driver of SR, and the biodiversity model calibrated with exclusively climatic variables will be accurate and it will have high values of explained variance. (2) Do biodiversity estimations improve if other drivers are considered? If yes, what is the magnitude of this improvement? Our hypothesis was that the accuracy of the predictions would increase. Furthermore, as the drivers were included by steps and categories, we could evaluate the influence of the different drivers' categories.

2.3. Biodiversity modelling

For each of the four clusters of drivers generated previously, we modelled the observed SR (n = 397 plots) using both random forests (RF, Breiman, 2001), and Bayesian inference using the integrated nested Laplace approximation (INLA, Rue et al., 2009). RF was implemented using a maximum of 500 trees and a Poisson distribution (D'Amen et al., 2015). The process was repeated considering a spatial pattern. For RF, longitude and latitude were included as predictors (Sekulić et al., 2020). Bayesian spatial models included several covariates (see Table 1) and continuous spatially correlated random effects defined using a Matérn covariance function, defined using the SPDE approach with INLA (Krainski et al., 2019; Lindgren et al., 2011). Finally, we obtained 16

Table 1
List of biodiversity drivers considered after the selection of non-correlated variables classified by four main categories: microclimate, topography, anthropic and edaphic.

Abbreviation	Biodiversity driver (predictor)
Microclimate drivers (90 m):	
Prec.1	Precipitation of the driest month (January)
Prec.7	Precipitation of the wettest month (July)
Tmed.10	Mean temperature or the hottest month (October)
Tmed. Seasonality	Temperature seasonality = Mean temperature hottest month (October) - Mean temperature coldest month (July)
Topography drivers (90 m):	
Aspect.sd	Standard deviation of linear aspect (heterogeneity)
Aspect	Linear aspect
DEM.sd	Standard deviation of altitude (heterogeneity)
Slope.sd	Standard deviation of slope (heterogeneity)
Flow	Flow accumulation (moisture)
Distance	Geographical distance to main streams (moisture)
Anthropic driver (900 m):	
Human activity	Human footprint
Edaphic drivers (information available at plot level):	
Sand	Total sand in the soil (%)
Silt	Total silt in the soil (%)
Clay	Total clay in the soil (%)
C	Organic carbon content (%)
pH	Soil pH
K	Available potassium content (mg/kg)
Mg	Available magnesium content (mg/kg)
Ca	Available calcium content (mg/kg)
N	Total nitrogen content (%)
C:N	Ratio between carbon content and nitrogen content

biodiversity models (4 clusters of predictors × 2 modelling techniques x 2 spatial options).

The predictive performance of the 16 biodiversity models was assessed by cross-validation. The models were fitted to a portion of the data, and these fitted models were used to make predictions on the remaining data. A good model is supposed to make good predictions on portions of the data that were not included during the model fitting process. In contrast, an overfitted model will make very accurate predictions on the data that were used to fit the model, but poor predictions based on other observations, even if taken from the same population. We followed a cross-validation procedure, where the original dataset (397 plots) was randomly divided into two partitions with a repeated (10 times) procedure, using the 80% partition for training the models and the other 20% for model validation (D'Amen et al., 2015). For each split-sample repetition, a Spearman rank correlation between observed and predicted SR value was calculated as a metric of the predictive ability of the model. Finally, the mean and the standard deviation of the correlation values between the 10 predictions were calculated as the overall quality of the model. RF was the technique with higher correlation values (see Table 2) and the fastest (see, Mateo et al., 2019a), therefore it was selected as the reference technique. From now on, the analysis explained were executed only for RF to simplify the interpretation of results.

We ran a final biodiversity model with 100% of the original dataset (397 plots) to avoid biases associated with subsampling (Araújo et al., 2005). For RF, as model averaging enable model coefficients to fluctuate and improve the spatial transferability (Mateo et al., 2010; Yates et al., 2018), we ran 100 times (replicates) with a repeated split-sample procedure, and the replicates were fitted on the 80% data partition and the other 20% for validation. The final biodiversity model was the average of the 100 replicates. The accuracy of this model was assessed by the mean of squared residuals, the percentage of variance explained, and the relative under- or over-estimation of species ([observed SR – predicted SR] / observed SR), which could be seen as model residuals weighted by the number of observed species.

The weighted residuals were plotted by forest types and altitude. Forest types classification was obtained from Arellano et al. (2015). The most distinct forest formation is the semideciduous dry forest, characterized by lack of precipitation during 4–5 months per year. The other forest types were characterized by regular altitudinal belts: lowland Amazonian forest (below 1000 m); lower montane forest (1000-1700 m); intermediate montane forest (1700-2400 m); upper montane forest (2400-3100 m); and high Andean forest (3100-3731 m).

Edaphic data were only available for the plots, so extrapolation to the complete study area could not include edaphic predictors. Therefore, spatial projections of the models were only generated for three predictor clusters: 1) climate, topography, and anthropic (CTA); 2) climate and topography (CT), and 3) climate (C). To explore if the biodiversity maps generated were different, we calculated the Spearman rank correlation coefficient between all pairs (Mateo et al., 2010).

3. Results

3.1. Field work

Our plant database included 2257 species or morphospecies based on standardized taxonomy. The observed SR varies from 11 to 134 woody plant species per 0.1-ha plot.

3.2. Comparison of modelling techniques

RF biodiversity predictions outperformed Bayesian models when the spatial component was not considered. Higher correlation values were obtained for the four biodiversity driver models (Table 2). However, when a spatial component was considered, the results obtained were very similar for both approaches.

3.3. Biodiversity drivers and species richness patterns

Counting RF biodiversity predictions, whether the spatial component was considered or not, very similar values of correlation (Table 2), mean of squared residuals (Table 3), and percentage of variance explained (Table 3) were obtained, for the four biodiversity driver clusters. In addition, high correlation values (0.86 to 0.99, Table 4) were found when biodiversity maps were subject to pairs comparison: the biodiversity model did not gain any considerable improvement by including more biodiversity drivers as predictors. Given that model complexity could have negative effects on ecological models (see Moreno-Amat et al., 2015 and references therein), we selected as the reference model the one calibrated with climatic variables only, i.e. it was considered the closest to the reality given the modelling technique and the available data (Hernandez et al., 2006). Otherwise, the model improves if a spatial component was included, the correlation value increase from 0.80 to 0.85 (Table 2), and the variance explained percentage raised from 60.18 to 67.74 (Table 3). We also tested the final model residuals spatial autocorrelation, adjusted with climatic variables and the spatial component through a Moran's I index (I) with 99,999 permutations. We obtained a non-significant result for this test (I = - 0.027, p-value = 0.7); we concluded that we did not left out any important spatial driver of SR (Chevalier et al., 2021).

An analogous trend was observed for the Bayesian model (similar correlation values, Table 2) when a spatial component was considered. However, if the spatial component was not included, the correlation values increase from 0.55 (only climatic variables) to 0.64 (climate, topography, anthropic, and edaphic).

Final average RF models of each cluster of drivers produced similar SR projections across the whole study area (Fig. 1, Table 4). However, at

Table 2
The predictive performance of the biodiversity models generated with random forest (RF) and Bayesian inference (Bayesian) with or without spatial component (spatial) was assessed by the Spearman rank correlation between observed and predicted species richness value following a cross-validation procedure. The values in parentheses represent the standard deviation.

Biodiversity driver clusters	RF	RF + spatial	Bayesian	Bayesian + spatial
Climate, topography, anthropic, and edaphic	0.81 (0.02)	0.84 (0.02)	0.64 (0.09)	0.84 (0.05)
Climate, topography, anthropic	0.80 (0.02)	0.83 (0.02)	0.58 (0.09)	0.83 (0.05)
Climate, topography	0.80 (0.02)	0.83 (0.02)	0.54 (0.08)	0.83 (0.05)
Climate	0.80 (0.02)	0.85 (0.02)	0.55 (0.07)	0.82 (0.04)

Table 3
Mean and standard deviation (in brackets) values of percentage of variance explained and mean of squared residuals of the final RF model (100 replicates) with or without spatial component and under four different clusters of biodiversity drivers: a) climate; b) climate and topography; c) climate, topography, and anthropic; d) climate, topography, anthropic, and edaphic.

	Percentage of variance		Mean of squared residuals	
Biodiversity driver clusters	RF	RF + spatial	RF	RF + spatial
Climate, topography, anthropic, and edaphic	60.47 (2.52)	65.17 (2.30)	211.70 (14.29)	187.32 (11.96)
Climate, topography, anthropic	59.12 (2.57)	64.76 (2.46)	219.05 (13.37)	188.39 (11.82)
Climate, topography	54.60 (3.08)	63.74 (2.70)	244.64 (15.96)	192.93 (13.15)
Climate	60.18 (2.43)	67.34 (2.37)	212.95 (13.01)	175.02 (11.99)

Table 4
Spearman rank correlation value by pairs when comparing all the RF biodiversity maps generated, with or without spatial component (spatial) and under three different clusters of biodiversity drivers: climate (C); climate and topography (CT); climate, topography, and anthropic (CTA).

	C	CT	CTA	C + spatial	CT + spatial	CTA + spatial
C		0.95	0.89	0.87	0.87	0.86
CT			0.93	0.88	0.92	0.90
CTA				0.85	0.88	0.92
C+spatial					0.98	0.98
CT+spatial						0.99
CTA+spatial						

the local scale, the spatial patterns differences between them could be important. Indeed, our results suggest that climate drivers determine a general trend, which is then refined by spatial factors.

3.4. Forest types, altitudinal gradient, and species richness prediction

The reference biodiversity models (RF modelling technique and climate predictors) displayed a general trend to over-prediction in the less SR forests (high Andean and dry forest), and a slight under-prediction in the higher SR forests (lowland Amazonian, lower montane, and intermediate montane forests) (Fig. 2). Furthermore, the maximum SR observed was 134 species per 0.1 ha plot, and the maximum SR predicted was 110 species per pixel. The under-prediction error was reduced when a spatial component was included in the model (Fig. 2b).

4. Discussion

4.1. Biodiversity drivers and species richness patterns

Our results supported our two main hypotheses. Accurate biodiversity models can be generated at the local scale, and climatic drivers are important biodiversity predictor in tropical areas when an altitudinal gradient is considered. However, climate drivers alone are not a sufficient explanation for biodiversity patterns. Indeed, a spatial component, at least, should be considered for a proper SR prediction (Table 1). Although the maximum cross-correlation obtained for the best model was 0.85 (Table 2), and the maximum explained variance was 67% (Table 3), there is still room for improvement. For example, the model presented a general trend to over-prediction in the forest with lower SR, while displaying an under-prediction in the forests with higher SR (Fig. 2). The inclusion of biogeographical, evolutionary and historical drivers during the modelling process could be needed to improve the results (Mateo et al., 2017), such as the regional species pool, colonization time, dispersal capacities, or speciation rates (Benício et al., 2021). If this were the case, they could be included in a step by step process (SESAM framework, Guisan and Rahbek, 2011), or considering a hierarchical scale framework (Mateo et al., 2019a). Finally, the importance of stochastic factors in biodiversity patterns at the local scale (Chase, 2010), which was not possible to include in the modelling process (D'Amen et al., 2017), might be responsible for some of the unexplained variance. Moreover, some authors have postulated recently that climatic drivers exert greater control over plant species assemblage in temperate areas (Laughlin and Laughlin, 2013), whereas dispersal limitation and historical drivers have a greater influence on tree plant richness patterns in tropical regions (Kraft and Ackerly, 2010; Pouteau et al., 2019).

Recently, precipitation has been associated with changes in tree

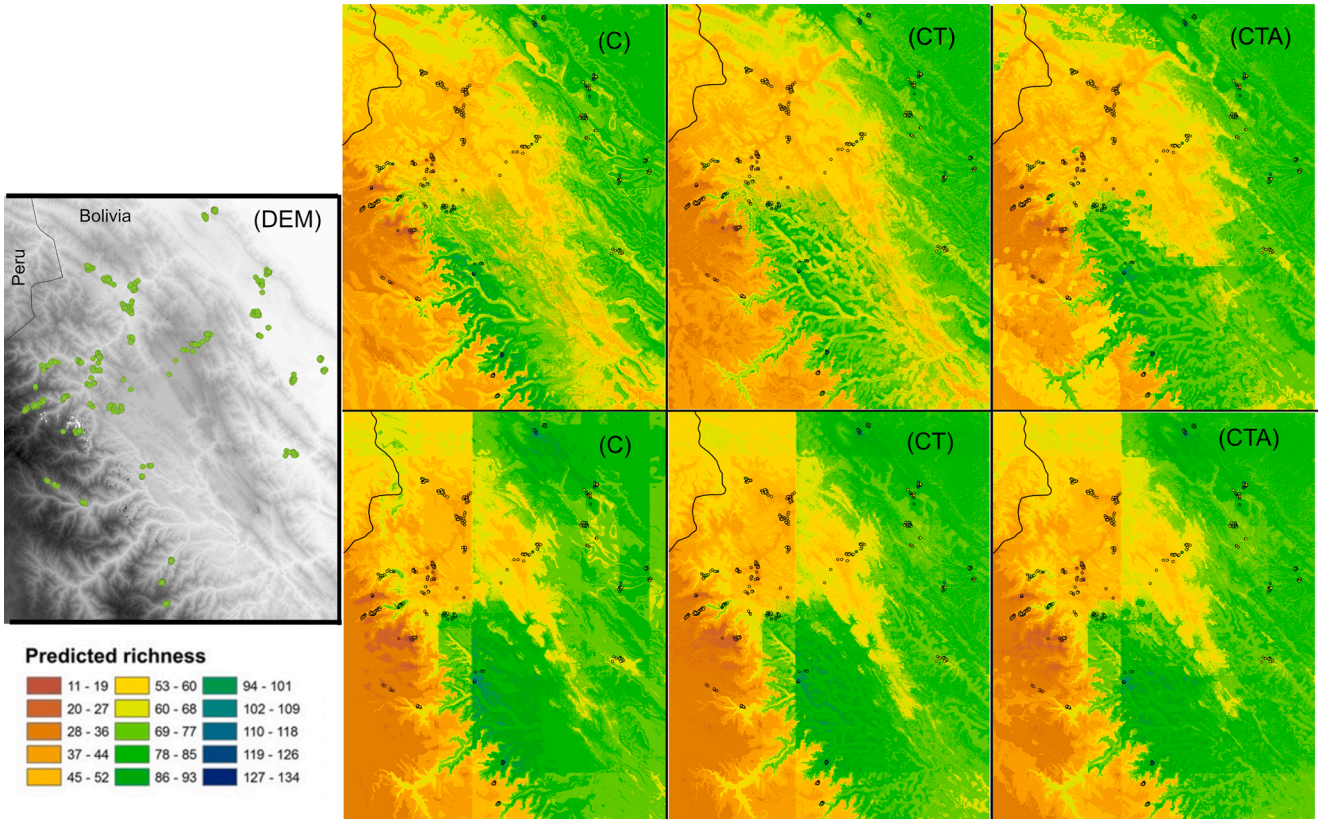

Fig. 1. Predicted species richness by the final RF model with (bottom) o without (top) spatial component and under three different clusters of biodiversity drivers: climate (C); climate and topography (CT); climate, topography, and anthropic (CTA). Plots are represented as green circles above a digital elevation model (DEM).

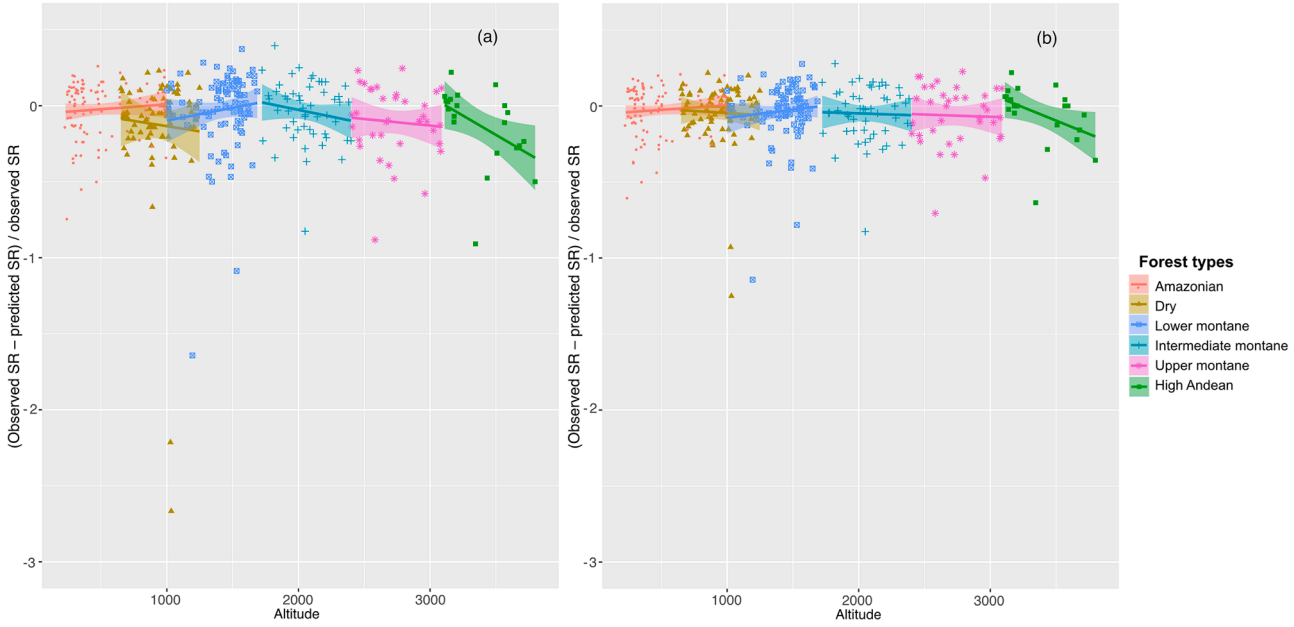

Fig. 2. Accuracy of the final averaged RF biodiversity model generated with only climatic predictors without spatial component (a) and with spatial component (b). It was measured by the calculation of residuals weighted by the number of observed species ([observed SR – predicted SR] / observed SR) and plotted by forest types and altitude.

species turnover in tropical areas (e.g., Esquivel-Muelbert et al., 2017; Hardy et al., 2012). These findings support the hypothesis that climate might drive the regional species pool, and subsequently the regional species pools have an important influence on the local tree communities (e.g., Lessard et al., 2012a; Lessard et al., 2012b). Our results meet with these past studies suggesting that precipitation is an important driver of woody biodiversity in tropical areas.

Edaphic variables are hypothesized to have an important role in plant richness patterns in tropical areas (e.g., Gentry, 1988; Tuomisto et al., 2016). However, our results suggest that SR can be accurately predicted without considering edaphic drivers directly. Indeed, when dropping edaphic drivers from the model, the correlation value remained high (0.80), and the explained variance decreased only slightly (from 67% to 65%; Table 3). In contrast, edaphic variables were found crucial for predicting the distribution of plant species at the local scale by using the S-SDMs modelling framework (Cianfrani et al., 2019), where each species was modelled independently, and the edaphic conditions are relevant in the distribution of individual plant species. Here, we were predicting the observed SR numbers and edaphic factors did not show an important role; when soil factors were removed, topographic factors became important. This might be explained because it is possible to approximate some edaphic conditions through topographic information. Soil texture and pH are variables strongly associated with topographic factors as elevation and slope (Dessalegn et al., 2014), which would justify the small reduction in explained variance in the richness models when these edaphic variables are removed in the analysis but topographic variables were retained. The large elevation gradient studied (from 250 to c. 4000 m) can influence microclimate and thus soil-forming processes. Soil pH values showed a decrease with elevation and coarse sand sized particles increased significantly. Slope is related to soil erosion, morphology, and deposition processes. Therefore, soil fertility is lower on ridges and upper slopes than in hollows and valleys (Scholten et al., 2017).

The anthropic variable did not seem to provide useful information during the modelling process. When we compared the models that included this variable (the climate, topography, and anthropic models) with models that did not include it (climate and topography models), they were practically equivalent (correlation value of 0.99 considering a spatial component, Table 4). This may be due to the coarse resolution of the information available for this variable (900 m). In the near future, information obtained by drones or other forms of high-resolution aerial or satellite imagery might be used to derive more precise and useful anthropic variables.

The RF model was mapped under three different clusters of biodiversity drivers (Fig. 1): climate; climate and topography; climate, topography, and anthropic. The three models mapped displayed similar regional trends for biodiversity patterns (see Fig. 1), however, at the local scale the differences between models could be important (see Fig. 1). Therefore, these comparisons among model projections reinforce our conclusion that climate alone is not a sufficient explanation for current biodiversity patterns, and other biodiversity drivers should be considered in biodiversity modelling frameworks.

4.2. *Macroecological biodiversity modelling framework*

Our results confirmed that random forests are reasonably resistant to overfitting (e.g., Mi et al., 2017), and we suggest their use to predict SR. Here, for the first time, we showed appropriate results for tropical areas. This means that it is possible to predict accurately SR, and better understand the role of different biodiversity drivers along an altitudinal gradient. A macroecological modelling (MEM) framework was selected to predict SR because the importance of different biodiversity drivers can be evaluated (Mateo et al., 2016), although species composition cannot be predicted (Guisan and Rahbek, 2011), which was not the objective of this study.

We achieved better results with RF than with the Bayesian procedure when we did not include space. For RF, we generated an ensemble model of 100 replicates with split-sample procedure, this could generate more flexible models (Mateo et al., 2010) than the Bayesian lineal models applied. However, when a spatial component was considered, the results obtained were very similar for both approaches. This highlights the importance of considering the spatial component during ecological landscape-scale modelling at precise spatial resolution. The inclusion of spatial components may be even more important than the statistical method employed.

The accurate modelling performance obtained here was conditioned by the employment of appropriate modelling practices (Araújo et al., 2019). We can emphasize three of them: (a) a proper selection of

ecologically meaningful biodiversity drivers in accordance with ecological theory (Mateo et al., 2017; McGill, 2010); (b) the generation of different variables at fine spatial resolution, as for example downscaled climatic variables (Mateo et al., 2019b) or environmental heterogeneity; (c) the availability of accurate and taxonomically standardized presence data at the local scale (D'Amen et al., 2017; Guisan et al., 2017). As a first and important step in studies related to biodiversity modelling, we suggest a cautious inspection of the data on the distribution of the species, the generation of appropriated environmental variables, and appropriate selection of the modelling approach and the parameterization.

4.3. Future lines of research

We have presented the first step to accurately predict SR in tropical areas at the local scale and precise resolution considering the importance of different biodiversity drivers. Future studies could consider and improve some aspects as: 1) Compare the results with other biodiversity modelling frameworks as S-SDMs (Dubuis et al., 2011), or hierarchical Bayesian approaches considering different aspects of scale (Mateo et al., 2019a). 2) Consider future climatic projections according to various climate change scenarios. 3) Model the effect of dispersal limitation and biotic interactions, which are important diversity drivers at local scales (Mateo et al., 2017; Pouteau et al., 2019). The integration and combination with other biodiversity modelling techniques that consider these drivers (Guisan and Rahbek, 2011) could be worthy. 4) Integrate biodiversity models with information obtained from remote sensing (Pouteau et al., 2018) or drones (Saarinen et al., 2018) to derive land use data at fine resolutions (meters), and include these data as independent variables in the modelling process.

5. Conclusions

We have ratified the importance of microclimate (precipitation and temperature) controlling plant SR patterns at the local scale. Our results suggest that climate drivers determine a general trend in plant richness patterns, which is then refined by spatial factors. Since climate change is expected to produce major changes in biological systems in this area (Beaumont et al., 2011), special conservation measures should be considered to prevent it (Edwards et al., 2019). The modelling approach proposed here, combined with the generation of precise biodiversity drivers (90 m resolution), could generate reliable and precise forecast predictions and upgrade previous methodological approaches, as multiple regression models (Fricker et al., 2015) or ordinary least squares (OLS) regression models (Tripathi et al., 2019), which usually have only been applied at regional or continental scales and coarse resolutions. The local and precise models obtained could serve as a valuable tool for local conservation planning (Mateo et al., 2019b) in the region. If accurate SR and spatial variables data are available, then the methodology presented here could be employed in other tropical areas to complement their conservation needs.

CRediT authorship contribution statement

Rubén G. Mateo: Conceptualization, Methodology, Software, Writing – original draft, Validation. **Gabriel Arellano:** Conceptualization, Data curation, Writing – review & editing. **Virgilio Gómez-Rubio:** Software, Validation. **J. Sebastián Tello:** Data curation, Writing – review & editing. **Alfredo F. Fuentes:** . **Leslie Cayola:** Data curation, Writing – review & editing. **M. Isabel Loza:** Data curation, Writing – review & editing. **Victoria Cala:** Data curation, Writing – review & editing. **Manuel J. Macía:** Conceptualization, Data curation, Supervision, Writing – review & editing.

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Data availability

Data will be made available on request.

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