

# Tropical high Andean drylands: species diversity and its environmental determinants in the Central Andes

Ana C. Godoy-Bürki<sup>1</sup> · Fernando Biganzoli<sup>2</sup> · Jesús M. Sajama<sup>3</sup> · Pablo Ortega-Baes<sup>3</sup> · Lone Aagesen<sup>1</sup>

Received: 25 November 2015 / Revised: 28 December 2016 / Accepted: 30 January 2017 /  
Published online: 7 February 2017  
© Springer Science+Business Media Dordrecht 2017

**Abstract** Diversity determinants have mostly been evaluated in high diversity areas, leaving behind regions with less species diversity such as drylands. Here we aim to analyze the patterns of plant diversity in tropical drylands in the southern Central Andes, and determine the importance of water, energy, and environmental heterogeneity as diversity determinants of the arid and semi-arid adapted flora. We examined the distribution of 645 native species from lowlands to 6000 m.a.s.l. in the north-western region of Argentina (NWA) and define hotspots of diversity within each NWA ecoregion. Diversity is concentrated in regions of middle elevation with intermediate values of water and energy, at the transition between arid and semi-arid regions. Furthermore, we showed that in tropical drylands energy input is as fundamental for plant diversity as water input is and, we found that the effects of these variables varied with elevation and, also with aridity. Water variables had the strongest effect on the flora in the arid high Andean ecoregions, where an increase in precipitation during the growing season stimulated species diversity. Energy only became more important than water when the arid adapted flora entered the low and semi-arid regions where energy increments reduce species diversity. Our analysis provides strong quantitative support for climate variables as the main determinants of plant diversity across different ecoregions of the southern Central Andes. Given the present climate

---

Communicated by Francis Brearley.

---

**Electronic supplementary material** The online version of this article (doi:[10.1007/s10531-017-1311-2](https://doi.org/10.1007/s10531-017-1311-2)) contains supplementary material, which is available to authorized users.

---

✉ Ana C. Godoy-Bürki  
agodoy@darwin.edu.ar

<sup>1</sup> Instituto de Botánica Darwinion, Labardén 200, Casilla de correo 22, B1642HYD San Isidro, Buenos Aires, Argentina

<sup>2</sup> Departamento de Métodos Cuantitativos y Sistemas de Información, Facultad de Agronomía UBA, Av. San Martín 4453, C1417DSE, Buenos Aires, Argentina

<sup>3</sup> Laboratorio de Investigaciones Botánicas (LABIBO), Universidad Nacional de Salta, Av. Bolivia 50, 4400 Salta, Argentina

change events, knowing how these variables affect the distribution of the arid adapted flora is crucial for planning strategies for achieve their present and future conservation.

**Keywords** Diversity · Arid/semi-arid climates · Water-energy variables · Argentina · Andes

## Introduction

Dryland systems cover more than 40% of Earth's surface and are inhabited by more than two billion people that depend on their ecological/cultural services (Bonkougou 2003; Safriel and Adeel 2005; UNEP 2006; Pernetta 2014). These lands are defined by water scarcity, and characterised by seasonal climatic extremes and unpredictable rainfall patterns. The lack of humidity prevents forest formations and high species richness in drylands but allow the development of a great variety of endemic biota with special adaptations to water deficit (Bonkougou 2003; Safriel and Adeel 2005; Pernetta 2014). At present, however, several of these regions are undergoing loss of habitat (see Myers et al. 2000). Worldwide these lands are threatened by the effects of climate change with decreasing mean annual precipitation (Dore 2005) and increments in temperature (Hughes 2003); both changes are expected to bring consequences for the flora and fauna found in drylands. Despite this, studies on species diversity in these ecosystems and the mechanisms driving it are still scarce (Li et al. 2013).

The spatial variation of vascular plant diversity in relation to climatic and environmental variables has been widely documented (Francis and Currie 1998; Ricklefs et al. 1999; Gaston 2000; Kreft and Jetz 2007; Blach-Overgaard et al. 2010). Water-energy variables have been indicated as the dominant predictors of global plant species richness (Francis and Currie 2003; Hawkins et al. 2003; Field et al. 2009—but see Stein et al. 2014), with global peaks of diversity found in topographical complex regions with high annual energy input and constant water supply (Kreft and Jetz 2007). However, most studies have been carried out in high diversity areas such as in the tropics or in temperate regions of the Northern Hemisphere where water acts as the limiting factor of plant richness at low latitudes and energy at higher latitudes (Hawkins et al. 2003; Whittaker et al. 2007; Eiserhardt et al. 2011). The Southern Hemisphere, which holds some of the most important centres of plant species richness such as the Atlantic Forest in Brazil and the Tropical Eastern Andes slopes (see Barthlott et al. 2005), is in lack of studies. Hawkins et al. (2003) suggested that in this hemisphere, as a consequence of a more oceanic climate, water could be the most important determinant of diversity irrespectively of latitude, while temperatures become the determinant factor only at high altitudes. To our knowledge, however, few studies have examined the drivers of species diversity in this part of the globe (Crisp et al. 2001; Moser et al. 2005; Distler et al. 2009; Eiserhardt et al. 2011) and none in tropical drylands (but see Li et al. 2013 for temperate drylands)—which is the principal aim of the present study.

The Tropical Andes comprise the Andean regions of Venezuela, Colombia, Ecuador, Peru, Bolivia, and the northern portions of Argentina and Chile (CEPF 2015, <http://www.cepf.net/>). Despite being recognized as a global hotspot for biodiversity, it is one of the most severely threatened areas in the tropics, with a large portion of its landscape being transformed by human activities (Myers et al. 2000; CEPF 2015). Its species richness have

been explained in terms of environmental factors; with the most outstanding diverse areas found on the eastern slopes of the northern Andes where a great input of energy and water occurs, in combination with a topographical complex environment (Kreft and Jetz 2007). Which factors drive the diversity of the southern portion of the Tropical Andes is, however, unknown. Towards the south, the Tropical Andes become increasingly dryer; with aridity acting as a strong filter for Andean elements in the southernmost part (Luebert and Weigend 2014).

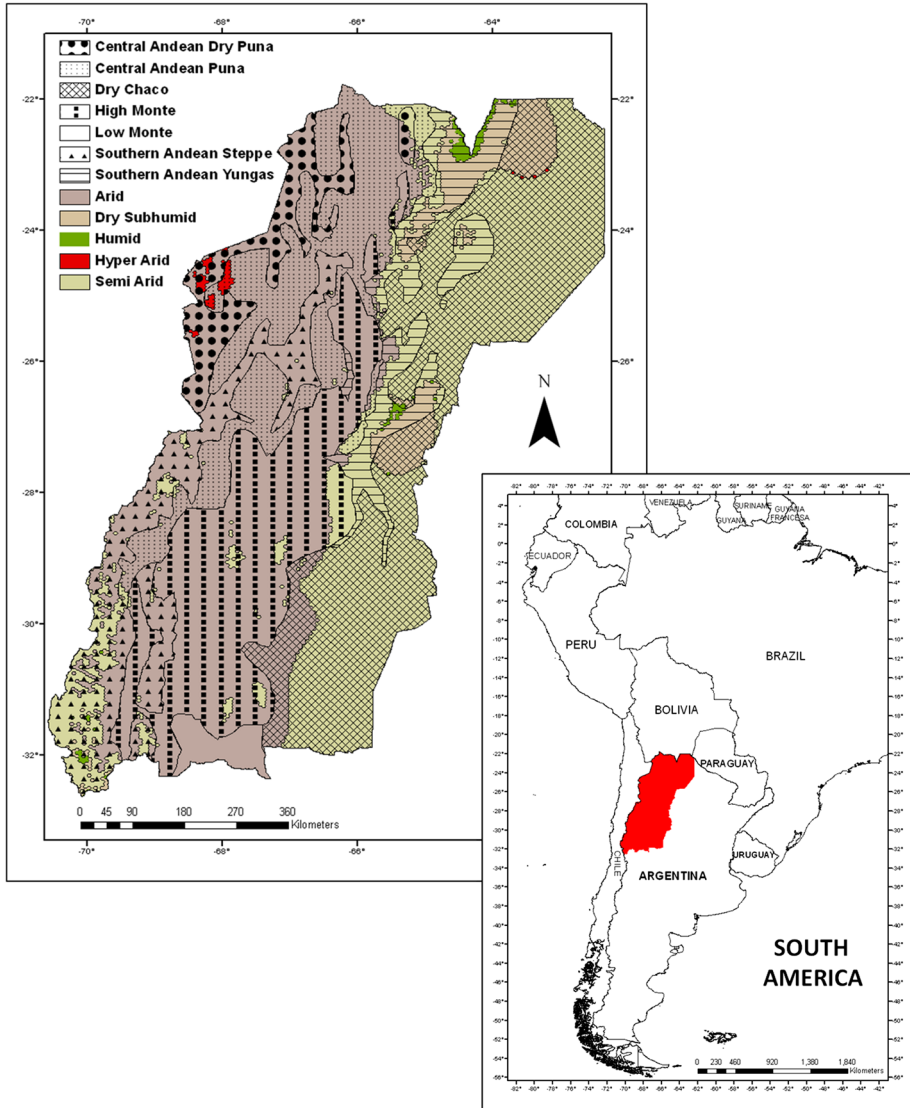
The high diversity and endemism that characterized the northern part of the Tropical Andes decline south of the Tropic of Capricorn and level out between 25°S and 29°S in north-western Argentina—hereafter abbreviated as NWA (Jorgensen et al. 2011; Kessler et al. 2011; Luebert and Weigend 2014). In this part of the Andes the complex topography combined with a steep climatic gradient, with tropical moist broadleaf forest on the eastern slopes and some of the world's most arid deserts towards the west, support a conspicuous east–west turnover in the flora and fauna. This turnover has been acknowledged by early South American biogeographers who divided the region into phytogeographic units (Lorentz 1876; Holmberg 1898; Castellanos 1944; Parodi 1945; Hauman-Merck et al. 1947; Cabrera and Willink 1973; Cabrera 1976; Ibsch et al. 2003; Josse et al. 2003) that are still recognized in contemporarily biogeographic schemes such as the ecoregions of Olson et al. (2001) and used by governmental and non-governmental organizations (Ribichich 2002). The main part of these ecoregions are found in arid to semi-arid climates at different altitudes, which makes them particularly sensible to damage caused by human activities or climate changes (Ezcurra 2006; Pernetta 2014). For vascular plants, the NWA region holds some of the most species rich ecoregions of the Southern Cone both in terms of endemism and diversity (Cabrera 1976; Zuloaga et al. 1999; Aagesen et al. 2012). Vascular plant endemism is mainly found in semi-arid to arid regions (Young et al. 2002; Roig et al. 2009; Aagesen et al. 2012; Godoy-Bürki et al. 2014) while the humid/sub-humid cloud forest on the eastern Andes slopes (Southern Andean Yungas) hold the highest species diversity (Cabrera 1976; Brown et al. 1993; Vides-Almonacid et al. 1998). These ecoregions are presently all threatened in a variable degree mainly by changes in land use (Grau et al. 2005; Izquierdo and Grau 2009) but also by the ongoing climate change (Gonzales 2009; Godoy-Bürki 2016). Furthermore, a recent study carried out in the area showed that the endemic flora of the NWA is nearly unprotected by the regional system of protected areas (Godoy-Bürki et al. 2014).

The traditional biogeographic scheme that has been developed for the NWA (e.g., Cabrera 1976; Cabrera and Willink 1973) is mainly based on qualitative observations but still widely used, among other by Olson et al. (2001) as mentioned above and by Morrone (2006, 2014) in his biogeographical regionalization of the region. The NWA is considered a part of the transition zone between the Neotropical and Andean flora and fauna that are composed by elements with different biogeographic history and with different climatic requirements (Morrone 2006). It is the aim of the present study to quantify plant diversity and environmental diversity drivers within each of these ecoregions, both to quantify the differences among these units that have been delimited by qualitative criteria, as well as to estimate if and where there is a turnover in the relative importance of water and energy within the transition zone. We analyze the distribution of the dry adapted flora found in the semi-arid to arid ecoregions of the tropical drylands surrounding the southernmost part of the Tropical Andes, and identify which are the main determinants of plant diversity in NWA region. Knowing which variables determine the distribution of the native flora adapted in each of these ecoregions is furthermore crucial knowledge for developing strategies for their present and future conservation.

## Methods

### Study area

The southernmost part of the Tropical Andes includes north-western Argentina and northern Chile. In this study we examine species diversity in the Argentinean portion of the region (Fig. 1). Specifically, we studied the flora of the arid and semi-arid drylands of the



**Fig. 1** Ecoregions and aridity climate classes (drylands) in north-western Argentina (NWA). Location of NWA in South America (*in red*). Ecoregions follow Olson et al. (2001). Climate classes were defined according to the Global Aridity Index (Trabucco and Zomer 2009)

region, which comprise the full range of drylands surrounding the southernmost part of the Tropical Andes (Fig. 1).

The NWA region is characterized by a climatic heterogeneity associated with the availability of moisture laden air masses along different altitudinal gradients (Bianchi and Yañez 1992). The altitudinal gradient, with mountains and hills oriented north–south, range from 300 m.a.s.l. at east to elevations above 4000 m.a.s.l. at west (Cabrera 1976). The highest peaks are located towards the southern-west in the Southern Andean Steppe ecoregion at approx. 6300 m.a.s.l. (Cabrera 1976; Olson et al. 2001). The precipitation follows a monsoon regime; with summer rain falling mainly from November to February and a dry winter period (Bianchi and Yañez 1992; Garreaud et al. 2003). The rainfall values range between 900 and 3500 mm year<sup>-1</sup> on the eastern Andes slopes, but decreases to less than 100 mm year<sup>-1</sup> on the western slopes (Bianchi and Yañez 1992). The temperature varies within the area, with the south-western side of the region presenting temperature occasionally under zero during the summer period (Cabrera 1976).

Predominantly, there are two climate types; warm and humid in the north-eastern part of the region, and cold and arid in the south-western portion. The changes in temperature and precipitation between these two extremes are reflected in the occurrence of seven ecoregions (Olson et al. 2001). Of those we will consider six: the Southern Andean Steppe, Central Andean Dry Puna, Central Andean Puna, High Monte, Dry Chaco, and the Southern Andean Yungas (Olson et al. 2001, Fig. 1). The Low Monte ecoregion was excluded from the analyses due to its reduced extension within the NWA region, which we considered non-representative (see Fig. 1). The Southern Andean Yungas, located in the north-eastern portion of the NWA represent the only ecoregion in the study with both humid and dry sub-humid climate (Fig. 1). The highest and coldest ecoregions are found towards the west and include the Southern Andean Steppe and the Central Andean Dry Puna (Fig. 1). For more details of each ecoregion see Table 1.

## Species data

As this study explores the dry adapted flora of the NWA region, we included only species inhabiting arid and semi-arid drylands, excluding those exclusively found in the Southern Andean Yungas forest or in the Dry Chaco ecoregions (dry sub-humid or/and humid climate, Fig. 1). Species found in hyper-arid drylands were analyzed together with the species found in arid climates because hyper-arid climate is only found in a very small fraction of the study region (Fig. 1). The dataset included species of the five most diverse families of vascular plants in the study area; Asteraceae, Cactaceae, Fabaceae, Poaceae, and Solanaceae (Cabrera 1976; Zuloaga et al. 1999—Online Resource 1). The Bromeliaceae family, despite being less diverse than some of the excluded plant families such as Cyperaceae, Malvaceae, and Verbenaceae (Zuloaga et al. 1999), were included because they are among the most characteristic families of the Neotropical region although one of the least studied (Versieux and Wendt 2007). All data for the families was obtained from the Vascular Plants Catalog Project the main database of Argentinean vascular flora, available and updated at <http://www.floraargentina.edu.ar> (Zuloaga et al. 2008—see Online Resource 1). The dataset includes information from herbarium specimens, literature, and field collections, all properly georeferenced following the point-radius method (see Wiczorek et al. 2004). Aagesen et al. (2012) provided the data for species that are endemic to the study region (Online Resource 1—indicated with an \*). The occurrence dataset was spatially filtered to reduce the effect of sampling bias which should reduce the degree of overfitting in species distribution models (Boria et al. 2014). For filtering, we

**Table 1** Determinants of plant diversity in each ecoregion of the NWA

Ecoregions	Climate class	Annual mean temperature mín–máx (°C)	PWQ mín–máx (mm)	PCQ mín–máx (mm)	Plant diversity determinants	Relative importance of variable 2 and 3 respect to variable 1 (%)	Category	Relationship
Southern Andean Steppe (3500–6000 m.a.s.l.)	ARID	–9.2 to 15.7	12.6 to 99.3	2.9 to	PCQ	–	Water	C–
				164.3	PWQ	85	Water	C+
Central Andean Dry Puna (3500–5500 m.a.s.l.)	ARID	–4.35 to 12.3	17 to 205.3	0 to 21.5	PWQ	26	Energy	C+
					PET	–	Water	C+
					PET	24	Energy	C+
Central Andean Puna (3000–4500 m.a.s.l.)	ARID	–5.78 to 15	19.6 to 370.4	0 to 59.1	PWQ	17	Heterogeneity	/
					PET	–	Water	C+
					PET	70	Energy	C+
High Monte (600–3500 m.a.s.l.)	ARID	–4.6 to 19.7	32.4 to 278.7	1.7 to 50.3	PET	8	Heterogeneity	/
					PWQ	–	Energy	C+
					PWQ	70	Water	C+
Southern Andean Yungas (800–2500 m.a.s.l.)	SEMIARID	4.5 to 23	106 to 650.3	2.8 to 81.8	PET	64	Water	C–
					PCQ	–	Energy	C–
					PCQ	33	Water	C–
Dry Chaco (200–1200 m.a.s.l.)	SEMIARID	11.9 to 23.3	131.8 to 553.9	3.6 to	PET	10	Heterogeneity	/
				107.8	PCQ	–	Energy	C–
					PCQ	13	Water	C–
					TB	5	Heterogeneity	/

Ecoregions characteristics (climate class, elevation, annual mean temperature and, precipitation), relative importance of the three more important plant diversity determinants, category each variable represents, the relationship each variable maintains with diversity  
*PCQ* precipitation of the coldest quarter, *PWQ* precipitation of the warmest quarter, *PET* potential evapotranspiration, *TB* temperature belts, / positive linear relationship, C+ positive quadratic relationship, C– negative quadratic relationship

randomly removed localities that were within 10 km of one another, keeping as many localities as possible (see also Anderson and Raza 2010).

Because the botanical collections in the study area are neither exhaustive nor uniformly distributed, we model the potential distribution of each species applying Maxent's ecological niche software (Phillips et al. 2006; Phillips and Dudik 2008). Maxent has specifically been developed to model species distributions with presence-only data (Phillips et al. 2006), and has shown to outperform most other modelling applications (Elith et al. 2006; Pearson et al. 2007), as it is least affected by location errors in occurrences (Graham et al. 2008), and has the best performance when few presence records are available (Wisz et al. 2008; Kumar and Stohlgren 2009). To model species distributions we combined the species data with bioclimatic variables obtained from WorldClim (<http://www.worldclim.org>, Hijmans et al. 2005) at a resolution of 30 s. These variables constitute derivatives of interpolated climatic data, in particular precipitation, temperature, and their seasonality. According to Bucklin et al. (2015), implementing species distribution models with only climate predictors provide an effective and efficient approach for initial assessments of environmental suitability. We do not apply any test to remove correlated variables because to obtain a correct prediction of the species occurrences (the best model), the correlation between variables is not a problem. As was shown by Elith et al. (2011) the correlation between variables does not interfere in the accuracy of the predictions. For each species we defined the modelling area, applying a minimum convex polygon bounded by a buffer of 200 km. The species dataset was divided in two groups and different modeling techniques were applied for each group. For those species with less than 25 occurrences we followed Shcheglovitova and Anderson (2013) and for those species with more than 25 occurrences we model according to Radosavljevic and Anderson (2014). For additional information of each procedure see Online Resource 2.

As a result, we obtained the geographic distributions of 645 species; among which 262 species are endemic to the region (Online Resource 1).

## Data analyses

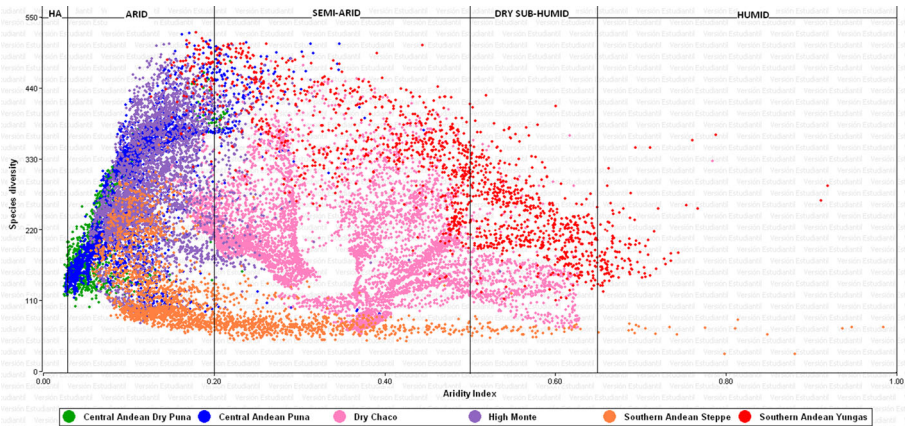
### *Patterns of species diversity*

The oldest and most fundamental concept of species diversity is species richness or species number in a given area (Peet 1974). Here we use the two terms species diversity and species richness interchangeable.

After modelling the species distributions, we divided the study area in hexagonal cells of 25 km<sup>2</sup> (21,058 cells). Using ArcGIS 10 software (ESRI 2011) we calculate the species richness of each cell by superposing all modelled species distribution and counting the number of species in each cell. We refer to hotspots as cells or groups of cells with high species diversity, while coldspots refer to cells or group of cells with low species diversity.

To identify which cells within the NWA region correspond to arid drylands and which cells correspond to semi-arid drylands, the Global Aridity Index classification (AI) was applied. The AI data were obtained from CGIAR-CSI GeoPortal (Trabucco and Zomer 2009). We associate the diversity of each cell to an aridity value of this index (Fig. 2). According to the AI, arid lands (the arid climate class) include those areas with an AI between 0.03 and 0.2 while semiarid lands (semi-arid climate class) comprise those lands with an AI between 0.2 and 0.5 (Fig. 2).





**Fig. 2** Plant diversity throughout NWA's aridity climate classes distinguished between ecoregions (Olson et al. 2001). Each point in the graph represents a cell of the study area. Species diversity is the total number of species per cell

### Potential determinants of species diversity

We first analyzed the entire dataset as a single unit and then by ecoregion. To identify which environmental variables affect the species diversity levels in each NWA ecoregion, we built a generalized least squares model (*gls* function, *nlme* package, Pinheiro et al. 2012). We evaluate 14 variables representing water, energy, and environmental heterogeneity (Online Resource 3). All variables were downloaded at a 30 s resolution. Potential evapotranspiration and aridity data were obtained from the CGIAR-CSI GeoPortal (Trabucco and Zomer 2009) while the soil types (ST) were provided by the FAO ([www.fao.org](http://www.fao.org)). The remaining variables (Online Resource 3) provided from Worldclim (Hijmans et al. 2005). Belts were calculated according to Kreft and Jetz (2007) and represent a measure of environmental heterogeneity related to elevation, temperature, or precipitation (Online Resource 3). The idea behind the belts is to reflect the association of discrete plant communities to a determined range of temperature, elevation or precipitation (belt).

To avoid multicollinearity between variables, we excluded those variables that were highly correlated based on pair correlations (Pearson correlation coefficient  $>0.7$ , Online Resource 4). As a result we discarded 8 variables (Online Resource 4), to finally maintain 6 variables plus three quadratic terms for PCQ (winter precipitation), PWQ (summer precipitation), and PET (potential evapotranspiration). We evaluated autocorrelation between errors potentially arising due to spatial proximity of hexagonal cells with the *correlation* option and the Gaussian Correlation Structure (Zuur et al. 2009). We also modeled variance heterogeneity of errors with the option *weights*. All variables were standardized to allow comparison between each variable importance as driver of species diversity, and to avoid collinearity among linear and quadratic terms of PCQ, PWQ, and PET (Montgomery et al. 2012). We ran this ecoregional level model, to find the primer determinants of species diversity in each ecoregion. In Online Resource 5 we show the final models for each case (b), including the analyses of the entire dataset as a single unit (a).

As no consensus appears on a single goodness of fit index for generalized least squared models, we present three metrics (Online Resource 5). First, a likelihood ratio test among the full model and the intercept only model, where rejection of the no effects hypothesis



means significant improvements of predictions with the addition of the independent variables. Second, the McFadden pseudo R-squared, calculated with  $1 - (\log\text{-likelihood (Full model)} / \log\text{-likelihood (Intercept only model)})$ , where a value greater than 0.2 represent excellent fit (McFadden 1979). Third, we present the common coefficient of determination (R-squared) among the observed and fitted richness, as a measure of ability of our models to predict the observed richness with the independent variables.

To compare the relative importance among variables with very different scales we sorted the effect-estimates from higher to lower, after fitting models with the standardized variables (Online Resource 5). We refer to these as proportion of the higher one and discuss the highest three for each ecoregion (Table 1).

## Results

### Patterns of species diversity

We found that the cells with the highest species diversity (421–525 species) were located towards the north of the study area (north 29°S, Fig. 3), at the limit between the arid and semi-arid climate classes, in cells with a mean AI of approx 0.2 (Fig. 2). The high diverse cells were primary found in the Central Andean Puna and in the High Monte ecoregions, especially in the montane grasslands (*sensu* Cabrera 1976) that form the transition zones between these ecoregions and the Southern Andean Yungas (Figs. 2, 3). The coldspots (less than 105 spp.) were mainly found in the Southern Andean Steppe and in the Central Andean Dry Puna (Figs. 2, 3).

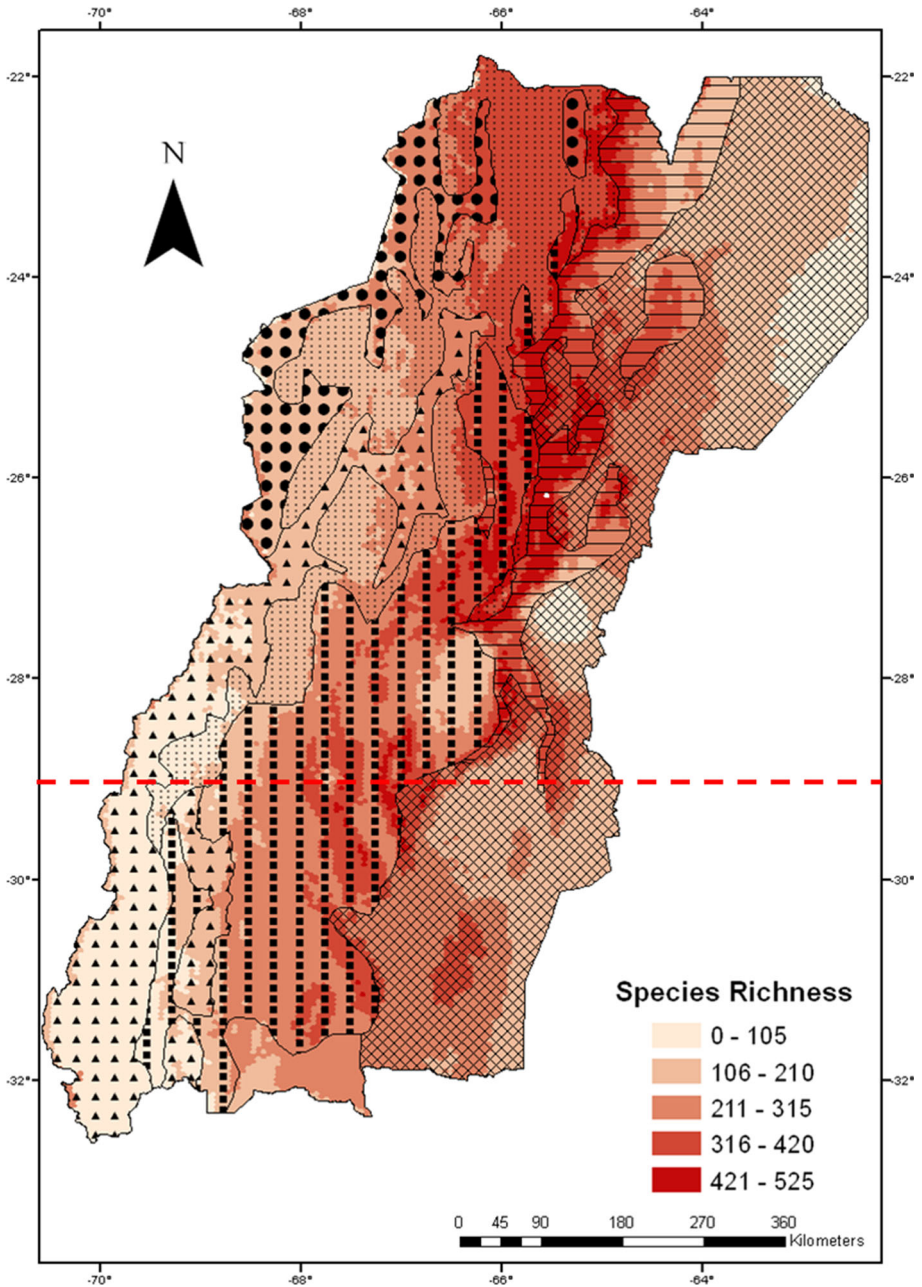
### Potential determinants of species diversity

As the results obtained when analyzing the entire dataset as a single unit simply reflects the conditions found in the two most extensive ecoregions (High Monte and Dry Chaco—Online Resource 5a), we base our discussion on the results found when analysing the data set by ecoregion (Online Resource 5b). The results from the regression analyses of the three main drivers of species diversity and their effect-estimates are found in Table 1. Model fitting values of all evaluated variables are found in Online Resource 5.

Species diversity was mainly affected by water and energy variables PWQ, PCQ, and PET while heterogeneity explained little of the diversity found in the NWA (Table 1). Water and energy variables differed in their relative importance, depending on the ecoregion (Table 1).

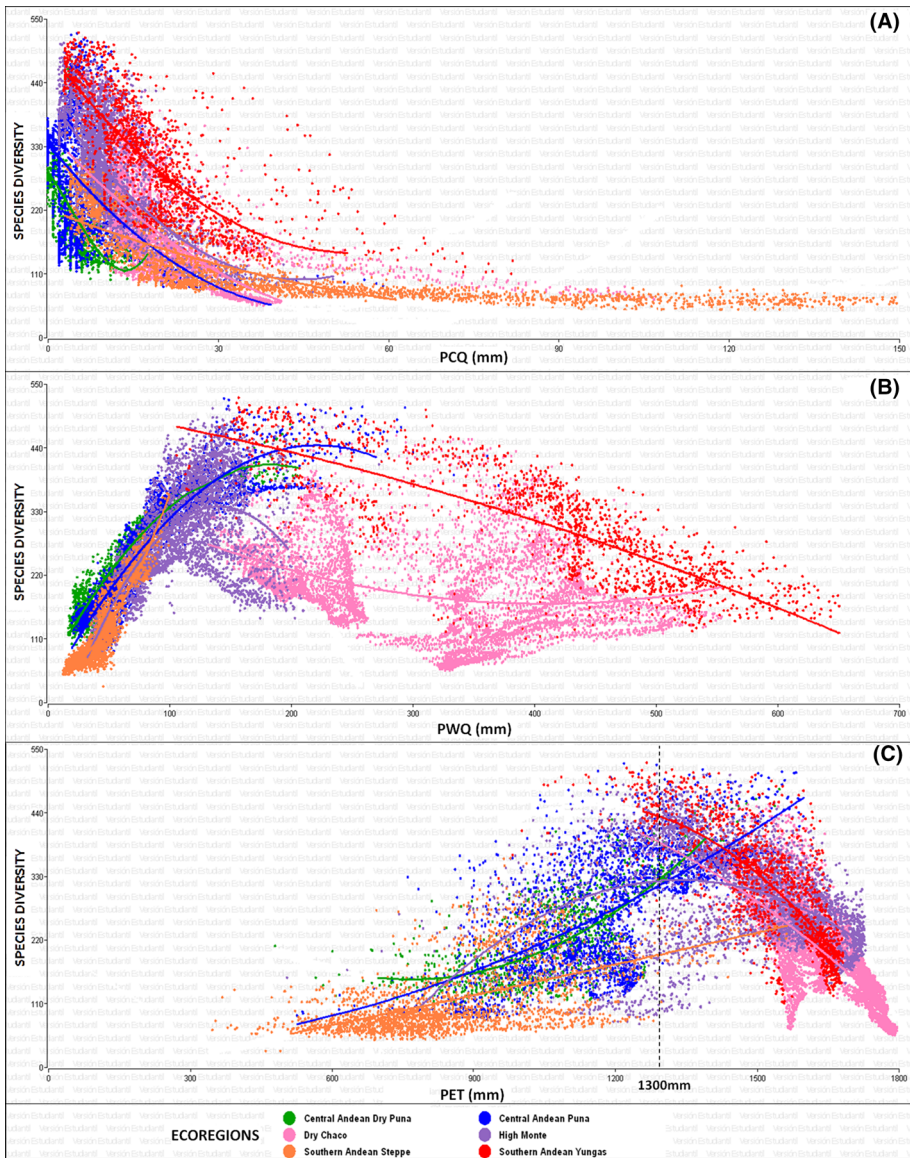
We found that in the highest, driest, and coldest ecoregions—the Southern Andean Steppe and the Central Andean Dry Puna, species diversity was strongly influence by water variables (Table 1). PCQ appeared as the most important factor for the arid flora in the Steppe, where it had a negative impact on species richness (Fig. 4a). PWQ was also important (Table 1) and positively related to species richness in this ecoregion (Fig. 4b). Increments in PWQ generated an increase in plant species richness up till 100 mm year<sup>-1</sup> (Fig. 4b), which is the maximum amount of summer rainfall in this ecoregion (Table 1). PET also presented a positive relationship with the Southern Andean Steppe flora (Fig. 4c) but with less influence on species richness than PWQ (Table 1).

In the Central Andean Dry Puna, which covers lower and slightly warmer areas than the Southern Andean Steppe, diversity was mainly determined by summer precipitation



**Fig. 3** Hotspots of plant diversity in NWA. Diversity is the total number of species per cell

(Table 1). Increments in PWQ generated an increase in species richness up till  $200 \text{ mm year}^{-1}$  (Fig. 4b); which is the maximum amount of summer precipitation occurring in this ecoregion (Table 1). As in the higher and dryer Southern Andean Steppe,



**Fig. 4** Relationship between environmental predictors and plant diversity in each ecoregion of NWA: **a** Precipitation of the coldest quarter (PCQ) versus species diversity, **b** Precipitation of the warmest quarter (PWQ) versus species diversity **c** Potential evapotranspiration (PET) versus species diversity. Each point in the graph represents a cell of the study area. Species diversity is the total number of species per cell

an increment in PET had a small but positive effect on the species richness in the Central Andean Dry Puna (Table 1; Fig. 4c).

In the Central Andean Puna, the lowest ecoregion of the high Andes, species richness continued to be conditioned mostly by increments in PWQ (Fig. 4b), but PET also had a strong positive influence on the flora (Table 1; Fig. 4c). Plant species richness responded

positively to increments in PWQ up to 200 mm year<sup>-1</sup> where after the relationship remained constant until 300 mm year<sup>-1</sup>, which is the maximum amount of summer precipitation in this ecoregion (Table 1; Fig. 4b). An increase in PET also generated a positive response of the plant species richness up till 1500 mm which is the maximum value of potential evapotranspiration in the ecoregion (Fig. 4c).

In the High Monte, the lowest and warmest area of the sampled ecoregions, species richness was mainly determined by PET (Table 1). In this ecoregion the diversity of the flora increased with increments in PET until 1300 mm from whereon increments in PET generated a decline in diversity (Fig. 4c). PWQ also had a strong influence on the flora (Table 1) and was related positively to species diversity (Fig. 4b). The flora responded positively to increments in PWQ up to 200 mm year<sup>-1</sup>, as in the Central Andean Puna (Fig. 4b). However, different cells within the High Monte responded differently to an increase in PWQ between approx. 100 and 200 mm year<sup>-1</sup> (Fig. 4b). The highlands cells which received this maximum precipitation present a higher diversity than the lowlands cells receiving the same amount of rain. Winter precipitation (PCQ), as in the Southern Andean Steppe, had a negative influence on the diversity in the High Monte ecoregion (Fig. 4a).

The Southern Andean Yungas and the Dry Chaco whose flora was not sampled here, contain part of the arid flora of NWA (Fig. 2). We found that in these ecoregions energy (PET) acted as the main diversity determinant and presented a far stronger negative effect on the arid adapted flora than water or heterogeneity variables did (Table 1; Fig. 4c).

## Discussion

When analyzing the distribution of the native flora found in the semi-arid to arid ecoregions of NWA, we found that the relative effects of water and energy on plant species richness vary with elevation (along the energy gradient) and also with aridity (from arid to semi-arid). The present study supports that water determines the species richness of the native flora at high elevations (3000–6000 m.a.s.l.) in the southernmost tropical Andes, while energy becomes increasingly important below 3000 m.a.s.l. (Table 1). Species diversity responds positively to water increments (available as PWQ) in the arid ecoregions while high quantities of energy reduce the number of species in the semi-arid regions (Fig. 4b, c). Consequently, the most diverse part of the arid flora of the Southern Central Andes is located at the limit between arid and semi-arid climates (AI: 0.2—Fig. 2) in mountain regions with intermediate values of water and energy. These areas correspond to the Central Andean Puna and the High Monte ecoregions and to the montane grasslands that are found at the transition zones between these two regions and the Southern Andean Yungas (Figs. 2, 3). Recent studies carried out in the region supported our results highlighting the high concentrations of endemic plants found in the above mentioned ecoregions, especially in the montane grasslands of the Yungas ecoregion (Aagesen et al. 2012; Godoy-Bürki et al. 2014).

Water and energy variables dominate the diversity of the native flora in the tropical drylands of the southernmost Tropical Andes, as found in previous studies at global level (Francis and Currie 2003; Hawkins et al. 2003; Whittaker et al. 2007; Field et al. 2009; Eiserhardt et al. 2011). These studies have indicated that either water or energy are the dominant predictors of global plant species richness regardless of the location of the study area. In agreement with the patterns found in temperate drylands of China (Li et al. 2013),



we found that water variables had the strongest effect on the diversity of the arid drylands (Table 1). In the present study, PCQ had the strongest effect on the arid flora in the Southern Andean Steppe, the only ecoregion within the NWA that receives more winter than summer rainfall (Table 1). However, PCQ has a negative effect on the species diversity of the native flora (Fig. 4a), which is interpreted as an artefact of our study caused by sampling bias in this ecoregion. As a consequence of the higher amount of winter rain, compared to summer precipitation, a floristic change occurs in the southern part of the Andean Steppe (Villagrán et al. 1983; Martínez-Carretero 1995). In the present study, we specifically sampled the monsoon regime flora and this flora disappears in regions where winter rain dominates over summer rain. In the Central Andean Dry Puna and the Central Andean Puna ecoregions where summer rain prevails, PWQ appears as the main diversity driver (Table 1). Moreover, it is the second most important diversity driver in the High Monte and in the Southern Andean Steppe ecoregions with a high influence on its flora (Table 1). An increment in the precipitation of the warmest quarter affects positively species diversity, indicating that summer rainfall always stimulates species richness (Fig. 4b). However, this increment stops when the precipitation reaches the maximum value received in the arid and semi-arid ecoregions (between 100 and 200 mm year<sup>-1</sup> depending on the ecoregion, Fig. 4b). In sites where the summer rainfall is higher than approx. 200 mm year<sup>-1</sup> the vegetation changes into southern Yungas forest or Chacoan shrubland both recognized as distinct biogeographic units (Fig. 4b). The dry adapted flora that was sampled in the present study enters these more humid ecoregions and the diversity peaks in the transition zone to these where after there is a conspicuous decline in diversity with raising PWQ (Fig. 4b). As the Southern Andean Yungas forest is recognized as one of the most species rich ecoregions in the Southern Cone (Cabrera 1976; Brown et al. 1993; Vides-Almonacid et al. 1998; Ibisch et al. 2003) this decline represent the transition into a flora that was not sampled here—composed of species restricted to dry sub-humid and humid climate.

According to our results, energy (expressed as PET) shifts its relative importance and its effect on the native flora of the arid and semi-arid ecoregions along with the elevation differences that exist between these ecoregions (Table 1; Fig. 4c). In the Southern Andean Steppe (3500–6000 m.a.s.l.) and in the Central Andean Dry Puna (3500–5500 m.a.s.l.) PET presented a weak influence on the flora (Table 1) but affects species richness positively (Fig. 4c). Although the two ecoregions are the most arid ones in the NWA region, an increase in PET does not impact the diversity negatively as is predicted by the water-energy hypothesis (Francis and Currie 2003; Kreft and Jetz 2007—Fig. 4c). The weak relationship between PET and diversity may be indicating that the flora of the Southern Andean Steppe and Central Andean Dry Puna is well adapted to low temperatures but is sensitive to water availability; as the slightest increase in summer rainfall generates a positive linear response in species richness (Fig. 4b). In the Central Andean Puna (3000–4500 m.a.s.l.) energy attained more importance but water still had a considerable effect on the flora (Table 1); which may indicate a transition towards a flora more dependent on energy input but still sensitive to the precipitation received. This pattern is consistent with the biogeographic scheme of Morrone (2006, 2014) who places the Puna in the American Transition Zone, where a transition between the Andean and Neotropical taxa occur. In contrast to the temperate drylands of China where water always had a stronger influence on plant species richness than energy (Li et al. 2013), in the tropical drylands of the southernmost Central Andes, energy input is as fundamental for plant diversity as water input is. According to our analyses, energy becomes the variable with highest effect on plant diversity at middle altitudes in the High Monte and in areas where

the native flora of the arid and semi-arid regions enter more humid ecoregions such as the Southern Andean Yungas and the Dry Chaco (Table 1). In these regions PET values above 1300 mm generated a decline in the species richness (Fig. 4c). Beyond this amount of energy, the native flora of the Central Andes drylands disappears to be replaced by the more tropical and humid adapted flora of the eastern Andes slopes and the Chaco lowlands.

## Conclusion

Our study contribute to the limited knowledge on plant species diversity patterns in the drylands of the Southern Cone, an understudied but outstanding region in terms of diversity and endemism. We indicate where are located the hotspots of dry adapted flora and, which environmental factors determine them. The knowledge on where hotspots are will help to develop better conservation strategies to create new protected areas systems or expand the existent reserves allowing a long term conservation of the flora of the region, rich in endemic species. We show which particular climate conditions of the southernmost Tropical Andes affects the regional dry adapted flora; water variables had the strongest effect on the flora in the arid high Andean ecoregions, while energy only became more important than water when the arid adapted flora entered the lower and semi-arid regions. Water has a positive effect on plant diversity, as increments in summer rainfall stimulated species numbers. Conversely, energy increments tend to reduce species diversity of the arid adapted flora. This knowledge would help predicting which areas will be most affected under different scenarios of future climate change and consequently developing more effective conservation strategies. We hope this study serve to promote quantitative studies on biodiversity patterns for other plant families and other megadiverse clades in the Tropical Andes, to improve our understanding of diversity gradients and, the role each potential diversity determinant has in such enigmatic regions as drylands.

## References

- Aagesen L, Bena MJ, Nomdedeu S, Panizza A, López R, Zuloaga F (2012) Areas of endemism in the Southern Central Andes. *Darwiniana* 50:218–251
- Anderson RP, Raza A (2010) The effect of the extent of the study region on GIS models of species geographic distributions and estimates of niche evolution: preliminary tests with montane rodents (genus *Nephelomys*) in Venezuela. *J Biogeogr* 37:1378–1393
- Barthlott W, Mutke J, Rafiqpoor MD, Kier G, Kreft H (2005) Global centres of vascular plant diversity. *Nova Acta Leopold* 92:61–83
- Bianchi AR, Yañez CE (1992) Las precipitaciones en el noroeste argentino. INTA, Salta
- Blach-Overgaard A, Svenning JC, Dransfield J, Greve M, Balslev H (2010) Determinants of palm species distributions across Africa: the relative roles of climate, non-climatic environmental factors, and spatial constraints. *Ecography* 33:380–391
- Bonkougou EG (2003) Biodiversity in the drylands: challenges and opportunities for conservation and sustainable use. Challenge Paper. The Global Drylands Initiative, UNDP Drylands Development Centre, Nairobi
- Boria RA, Olson LE, Goodman SM, Anderson RP (2014) Spatial filtering to reduce sampling bias can improve the performance of ecological niche models. *Ecol Model* 275:73–77
- Brown AD, Placci LG, Grau HR (1993) Ecología y diversidad de las selvas subtropicales de la Argentina. In: Goin F, Goñi F (eds) Elementos de política ambiental. H. Cámara de Diputados, Buenos Aires, pp 215–222
- Bucklin DN, Basille M, Benscoter AM, Brandt LA, Mazzotti FJ, Romañach SS et al (2015) Comparing species distribution models constructed with different subsets of environmental predictors. *Divers Distrib* 21:23–35

- Cabrera AL (1976) Regiones fitogeográficas argentinas. *Enciclopedia Argentina de Agricultura y Jardinería* 2:1–85
- Cabrera AL, Willink A (1973) *Biogeografía de América latina*. Monografía 13, Serie de Biología, Organización de Estados Americanos, Washington, DC
- Castellanos A (1944) Los tipos de vegetación de la Republica Argentina. *Monografías del Instituto de Estudios Geográficos*. Universidad Nacional de Tucumán 4:66–94
- CEPF Critical Ecosystem Partnership Fund (2015) *Ecosystem Profile Technical Summary Tropical Andes Biodiversity Hotspot*. NatureServe and EcoDecisión, p 53
- Crisp MD, Laffan S, Linder HP, Monro A (2001) Endemism in the Australian flora. *J Biogeogr* 28:183–198
- Distler T, Jorgensen PM, Graham A, Davidge G, Jimenez I (2009) Determinants and prediction of broad-scale plant richness across the Western Neotropics 1. *Ann Mo Bot Gard* 96:470–491
- Dore MH (2005) Climate change and changes in global precipitation patterns: what do we know? *Environ Int* 31:1167–1181
- Eiserhardt WL, BJORHOLM S, Svenning JC, Rangel TF, Balslev H (2011) Testing the water–energy theory on American palms (Arecaceae) using geographically weighted regression. *PLoS ONE* 6:e27027
- Elith J et al (2006) Novel methods improve prediction of species’ distributions from occurrence data. *Ecography* 29:129–151
- Elith J, Phillips SJ, Hastie T, Dudík M, Chee YE, Yates CJ (2011) A statistical explanation of MaxEnt for ecologists. *Divers Distrib* 17:43–57
- ESRI (2011) *ArcGIS desktop: release 10*. Environmental Systems Research Institute, CA
- Ezcurra E (2006) Natural history and evolution of the world’s deserts. In: Ezcurra E (ed) *Global deserts outlook*. UNEP, Copenhagen, pp 2–26
- FAO (1971) *Food and Agriculture Organization of the United Nations*. Mapa mundial de suelos. UNESCO, Paris 1971 ([www.fao.org](http://www.fao.org))
- Field R, Hawkins BA, Cornell HV, Currie DJ, Diniz-Filho JA, Guégan JF, Kaufman DM, Kerr JT, Mittelbach GG, Oberdorff T, O’Brien EM, Turner JRG (2009) Spatial species–richness gradients across scales: a meta-analysis. *J Biogeogr* 36:132–147
- Francis AP, Currie DJ (1998) Global patterns of tree species richness in moist forests: another look. *Oikos* 81:598–602
- Francis AP, Currie DJ (2003) A globally consistent richness: climate relationship for angiosperms. *Am Nat* 161:523–536
- Garreaud R, Vuille M, Clement AC (2003) The climate of the Altiplano: observed current conditions and mechanism of past changes. *Paleogeogr Palaeoclimatol Palaeoecol* 194:1–18
- Gaston K (2000) Global patterns in biodiversity. *Nature* 405:220–227
- Godoy-Bürki AC (2016) Efectos del cambio climático sobre especies de plantas vasculares del sur de los Andes Centrales: un estudio en el noroeste de Argentina (NOA). *Ecol Austral* 26:83–94
- Godoy-Bürki AC, Ortega-Baés P, Sajama J, Agesen L (2014) Conservation priorities in the Southern Central Andes: mismatch between endemism and diversity hotspots in the regional flora. *Biodivers Conserv* 23:81–107
- Gonzales JA (2009) Climatic change and other anthropogenic activities are affecting environmental services on the Argentina Northwest (ANW). *Earth Environ Sci* 6:1–2
- Graham CH, Elith J, Hijmans RJ, Guisan A, Townsend-Peterson A, Loisele BA (2008) The influence of spatial errors in species occurrence data used in distribution models. *J Appl Ecol* 45:239–247
- Grau RH, Gasparri IN, Aide MT (2005) Agriculture expansion and deforestation in seasonally dry forests of north-west Argentina. *Environ Conserv* 32:140–148
- Hauman-Merck L, Burkart A, Parodi LR, Cabrera AL (1947) La vegetación de la Republica Argentina. In: *Geografía de la Republica Argentina vol 8*, pp 5–349
- Hawkins BA et al (2003) Energy, water and broad scale geographic patterns of species richness. *Ecology* 84:3105–3117
- Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. *Int J Climatol* 25:1965–1978
- Holmberg EL (1898) La flora de la Republica Argentina. *Segundo Censo Rep Argent* 1895(1):385–474
- Hughes L (2003) Climate change and Australia: trends, projections and impacts. *Austral Ecol* 28:423–443
- Ibisch PL, Beck SG, Gerkmann B, Carretero A (2003) *Diversidad Biológica: Ecoregiones y ecosistemas*. In: Ibisch P, Merida G (eds) *Biodiversidad: La riqueza de Bolivia*. Editorial FAN, Santa Cruz de la Sierra, pp 73–75
- Izquierdo AE, Grau HR (2009) Agriculture adjustment, land-use transition and protected areas in North-western Argentina. *J Environ Manag* 90:858–865
- Jorgensen PM, Ulloa Ulloa C, León B et al (2011) Regional patterns of vascular plant diversity and endemism. In: Herzog SK, Martínez R, Jørgensen PM, Tiessen H (eds) *Climate change and*



- biodiversity in the tropical andes. Inter-American Institute for Global Change Research, São José dos Campos, pp 192–203
- Josse C et al (2003) Ecological systems of Latin America and the Caribbean: a working classification of terrestrial systems. NatureServe, Arlington
- Kessler M, Grytnes JA, Halloy SR et al (2011) Gradients of plant diversity: local patterns and processes. In: Herzog SK, Martínez R, Jørgensen PM, Tiessen H (eds) Climate change and biodiversity in the tropical andes. Inter-American Institute for Global Change Research, São José dos Campos, pp 204–219
- Kreft H, Jetz W (2007) Global patterns and determinants of vascular plant diversity. PNAS 104:5925–5930
- Kumar S, Stohlgren TJ (2009) Maxent modelling for predicting suitable habitat for threatened and endangered tree *Canacomyrica monticola* in New Caledonia. J Ecol Nat Environ 1:94–98
- Li L, Wang Z, Zerbe S, Abdusalih N, Tang Z, Ma M, Yin L, Mohammad A, Han W, Fang J (2013) Species richness patterns and water-energy dynamics in the Drylands of Northwest China. PLoS ONE 8:e66450
- Lorentz PG (1876) Cuadro de la vegetación de la Republica Argentina. In: Napp R (ed) La Republica Argentina, Buenos Aires, pp 77–136
- Luebert F, Weigend M (2014) Phylogenetic insights into Andean plant diversification. Front Ecol Evol 2:27
- Martínez-Carretero E (1995) La Puna Argentina: delimitación general y división en distritos florísticos. Bol Soc Argent Bot 31:27–40
- McFadden D (1979) Quantitative methods for analyzing travel behavior of individuals: some recent developments. In: Hensher DA, Stopher PR (eds) Behavioral Travel Modelling, Chapter 13. Groom Helm London, London, pp 279–318
- Montgomery DC, Peck EA, Vining GG (2012) Introduction to Linear Regression Analysis, 5th edn. Wiley, New York
- Morrone JJ (2006) Biogeographic areas and transition zones of Latin America and the Caribbean islands based on panbiogeographic and cladistic analyses of the entomofauna. Annu Rev Entomol 51:467–494
- Morrone JJ (2014) Biogeographical regionalization of the Neotropical region. Zootaxa 3782:1–110
- Moser D, Dullinger S, Englisch T et al (2005) Environmental determinants of vascular plant species richness in the Austrian Alps. J Biogeogr 32:1117–1127
- Myers N, Mittermeier RA, Mittermeier CG, Da Fonseca GBA, Kent J (2000) Biodiversity hotspots for conservation priorities. Nature 403:853–858
- Olson DM, Dinerstein E, Wikramanayake ED et al (2001) Terrestrial ecoregions of the World: a new map of life on Earth. BioSci 51:933–938
- Parodi LR (1945) Las regiones fitogeográficas argentinas y sus relaciones con la industria forestal. In: Verdoorn F (ed) Plants and plant science in Latin America. Chronica Botanica Company, Waltham, pp 127–132
- Pearson RG, Raxworthy CJ, Nakamura M, Peterson AT (2007) Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. J Biogeogr 34:102–117
- Peet R (1974) The measurement of species diversity. Annu Rev Ecol Syst 5:285–307
- Pernetta AP (2014) Conserving dryland biodiversity. Biodiversity 15(2-3):237–238
- Phillips S, Dudík M (2008) Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. Ecography 31:161–175
- Phillips S, Anderson R, Schapire R (2006) Maximum entropy modeling of species geographic distributions. Ecol Model 190:231–259
- Pinheiro J, Bates D, DebRoy S, Sarkar D, Team RC (2012) nlme: linear and nonlinear mixed effects models. R package version 3, 103. <http://CRAN.R-project.org/package=nlme>
- Radosavljevic A, Anderson RP (2014) Making better Maxent models of species distributions: complexity, overfitting and evaluation. J Biogeogr 41:629–643
- Ribichich AM (2002) El modelo clásico de la fitogeografía de Argentina: un análisis crítico. Interciencia 27:669–675
- Ricklefs RE, Latham RE, Qian H (1999) Global patterns of tree species richness in moist forests: distinguishing ecological influences and historical contingency. Oikos 86:369–373
- Roig FA, Roig-Juñent S, Corbalán V (2009) Biogeography of the Monte Desert. J Arid Environ 73:164–172
- Safriel U, Adeel Z (2005) Dryland systems. In: Hassan R, Scholes R, Ash N (eds) Ecosystems and human well-being, current state and trends, vol 1. Island Press, Washington, pp 625–658
- Shcheglovitova M, Anderson RP (2013) Estimating optimal complexity for ecological niche models: a jackknife approach for species with small sample sizes. Ecol Model 269:9–17
- Stein A, Gerstner K, Kreft H (2014) Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. Ecol Lett 17:866–880
- Trabucco A, Zomer RJ (2009) Global aridity index (global-aridity) and global potential evapo-transpiration (Global-PET) Geospatial Database. CGIAR

- UNEP (2006) Don't desert drylands! Facts about deserts and desertification. [www.unep.org](http://www.unep.org)
- Versieux LM, Wendt T (2007) Bromeliaceae diversity and conservation in Minas Gerais state, Brazil. *Biodivers Conserv* 16:2989–3009
- Vides-Almonacid R, Ayarde H, Scrocchi GJ, Romero F, Boero C, Chani JM (1998) Biodiversidad de Tucumán y el Noroeste Argentino. *Opera Lilloana*, pp 43–89
- Villagrán C, Arroyo MK, Marticorena C (1983) Efectos de la desertización en la distribución de la flora andina de Chile. *Rev Chil Hist Nat* 56:137–157
- Whittaker RJ, Nogués-Bravo D, Araújo MB et al (2007) Geographical gradients of species richness: a test of the water-energy conjecture of Hawkins (2003) using European data for five taxa. *Glob Ecol Biogeogr* 16:76–89
- Wieczorek J, Guo Q, Hijmans RJ (2004) The point-radius method for georeferencing locality descriptions and calculation associated uncertainty. *Int J Geogr Inf Sci* 18:745–767
- Wisn MS, Hijmans RJ, Li J, Peterson AT, Graham CH, Guisan A (2008) Effects of sample size on the performance of species distribution models. *Divers Distrib* 14:763–773
- Young KR, Ulloa Ulloa C, Luteyn JL, Knapp S (2002) Plant evolution and endemism in Andean South America: an introduction. *Bot Rev* 68:4–21
- Zuloaga FO, Morrone O, Rodríguez D (1999) Análisis de la biodiversidad en plantas vasculares de la Argentina. *Kurtziana* 27:17–167
- Zuloaga FO, Morrone O, Belgrano MJ (2008) Catálogo de las Plantas Vasculares del Cono Sur. *Monogr Syst Bot Mo Bot Gard* 107:609–967. (<http://www2.darwin.edu.ar>)
- Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) *Mixed effects models and extensions in ecology with R*. Springer, New York, p 574