



## Regional-scale vegetation heterogeneity in northeastern Patagonia: Environmental and spatial components

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**Abstract:** Our aim was to describe vegetation heterogeneity at a regional scale in northeastern Patagonia and to identify the environmental variables associated to it. The study area encompasses 13 144 km<sup>2</sup> and is characterized by a mixture of species typical of Patagonian steppes and Monte Desert. We performed 48 vegetation relevés, which were randomly assigned to a training set and to a validation set (32 and 16 relevés, respectively). Training set was subjected to cluster analysis, which allowed the identification of two plant communities one related to Patagonian steppes and another to the Monte desert. We derived 3 attributes of the seasonal curve of the NDVI as indicators of ecosystem function: the seasonal amplitude (SA), the date of the maximum (DOM), and the large seasonal integral (LSI). We explored the relationship between NDVI attributes and communities by classification tree analysis. LSI was the strongest predictor among NDVI attributes, separating both communities without misclassification errors. Patagonian steppes occupy areas with higher LSI. The partial RDA analysis explained 38.1% of total data variation, of which 16.5% was ascribed to environment, 7.9% to space, and 13.7% to spatial component of environment. Patagonian steppes are closer to the coast, in areas exhibiting higher annual precipitation and lower annual temperature range than Monte deserts. Our results indicate the occurrence of two plant communities in the study area and highlight the significance of climatic variables to explain their spatial distribution. As most scenarios of future climate predict greater annual thermal amplitude in the study area, the limit between both communities could be displaced eastward.

**Abbreviations:** CT–Classification Tree; DEM–Digital Elevation Model; DOM–Date Of Maximum NDVI; IV–Indicator Value; LSI–Large Seasonal Integral of NDVI; MAT–Mean Annual Temperature; NDVI–Normalized Difference Vegetation Index; PCNM–Principal Coordinates of Neighbor Matrices; PPT–Precipitation; RDA–Redundancy Analysis; SA–Seasonal NDVI Amplitude; TEMP–Temperature.

**Nomenclature:** Flora Argentina (<http://www.floraargentina.edu.ar>).

### Introduction

Vegetation is heterogeneous at a wide range of spatial scales varying from microsite to region (Crawley and Harral 2001). Biotic and abiotic factors were identified as important sources of this heterogeneity. In general, it is accepted that biotic factors are relevant at high detailed scales (i.e., microsite, patch) whereas abiotic factors had increasing importance at landscape or regional scale (Reynolds and Wu 1999).

A hidden spatial structure can cause problems in the statistical detection of significant vegetation-environment relationships, since the use of classical statistical methods may be invalidated if there is a strong spatial structure in the data (Heikkinen and Birks 1996). In addition, it is becoming increasingly evident that environmental factors and vegetation heterogeneity are scale dependent, and consequently the explicit consideration of multiple spatial scales in the analysis could be helpful (Dray et al. 2012).

Vegetation heterogeneity has been studied in northeastern Patagonia by different authors, but these studies were restricted to microsite, patch, and patch mosaic scales (e.g., Bisigato

and Bertiller 1997, 2004, Ares et al. 2003, Kröpfl et al. 2007). These studies highlighted that biotic (facilitation, competition) and abiotic (water redistribution) factors play an important role in generating these patterns. In contrast, studies at landscape or regional scale are lacking (Bisigato et al. 2009).

Vegetation in extra-andean Patagonia belongs to two different Phytogeographic Provinces: Monte and Patagonia. Shrublands characteristic of the Monte Province are dominated by species of the genus *Larrea*, whereas Patagonian Province is characterized by grass steppes, shrub steppes and semi-deserts (León et al. 1998). At a country scale, the Monte Province occupies areas with mean annual temperature higher than 12°C (Labraga and Villalba 2009), annual precipitation lower than 250 mm (León et al. 1998), concentrated in summer or evenly distributed along the year. In contrast, the Patagonian Province occupies areas exhibiting mean annual temperature lower than 12°C, and an annual precipitation that varies between 150 and 500 mm and it is concentrated in winter months (Páruelo et al. 1998).

Although abiotic factors were associated to the distribution of both Phytogeographic Provinces at a country-level

scale, different authors did not agree in the location of the boundary between them (Morello, 1958) and other authors have proposed the existence of a more or less extended ecotone (León et al. 1998, Abraham et al. 2009). This discrepancy among authors is particularly notorious in the northeastern Chubut province.

In this article we evaluate vegetation heterogeneity in a 13 144 km<sup>2</sup> area located in northeastern Chubut province, Argentina. The landscape is characterized by plateaus with elevations ranging from 50 to 130 m a.s.l. (Beeskow et al. 1987). The geological substratum from which soils have developed is gravelly sand to sandy clay alluvial stratum of which the thickness ranges between 50 and 100 cm. This deposit of Holocene age rests on the Plio-Pleistocene formation locally known as ‘Patagonian Gravel’ (Fidalgo and Riggi 1970, Haller et al. 2005). Climate is arid with annual precipitation lower than 250 mm and mean temperature ranging between 12.5 and 13.6 °C depending on relief and distance from the ocean (Coronato 1994, Palacio et al. 2014). Vegetation physiognomy in the area is characterized by shrub steppes with low plant cover and variable species composition (Beeskow et al. 1987). Some authors have considered that the study area is entirely within the Monte Province (e.g., Soriano 1950, Morello 1958, Rundel et al. 2007, Villagra et al. 2009) while other authors have proposed that the limit between both Provinces crosses the study area (Abraham et al. 2009, Carrera et al. 2009). So, we aimed to: a) describe the vegetation heterogeneity at a regional scale, b) delimit both Phytogeographic Provinces more accurately, and c) identify the role of environmental and spatial variables obtained from coordinates in explaining the species composition patterns.

## Materials and methods

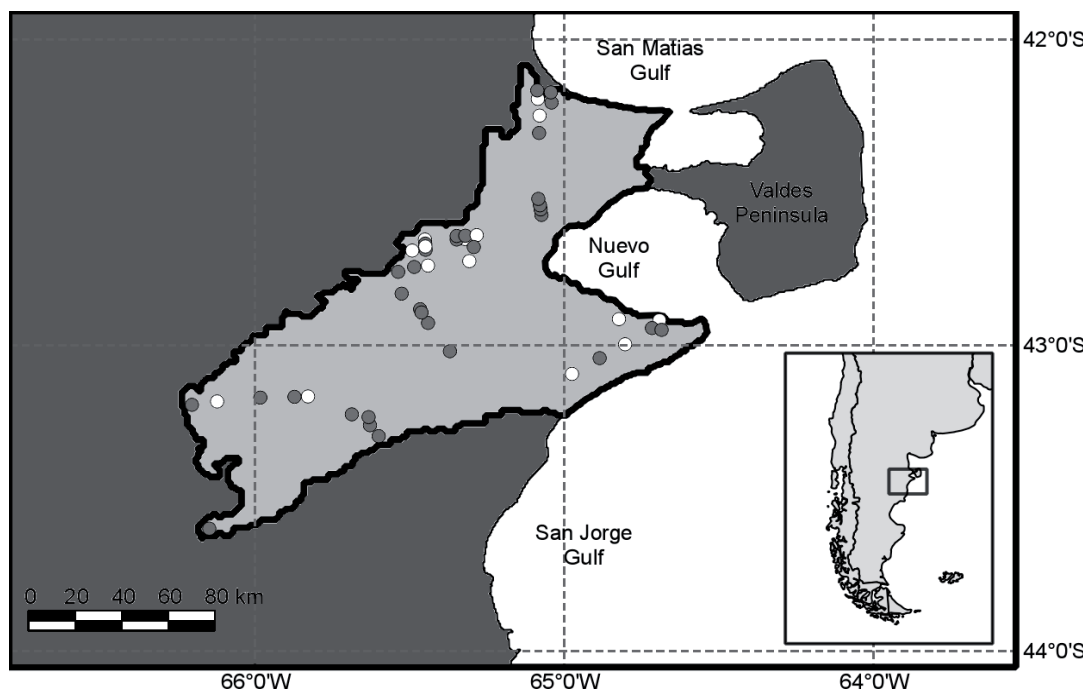
### *Vegetation surveys*

Vegetation was sampled in forty-eight 1 ha sites (Fig. 1) using the Braun-Blanquet relevé method (Mueller-Dombois and Ellenberg 1974). We decided to use that plot size because many species in the study area have clumped distributions at small scales (i.e., a few meters). As a consequence of that, the employment of smaller areas or transects would conduct to biased estimations of plant species cover. Moreover, as environmental data were available at spatial resolution of 1 × 1 km<sup>2</sup> (see below), the choice of smaller areas for vegetation surveys could conduct to a big discrepancy between the scales at which vegetation and environmental information were collected.

Sampling sites were selected on the basis of their representativeness, accessibility and avoiding highly disturbed areas. Grazing is the most important anthropogenic disturbance in the area (Bisigato and Bertiller 1997), so heavily grazed areas near artificial water points were avoided during sampling. Wild fires are the commonest natural disturbance in the area but, as they represent different successional stages, recently burned areas were excluded from the analysis. All sites are grazed with the usual stocking rate in the area (about 0.1–0.2 sheep ha<sup>-1</sup> throughout the year).

### *Ecosystem function*

We used the 16-day composite MODIS NDVI dataset at a 250-m resolution, spanning the period from 2000 to 2010 (the



**Figure 1.** Locations of 48 sampling points in the study area. Training and evaluation sets are indicated by gray and white points, respectively.

MOD13Q1 product, Huete et al. 2002). We derived 3 attributes of the seasonal curve of the NDVI, which are related to ecosystem function: 1) the difference between the maximum and minimum NDVI through the year (Seasonal Amplitude, SA), 2) the Date Of the Maximum NDVI (DOM), and 3) the Large Seasonal Integral (LSI), i.e., the integral of the function describing the NDVI variation from the beginning to the end of the season. To obtain these attributes we estimated the start and the end of season using the Midpoint pixel method as described by White et al. (2009). We also calculated mean annual NDVI (NDVI) as a proxy of ANPP (aboveground net primary production).

#### *Environmental data*

Since climate and altitude have a strong influence on the distribution of plant communities at a regional scale (e.g., Baruch 2005, Bergamin et al. 2012), we included climatic and topographic variables in the analysis. We considered the following climatic variables: 1) mean monthly temperature (TEMP\_(month)); 2) mean annual temperature (MAT), both of them were taken from World-Clim (<http://www.worldclim.org/>, Hijmans et al. 2005); 3) Mean annual precipitation (PPT) was estimated by kriging values of De Fina (1978) which included 59 weather stations in and around the study area (mainly private ranches). We decided to employ De Fina's database instead of World-Clim precipitation data because of some inconsistencies detected in the later referred to the study area. Topographic variables (i.e., elevation, slope, and aspect) were derived from a 90 m resolution Digital Elevation Model (DEM) from the Shuttle Radar Topography Mission (SRTM; <http://dds.cr.usgs.gov/srtm/>). All data were incorporated into a GIS database (GRASS-GIS), reprojected into UTM Zone 20 South coordinates system and resampled to 1 km x 1 km pixels using a cubic convolution resampling algorithm to minimize the loss of spatial accuracy of the data.

#### *Statistical analyses*

Vegetation relevés were randomly assigned to two groups: a training set (n=32) and an evaluation set (n=16). To identify plant communities, the training set was subjected to a hierarchical cluster analysis using the Ward group linkage method. We used 'pvclust', a R package which automatically computes *p*-values for all clusters contained in the clustering of original data using multiscale bootstrap resampling and identifies the clusters strongly supported by data (Suzuki and Shimodairo 2011). Indicator species analysis (Dufrène and Legendre 1997) was used to find the indicator species of each cluster (community). The indicator values of the species were calculated using the function 'indval' in the R-package 'labdsv' (Roberts 2013). We also calculated mean specific cover, richness (S) and evenness (J') of each community (cluster). Evenness was calculated from

$$J' = H' / H'_{\max}$$

where  $H'$  = Shannon-Wiener index and  $H'_{\max}$  = maximum value of  $H'$ , equal to  $\ln(S)$ .

Differences among communities in mean annual NDVI were evaluated comparing the averages of annual NDVI of the sampling sites belonging to each community by one way ANOVA.

We used classification tree analysis (CT) to explore the relationship between NDVI attributes and the plant communities identified by cluster analysis. The classification tree algorithm works by a recursive binary partition of the data space into increasingly homogenous regions (Breiman et al. 1984). Applied to a categorical response variable (communities in our case), the objective of a classification tree is to separate the samples such that each node of a treelike diagram encompasses only one group type. We performed the CT with the 'rpart' package (Therneau and Atkinson 2010), which is the R implementation of CT, using a different class code for every plant community identified by cluster analysis (see above). Only vegetation relevés belonging to the training set were included.

Vegetation relevés belonging to the evaluation set were assigned to the communities identified by Cluster analysis on the basis of their similarity to the mean species plant cover in every community. We also assigned every vegetation relevé to a plant community on the basis of its NDVI attributes and the best classification tree, and evaluated the agreement between both categorizations (based on plant cover or NDVI).

In order to assess the contribution of environmental (i.e., climate and topography) and spatial variables to the vegetation heterogeneity at a regional scale, we used partial canonical redundancy analysis (partial RDA) (Borcard et al. 1992), using the package 'vegan' (Oksanen et al. 2013) of the R language (R Development Core Team). Prior to analysis, all rare species (i.e., species present in only a relevé) were removed from the analysis (Bergamin et al. 2012), and the remainder data were Hellinger-transformed (Legendre and Gallagher 2001). This transformation reduces the weight of the most abundant species in the analysis. Partial RDA analysis allows the variation partition into two or more sets of variables (Legendre and Legendre 1998, Borcard et al. 2011). In our case, it was possible to differentiate four components of variation of species composition: [a] pure environmental, [b] spatial component of environmental influence, [c] pure spatial and [d] undetermined (Borcard et al. 1992). We used the principal coordinates of neighbor matrices (PCNM) method to introduce space as an explanatory variable in the analysis (Borcard and Legendre 2002). As the PCNM method has been found to be best applied to detrended data (Borcard et al. 2004), before the PCNM analysis plant cover matrix was detrended by regressing it on the X-Y coordinates and retaining the residuals. By using this method complex spatial patterns can be modeled at different spatial scales (Jones et al. 2008). We computed PCNM variables with the 'PCNM' package (Legendre et al. 2013) of R language and used the 'packfor' package ( $\alpha = 0.05$ , 9999 random permutations) to select the best environmental and PCNM functions by forward selection (Dray et al. 2013). The selected variables were used as explanatory variables in the variation partitioning of the species composition data. We tested the significance of the spatial and environmental fractions by means of 199

permutations using the function `anova.cca` in the above mentioned ‘vegan’ package. After that, a RDA diagram was used to visualize the relations between explanatory variables and species composition across plant communities. RDA analysis was carried out using the function ‘`rda`’ in the ‘vegan’ package in R (Oksanen et al. 2013).

**Results**

*Plant communities*

A total of 40 species were recorded in the 32 surveys belonging to the training set (supplementary material, Table S1). Cluster analysis allowed the identification of two plant communities (Fig. 2; supplementary material, Table S1). The first community included 23 surveys, and its indicator species were *Pappostipa speciosa* (IV = 0.76), *Atriplex lampa* (IV = 0.73), *Chuquiraga erinacea* spp. *hystrix* (IV= 0.71), *Bougainvillea spinosa* (IV = 0.68) and *Nassauvia fuegiana* (IV = 0.61). The second community contained 9 surveys, and its indicator species were *Chuquiraga avellanadae* (IV = 0.92), *Condalia microphylla* (IV = 0.66), *Stipa tenuis* (IV = 0.60) and *Elymus* spp. (IV = 0.37). The first community

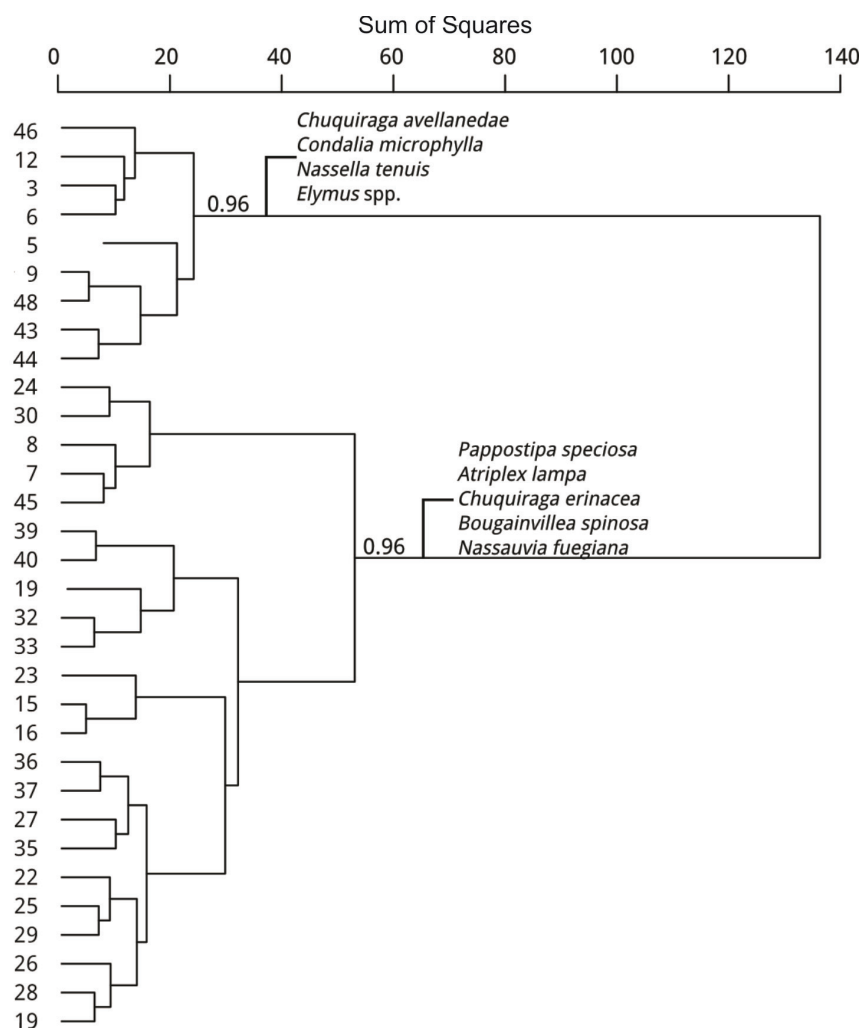
is related to the Monte desert, whereas the second is associated to Patagonian steppes. Plant communities did not differ in species richness ( $F_{1,30}=2.2, P>0.05, n=32$ , supplementary material Table S1), but the Monte desert community showed lower plant cover and higher evenness than the Patagonian steppe community ( $F_{1,30}=7.7, P<0.009, n=32$  and  $F_{1,30}=17.7, P<0.001, n=32$ , respectively; supplementary material Table S1).

*Plant productivity*

Mean annual NDVI was higher in the Patagonian steppe community ( $F_{1,30}=73.9, P<0.001, n=32$ ). A closer inspection of NDVI values of pixels containing the training set showed that mean NDVI ranges did not overlap (0.157-0.233 and 0.236-0.299 for Monte desert community and Patagonian steppe community, respectively).

*Classification tree*

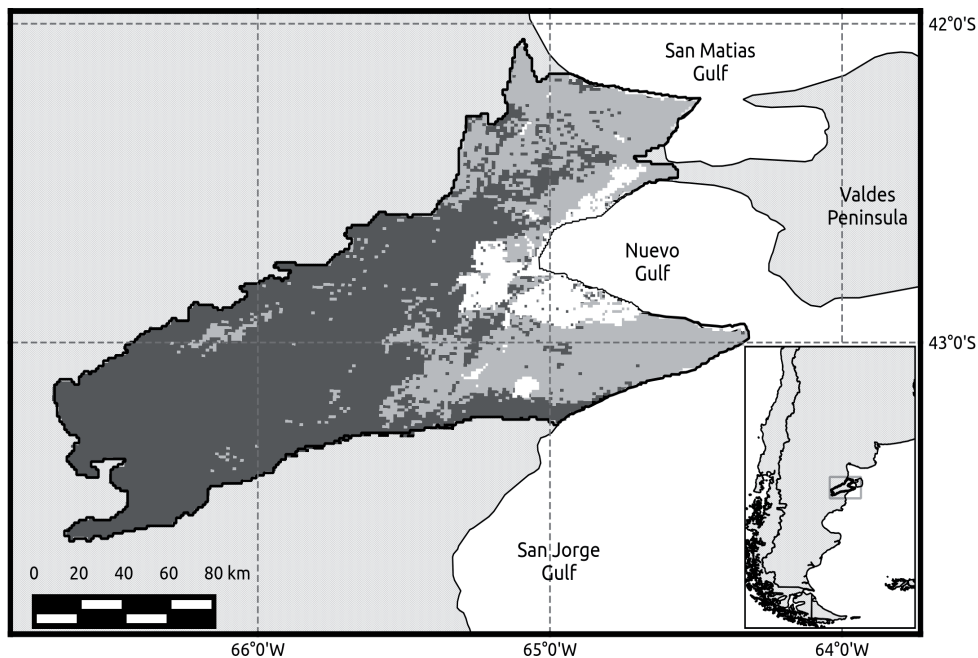
The classification tree indicated that LSI was the strongest predictor among NDVI attributes, separating the Monte desert community from the Patagonian steppe community at



**Figure 2.** Ward clustering of the vegetation relevés. Dufrière-Legendre indicator species of each cluster are indicated. Values near the edges are *p*-values after 1000 replicates (values higher than 0.95 are significant).

**Table 1.** Results of variation partitioning (partial RDA) according to environmental and spatial variables on plant species composition of 48 sites in the study area. Environmental variables used to compute fraction [a+b]: DFC, PPT, TEMP\_3, TEMP\_9, TEMP\_11 and TEMP\_RANGE. Spatial variables used to compute spatial fraction [b+c]: PCNM1, 4, 5, 6, and 10. P-values were obtained after 199 permutations.

Partial RDA fractions	Adjusted R <sup>2</sup>	Pseudo <i>F</i>	P
[a+b] = Environmental	0.302	4.39	0.005
[b+c] = Spatial	0.216	3.58	0.005
[a+b+c] = Environmental + Spatial	0.381	3.63	0.005
[a] = Pure environmental	0.165	2.86	0.005
[b] = Environmental Spatially Structured	0.137		
[c] = Pure spatial	0.079	2.05	0.005
[d] = Unexplained	0.619		



**Figure 3.** Spatial distribution of plant communities extrapolating the results of the classification tree to the whole area. White areas indicate wildfires (which were excluded from the analysis), light grey indicates Patagonian steppe and dark grey Monte desert.

a LSI value of 2.5316. Since this model perfectly separates both communities (i.e., misclassification errors were 0), additional NDVI attributes were ignored. When the results of the classification tree were extrapolated to the whole area both communities were spatially segregated: the Monte desert occupies the western part of the study area whereas the Patagonian steppe is found in the east (Fig. 3).

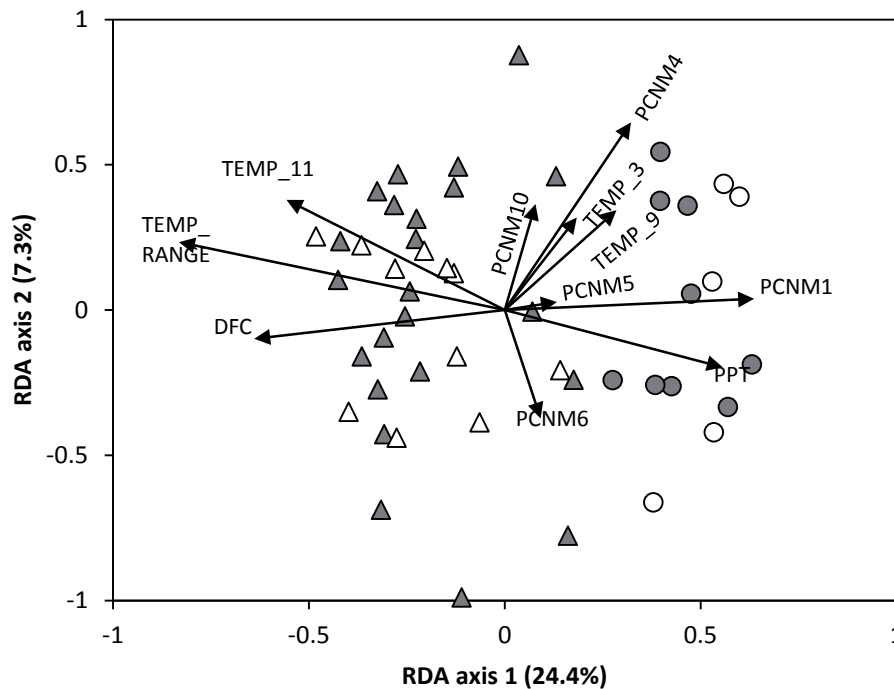
#### Model validation

When censuses belonging to the evaluation set were assigned to both plant communities on the basis of their species cover and on the basis of the extrapolation of the classifica-

tion tree, a perfect match between both classifications was found. This validates our results and the classification map (Fig. 3).

#### Variation partitioning of plant species composition

PCNM analysis generated 26 PCNM axes, but only 10 showed positive eigenvalues and were consequently retained. The environmental variables that were selected by the forward selection that exhibited the best relationship with the species composition were DFC, PPT, TEMP\_RANGE, TEMP\_3, TEMP\_9 and TEMP\_11. Five large scale PCNM axes were also selected: PCNM 1, 4, 5, 6 and 10. The partial



**Figure 4.** Redundancy analysis (RDA) of the 48 vegetation relevés. The percentage of the variance explained by each axis is indicated in parenthesis. Circles indicate the Patagonian steppe sites and triangles the Monte Desert sites. Filled symbols indicate the training set and empty symbols the evaluation set. Significant environmental and spatial variables are shown by arrows.

RDA explained 38.1% of total data variation, of which 16.5% was ascribed to environment, 7.9% to space, 13.7% to spatial component of environment, and 61.9% remained undetermined (Table 1). These results indicate that a relatively high proportion of variation explained by environment could not be separated from space.

The main pattern found by the RDA shows a gradient along the first axis associated to some environmental (DFC, TEMP\_11, PPT, and TEMP\_RANGE) and spatial (PCNM1) variables (Fig. 4). On the right side of this axis are the Patagonian steppe sites which are near the coast and are associated to higher PPT, and to lower TEMP\_RANGE and TEMP\_11. All Monte desert sites have low scores on the first axis ( $< 0.18$ ). Except for PCNM1, all PCNM variables and TEMP\_3 and TEMP\_9 were mostly related to RDA2 and consequently they did not explain differences between communities. The importance of the component [b] in the variance partitioning can be appreciated in the diagram since most of PCMNs coincides with environmental variables.

## Discussion

Our results indicated the existence of two plant communities in the study area, phytogeographically related to the Monte desert and the Patagonian steppe, as described by Beeskow et al. (1995) and Bisigato and Bertiller (1997). At a regional scale, both communities are spatially segregated, occupying the western and the eastern section of the study area, respectively (Fig. 3). This result agrees with those authors who proposed that the limit between the two Phytogeographic provinces crosses the study area, particularly with Abraham et al. (2009). However, our results indicate that the limit is displaced towards the west, in a way that the northeastern extreme of the study area (i.e., west from the Valdes peninsula) is more related to Patagonian steppes than to the Monte

desert. The Patagonian steppe community identified in our study is closely related to the dominant plant community in Valdes peninsula (Catorci et al. 2012).

In both communities, indicator species (supplementary material, Table S1) were among the commonest species and included species that belong to different life forms and exhibit contrasting palatability. In the case of the Patagonian steppe, indicator species encompassed an evergreen shrub (*C. avellanadae*), a deciduous shrub (*C. microphylla*) and a perennial grass (*N. tenuis*). On the other hand, indicator species of the Monte desert community included two evergreen shrubs (*A. lampa* and *C. erinacea* ssp. *hystrix*), a deciduous shrub (*B. spinosa*), a dwarf shrub (*N. fuegiana*) and a perennial grass (*P. speciosa*). It should be mentioned here that *A. lampa* is the unique species exhibiting the C<sub>4</sub> photosynthetic pathway (Frayssinet et al. 2007) found in this study, and therefore it is more common in the warm Monte desert than in the cold Patagonian steppe. Likewise, *B. spinosa* was identified by several authors (e.g., Morello 1958) as one species typical of the Monte desert. In general, palatability is low among these species with the exception of *N. tenuis* (Catorci et al. 2012). Most of above mentioned shrubs are spiny and *A. lampa* leaves contain high salt content what reduces their palatability (Fernández et al. 1999).

When examining the relationships between species composition and environmental and spatial variables it is clear that they are intercorrelated and that the comprehension of their relative importance in determining floristic composition is not easy. The overlap between environment and space can be interpreted as an historical-environment factor influencing the current vegetation distribution. A relatively high proportion of floristic variation (61.9%) was not related to the spatial and environmental variables included in our analysis. This variation can be attributed to random processes (such as dispersal and mortality) but also to unmeasured environmen-

tal variables such as soil attributes and/or land use (Bergamin et al. 2012). However, it is worth to mention that comparable studies carried out in other deserts around the world exhibit similar ranges of unexplained variation. For example, Lu et al. (2006) evaluated the influence of environmental and spatial variables on shrub and herb cover in China and found that unexplained variation varied between 52% and 73%. Similarly, Maestre et al. (2003) found that between 26% and 67% of variation in seedling distribution remain unexplained after considering environmental and spatial influences. Likewise, Speziale et al. (2009) and Pan et al. (1998) found that environmental and spatial variables only explained half of variation in species richness and plant cover in northwestern Patagonia and China, respectively.

The explicit consideration of space in our analysis highlighted the fact that almost half of environmental variation (a+b in Table 1) is indistinguishable from spatial variation (b+c). It is not surprising, since almost all the climatic and topographic variables incorporated in the analysis (with the exception of aspect) have a strong spatial dependence. We included space into the analysis by means of PCNM analysis. This analysis identified 5 large-scale PCNM axes significantly correlated with species composition. The fact that fine scale PCNM axes were not significant could be consequence of our irregular sampling scheme, which reduces the ability to find fine-scale spatial structures (Lacey et al. 2007). Beyond that, the variation partitioning emphasizes the importance of considering space when environmental data are suspected of having a strong spatial structure (Dray et al. 2012).

Our results also suggest that the Patagonian steppe community is more productive than the Monte desert community (i.e., it exhibits higher mean annual NDVI). Coincidentally, ranches located near the coast are the most productive across the study area, supporting stocking rates as high as twice those of the ranches located at the western area (Dirección General de Estadísticas y Censos – Provincia del Chubut 2012). Likewise, most wild fires occurred in this area (Fig. 3) indicating that fuel biomass, especially fine fuel, is higher allowing fire dispersion (Rostagno et al. 2006). Accordingly, the RDA results show that the Patagonian steppe sites occupy areas with higher annual precipitation (PPT). Unexpectedly, mean annual temperature was not related to vegetation heterogeneity. These results contrast with previous studies which highlight the importance of temperature as an environmental variable controlling the limits of the Monte desert at a country-level scale (Labraga and Villalba 2009). The discrepancy between our results and that of Labraga and Villalba (2009) could stem in part from the inclusion of a greater spatial extent in the above mentioned article, which implies wider ranges of variation in climatic and topographic variables. Likewise, our study incorporates detailed climatic information instead of annual means (i.e., monthly mean TEMP) allowing the identification of significant relationships with specific periods of the year.

Although our analysis is among the most comprehensive for northeastern Patagonia so far, there are some limitations in the data that may have influenced our results. One of the most important is that surveys are concentrated in some ranches, in

which we were allowed to sample. However, by taking into consideration spatial autocorrelation in our analysis we think that our results lack of biases due to spatial distribution of sampling points. Another problem with our data is related to a mismatch between the spatial scale of the surveys (1 ha) and the environmental variables ( $1 \times 1$  km<sup>2</sup> grid). Nevertheless, as we carefully selected the sites on the basis of their representativeness, we believe that this problem is not so serious. Finally, it should be recognized here that we were unable to include in the analysis other detailed climatic (e.g., monthly precipitation), edaphic (e.g., soil texture, soil water retention, etc.), and land use variables (e.g., grazing pressure), because they are unavailable. However, previous studies showed that these variables can also affect the distribution of plant communities as found in other areas arid ecosystems around the world (e.g., Pan et al. 1998, Zhang et al. 2006, Hegazy et al. 2007, Catorci et al. 2014).

Our results suggest that the limit between the two Phytogeographic Provinces could be displaced towards the East as a consequence of ongoing climate change. Estimates of global climate models predict greater annual thermal amplitude in northeastern Patagonia, owing to a larger warming in summer than in winter (Labraga and Villalba 2009). Since the Patagonian steppe community occupies areas exhibiting lower spring temperature (TEMP\_11) and lower TEMP\_RANGE, we speculate that many of the areas covered by this community could be colonized by species characteristics of the Monte desert during the next century.

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## Electronic Appendix

**Table S1.** Specific and total plant cover (%), richness and evenness at the Patagonian steppe community and at the Monte desert community in the training set.

The file may be downloaded from [www.akademaii.com](http://www.akademaii.com).