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ORIGINAL PAPER

The relative importance of soil properties and regional climate as drivers of productivity in southern Patagonia's *Nothofagus antarctica* forests

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Abstract

• ***Key message*** **Soil texture and temperature-related variables were the variables that most contributed to *Nothofagus antarctica* forest height in southern Patagonia. This information may be useful for improving forest management, for instance related to the establishment of silvopastoral systems or selection of suitable sites for forest reforestation in southern Patagonia.**

• ***Context*** Changes in forest productivity result from a combination of climate, topography, and soil properties.

• ***Aims*** The relative importance of edaphic and climatic variables as drivers of productivity in *Nothofagus antarctica* forests of southern Patagonia, Argentina, was evaluated.

• ***Methods*** A total of 48 mature stands of *N. antarctica* were selected. For each study site, we measured the height of three mature dominant trees, as an indicator of productivity. Seven soil, five spatial, and 19 climatic features were determined and related to

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Contribution of the co-authors

Héctor A. Bahamonde contributed with field sampling, analyzing the results, writing the main manuscript, and revising it.

Guillermo Martínez Pastur contributed with the field sampling and revision of the manuscript.

María V. Lencinas contributed with the data analysis and the revision of the manuscript.

Rosina Soler contributed with the field sampling and the revision of the manuscript.

Yamina M. Rosas contributed with the field sampling planning and the soil analysis.

Brenton Ladd contributed with the data analysis, the revision of the manuscript, and the thorough revision of the English.

Sandra Duarte Guardia contributed with the field sampling planning and the data analysis.

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forest productivity. Through partial least squares regression analyses, we obtained a model that was an effective predictor of height of mature dominant trees in the regional data set presented here.
• ***Results*** The four variables that most contributed to the predictive power of the model were altitude, temperature annual range, soil texture, and temperature seasonality.
• ***Conclusion*** The information gathered in this study suggested that the incidence of the soil and temperature-related variables on the height of dominant trees, at the regionally evaluated scale, was higher than the effect of water-related variables.

Keywords Carbon sequestration · Native forest · *Nothofagus antarctica* · ñire · South America · Trees

1 Introduction

Forest site quality is influenced by an array of factors, including climate, topography, and soil properties that determine forest productivity (Skovsgaard and Vanklay 2008). Related to this, Schoenholtz et al. (2000) examined the use of physical and chemical characteristics of soils as indicators of forest site quality, and determined that the most common variables to assess forest soil quality are organic matter, total N, available P, pH, texture, and soil depth. *Nothofagus* forests of southern Patagonia are the southernmost broadleaf woodlands of the world, being the deciduous *N. antarctica* (G. Forster) Oerst. (ñire) which occupies a broad variety of environmental conditions, from temporarily flooded soils to drier sites on the boundary with the Patagonian steppe (Veblen et al. 1996). *N. antarctica*'s natural distribution is the broadest of the South American *Nothofagus* species and ranges from 36° 30′ to 56° 00′ SL and from 0 to 2000 m a.s.l. (Donoso et al. 2006). In Argentina, it covers about 750,000 ha (SAyDS 2005), 60% of which are located in the southern part of its distribution area (i.e., Santa Cruz and Tierra del Fuego Provinces) (Peri et al. 2016). Unfortunately, the existing information on the genetic diversity of this broadly distributed species is still scarce. However, in a broad study about phylogenetic analyses of five species of the subgenus *Nothofagus*, including samples of *N. antarctica* from all its distribution, Premoli et al. (2012) reported a major latitudinal divergence among chloroplast lineages within subgenus *Nothofagus* that dates back to the Early Oligocene and at least no younger than the Middle Miocene. Particularly, in the case of *N. antarctica*, the authors found that populations located in southern Patagonia, including Santa Cruz (in the mainland) and Tierra del Fuego (Island) provinces, belong to the same lineage, which was different to that of northern Patagonia populations. Similarly, in a recent study where *N. antarctica* seedlings from four provenances (including Santa Cruz and Tierra del Fuego) were compared in a common garden experiment, Bahamonde et al. (2017) found that all provenances had a similar physiological performance which suggests that environmental conditions may be the main driver for phenotypic differences in this species. Also, Premoli et al. (2012) indicated that *N. antarctica* was sister to a clade of evergreen species (*N. betuloides*, *N. dombeyi*, *and N. nitida*).

N. antarctica forest productivity has been characterized through site quality index equations (Ivancich et al. 2011), which proposed a classification with five site classes (SC), where best site class stands present dominant tree height up to 14 m (SC1), whereas the poor site class (SC5) was represented by stands with mature dominant trees 8 m. Related to this, (i) carbon accumulation of mature trees increased site class quality (Peri et al. 2010); (ii) understory productivity was positively correlated with SC (Bahamonde et al. 2012a); (iii) nutrient stocks in root biomass increased with decreasing site class quality (Gargaglione et al. 2013); and (iv) the seed rain and litter-fall were positively correlated with SC (Bahamonde et al. 2015, 2016). In these studies, a clear correlation among SC and other biological and ecological processes for these ecosystems has been reported.

Furthermore, it is broadly recognized that nitrogen is an important limiting growth factor in most temperate forests (Fisher and Binkley 2000), as well as in *N. antarctica* forests, where very low amounts of available N have been reported (Bahamonde et al. 2013). Besides, soil organic carbon in these *Nothofagus* forests is relatively abundant compared to that in other temperate forests, mainly due to low decomposition and soil respiration rates (Bahamonde et al. 2012b; Peri et al. 2015). This is a key issue, considering that soil organic matter in forests has been identified as an indicator of its productivity (Burger and Kelting 1999), e.g., Ladd et al. (2014) found a strong correlation between $\delta^{13}C_{SOM}$ (carbon isotope composition of soil organic matter) and LAI (leaf area index, an important proxy for primary productivity). Climatic variables also drive forest productivity (closely related to site index), e.g., temperature, radiation, and water availability (Boisvenue and Running 2006). Nevertheless, these abiotic factors can interact making more difficult the interpretation of their relative impact on site index in forests. Also, the main limiting climatic factor may be different for each region of the world (Churkina and Running 1998; Nemani et al. 2003). In temperate forests, water and irradiance have been identified as the most limiting climatic variables (Ladd et al. 2009; Martínez Pastur et al. 2014), which could be the case for *N. antarctica* forests. However, it is possible in the context of the prevailing low temperatures in Patagonia that temperature may also be strongly correlated with site index. Concerning

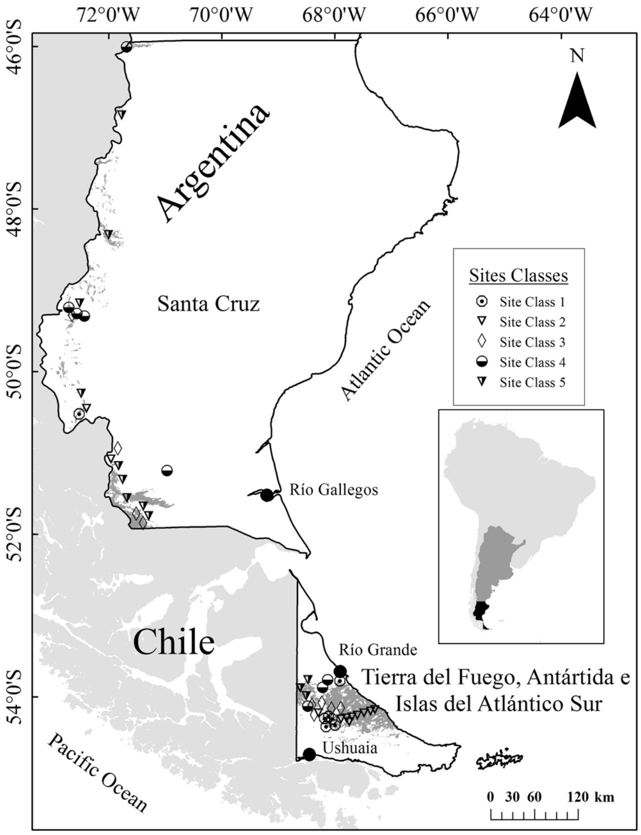

Fig. 1 Distribution of *Nothofagus antarctica* stands assessed in the study

this, knowledge about which soil and climatic variables are the main drivers of site index (as a proxy of productivity) in *N. antarctica* forests became a critical factor to consider for resource management. Under this perspective, the objectives of this study were (i) to relate soil and climatic variables to the productivity of *N. antarctica* forests using site class as a proxy, and (ii) to identify differences at the landscape level (Tierra del Fuego archipelago and Santa Cruz mainland) over the main identified drivers that influence forest productivity. Also, we propose the following hypothesis: Soil texture and water-related variables are more important as drivers of productivity in *N. antarctica* forests, in southern Patagonia.

2 Materials and methods

2.1 Study area

Our study included two provinces of southern Patagonia, Argentina: Santa Cruz (on the mainland) and Tierra del Fuego (an archipelago), which cover approximately 26.5 million ha with latitude ranging from 46° to 55° SL. The precipitation ranges from maximum values of 900 to 200 mm year^{-1} with west-east variation in Santa Cruz and a south-north rainfall gradient in Tierra del Fuego. The temperatures in southern Patagonia follow a north-south gradient with mean annual temperatures ranging from 12 °C in the north to 5 °C in the south (Paruelo et al. 1998; Kreps et al. 2012). In general terms, according to USDA classification, the soils are mollisols-haploxerolls (in the forest zone) and mollisols (in the steppe zone) with a silty loam texture and a slightly acidic pH.

2.2 Study sites and sampling

A total of 48 mature stands of *N. antarctica* were selected (27 in Tierra del Fuego and 21 in Santa Cruz) (Fig. 1). An exploratory survey was carried out analyzing the maps of site class distribution of *N. antarctica* forests in Santa Cruz and Tierra del Fuego (Collado 2001; Peri and Ormaechea 2013). Thus, we could ensure that all the established site classes for *N. antarctica* forests in southern Patagonia described by Ivancich et al. (2011) were included in the sampling. At each study site, we measured the height of three mature dominant trees (HMDT), as an indicator of productivity, and the site class of each stand was classified according to Ivancich et al. (2011). Soil depth was determined at each study site by digging to bedrock and then measuring with a tape measure, at three points randomly selected. Also, one composite sample (from three sub samples) from the first 30 cm of the soil profile was collected for all evaluated stands. Soil pH was determined with saturated soil pastes (30 mL deionized water mixed with 100 g soil). Organic matter (OM) was measured according to the loss on ignition method. Soil nutrient concentrations were determined as follows: (i) total N was measured by spectrophotometry; (ii) available P was determined by the Olsen method; and (iii) ammonium acetate-extracted potassium (K) was determined with a plasma emission spectrometer (Shimadzu ICPS-1000 III, Japan). The soil texture was determined using the densimeter method of Bouyoucos and sieving the sand fractions.

2.3 Spatial and climate variables

For each site, latitude, longitude, altitude, slope, and aspect were recorded. Also, 19 different climate parameters for each site were derived from the WorldClim data set (www.worldclim.org, Hijmans et al. 2005). This data set contains global geographical surfaces for the climatic parameters describing rainfall, temperature, and combination of these parameters at a resolution of approximately 1 km. The climate variables were temperature (annual, max of the warmest month or min of the coldest month), rainfall (annual or warmest quarter), and global potential evapotranspiration and global aridity index (Hijmans et al. 2005; Zomer et al. 2008). The climatic parameters are as follows: BIO1 (annual mean temperature); BIO2 (maximal monthly temperature − minimal monthly temperature); BIO3 (isothermality ((BIO2/BIO7) × 100)); BIO4 (temperature seasonality (standard deviation × 100)); BIO5 (maximal temperature of the warmest month); BIO6 (minimal temperature of the coldest month); BIO7 (temperature annual range (BIO5–BIO6)); BIO8 (mean temperature of the wettest quarter); BIO9 (mean temperature of the driest quarter); BIO10 (mean temperature of the warmest quarter); BIO11 (mean temperature of the coldest quarter); BIO12 (annual precipitation); BIO13 (precipitation of the wettest month); BIO14 (precipitation of the driest month); BIO15 (precipitation seasonality (coefficient of variation)); BIO16 (precipitation of the wettest quarter); BIO17 (precipitation quarter of the driest quarter); BIO18 (precipitation of the warmest quarter); and BIO19 (precipitation of the coldest quarter). The topography variables were defined by the altitude and the slope (Farr et al. 2007).

2.4 Data analysis

Initially, the complete data set was subjected to a partial least squares regression (PLSR). In this analysis, we used the height of the dominant trees at each sampling site as the dependent variable and the 33 independent variables described above (i.e., soil properties, climate, and topographic variables) as independent variables using XlStat (Addin Soft, Paris). PLSR is a statistical technique that combines elements of both principal component analysis and multiple regression. In PLSR, firstly, a large number of independent variables are reduced to a smaller number of components to reduce dimensionality and avoid problems with multicollinearity. These components (four in this case) are then used as independent variables in a multiple linear regression. With PLSR, it is also possible to calculate the relative importance of the underlying independent variables (i.e., altitude, temperature, soil chemistry) used to create the components used in the regression.

In the following statistical analyses, we separated the stands in different site classes according to the classification of Ivancich et al. (2011) mentioned in section 1 to facilitate the analysis of the environmental variables on forest productivity. Then, a principal component analysis (PCA) was performed to analyze the influence of the best correlated variables (altitude, total N, C/N, exchangeable K, BIO2, BIO3, BIO4, BIO5, BIO6, BIO7, BIO9, BIO10, and evapotranspiration) over the sample distribution in an ordination space. Latitude and longitude variables, also with high correlation, were excluded to avoid obvious relation with origin of the samples. Site classes (1 to 5) according to Ivancich et al. (2011) were used for grouping of samples. PCA included Monte Carlo permutation test ($n = 999$) to assess the significance of each axis. PCA was conducted in PCORD version 4.01 (McCune and Mefford 1999).

Data availability This study was financed by CONICET (Argentinean National Research Council) project. According to their specifications, at the end of the project and after publishing the results, the data can be deposited into an open access repository. Since this belongs to a still ongoing CONICET project, we cannot deposit the data in an open access repository at this moment.

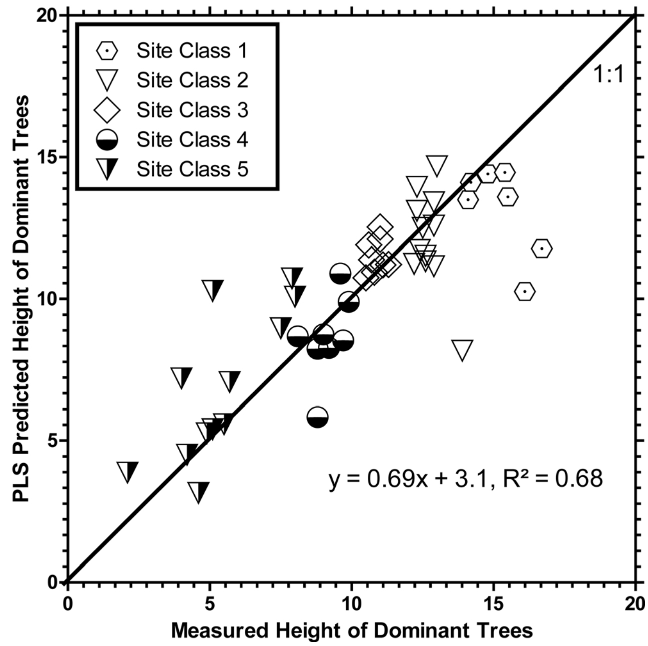

Fig. 2 The correlation between predictions of height of dominant trees from the PLS model and the measured values of height of dominant trees across the sites shown in Fig. 1

3 Results

3.1 Combined analysis for all sites

The partial least squares regression produced a model that was an effective predictor of height of dominant trees in the regional data set presented here (Fig. 2, $R^2 = 0.68$). In this analysis, the four variables that contributed most predictive power to the model were (1) altitude, (2) temperature annual range, (3) soil texture, and (4) temperature seasonality (see Figs. 3, 4, 5, 6, and 7).

Principal component analyses showed a clear separation of stands between the landscapes (archipelago and mainland locations) (Fig. 8). Eigenvalues for the first two axes were 7.578 ($p = 0.001$) and 1.8131 ($p = 0.110$), explaining 58.3 and 72.4% of the cumulated variation of total data set. The factors with the highest absolute coefficient for axis 1 were evapotranspiration > annual temperature range > max temperature in the warmest month > mean temperature of the driest quarter; and those for axis 2 were min temperature in the coldest month > mean temperature of the warmest quarter > annual temperature range > isothermality. Regardless of their productivity, the stands growing in Tierra del Fuego province were associated with less variability of the evaluated parameters.

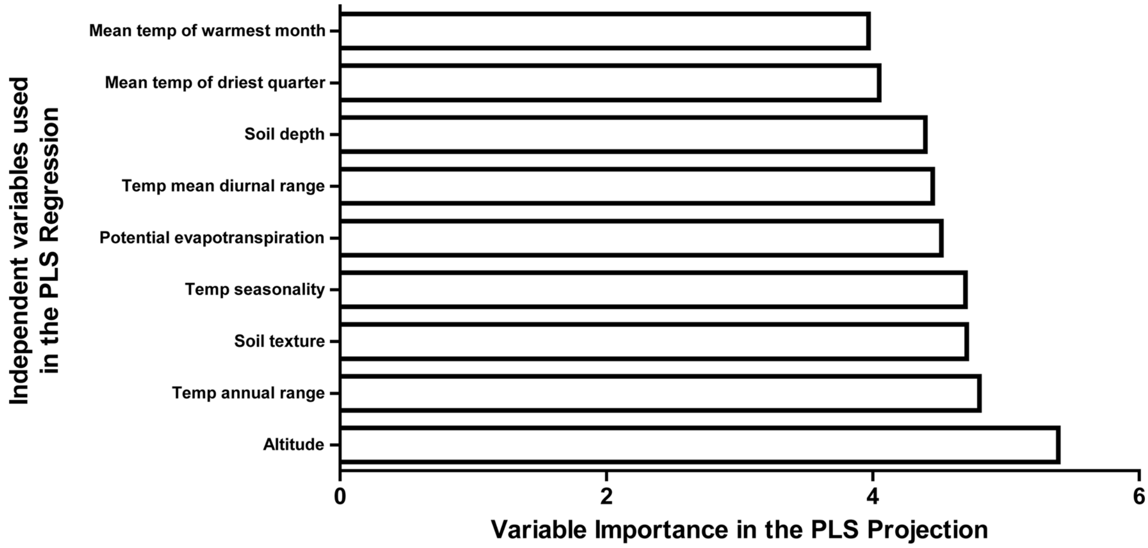

Fig. 3 Relative predictor importance for height of dominant trees prediction. The 9 more important variables are shown in ascending order (altitude being the most important variable in the PLS projection). Temp = temperature. Temperature seasonality = the standard deviation of the annual temperature range × 100, where range refers to the difference between the highest and lowest recorded values

4 Discussion

Forest productivity is strongly influenced by the prevailing soil and climatic conditions, but the magnitude of their incidence may be different according to the considered species and the interactions with environmental conditions (Schoenholtz et al. 2000; Skoovsgaard and Vanclay 2008). In a context of climate change, it is important to know the magnitude and range of environmental factors that influence tree productivity. Concerning Patagonia, *N. antarctica* forests are of major interest due to the broad environmental distribution of this species and its economic importance for silvopastoral systems (Peri et al. 2016). Moreover, *N. antarctica* has a major ecological relevance since it thrives in a broad range of environmental conditions, and that it is chiefly located in a transitional zone between more productive *N. pumilio* forests and Patagonian steppe. Due to their ecological significance, *N. antarctica* forests in southern Patagonia are part of the PEBANPA (Parcelas de Ecología y Biodiversidad de Ambientes Naturales en Patagonia Austral) network, which have been established for evaluating and measuring the economic, silvicultural, and ecological parameters related to forest use, management, and regeneration (Peri et al. 2016b). Thus, the ecological importance of this species is closely related to the productivity indicators evaluated in the present study.

The height of dominant trees (HDT, as a proxy of forest productivity) of the stands located further south and west, and at lower altitudes, was higher and is possibly a consequence of the combination of soil and climate variables, e.g., in this study, we found that total soil N was positively correlated with latitude and negatively correlated with the altitude (data not shown). Similarly, the mean annual temperature was negatively correlated with the latitude, longitude, and altitude. Thus, the correlations observed between spatial variables and tree productivity are indirectly representing the effect of soil and climate variables. Also, soil depth and texture were important

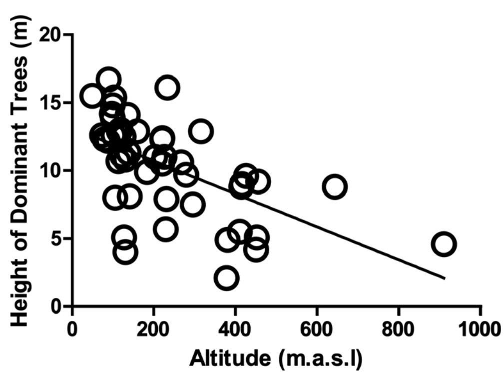

Fig. 4 Height of dominant trees according to altitude across the sites shown in Fig. 1

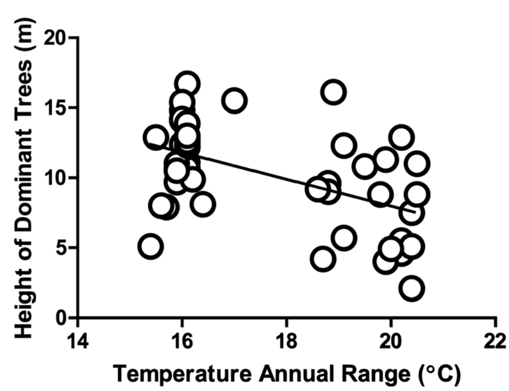

Fig. 5 Height of dominant trees according to temperature annual range across the sites shown in Fig. 1. Temperature annual range = maximal monthly temperature − minimal monthly temperature

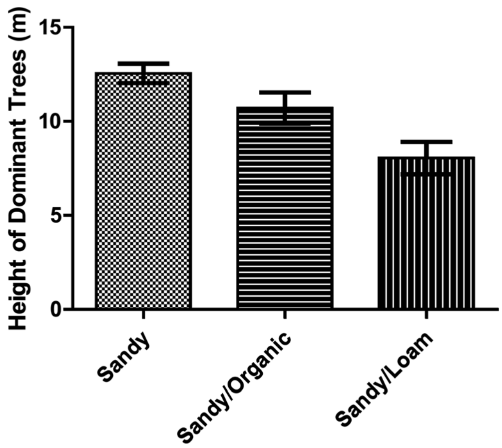

Fig. 6 Height of dominant trees according to soil texture across the sites shown in Fig. 1

variables explaining HDT. Other studies carried out in Patagonia with the closely related *N. pumilio* revealed similar trends, e.g., diameter and height growth of trees decreased with altitude (Barrera et al. 2000; Massaccesi et al. 2008), attributed mainly to climate variables negatively correlated with altitude.

Nemani et al. (2003) identified the main climatic constraints for plant growth around the world, and the temperature appears as the strongest limitation for southern Patagonian forests. Similarly, a study carried out in Alaska demonstrated that higher temperatures induced drought stress in boreal forests and consequently negatively affected tree growth and productivity (Barber et al. 2000). These studies are in agreement with our results, where less productive stands are located in extreme temperatures, whether high or low values.

Both soil- and temperature-related variables were correlated with the height of mature trees (as forest productivity indicator), suggesting that the incidence of the temperature-related variables at the regionally evaluated scale was higher than the effect of water-related variables, which made us reject our initial hypothesis.

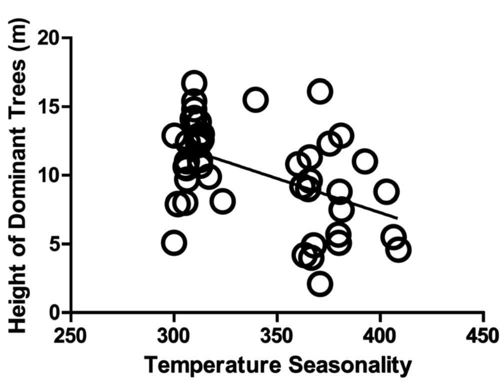

Fig. 7 Height of dominant trees according to temperature seasonality across the sites shown in Fig. 1. Temperature seasonality = the standard deviation of the annual temperature range × 100, where range refers to the difference between the highest and lowest recorded values

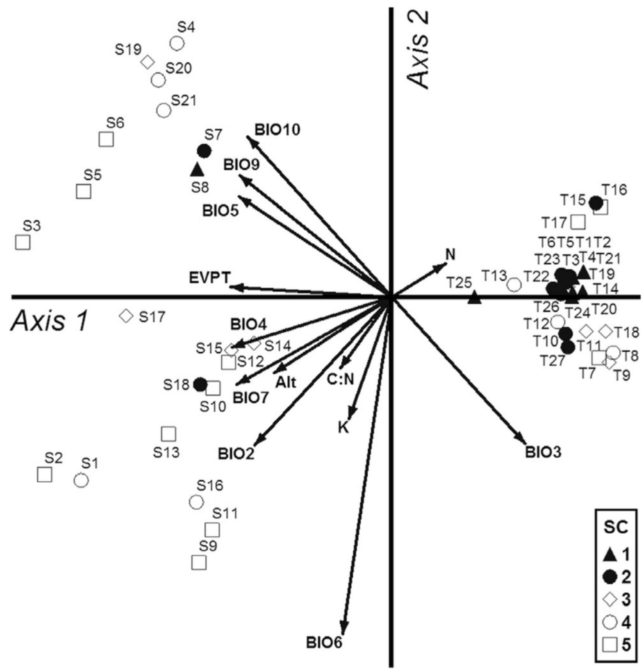

Fig. 8 Principal component analysis including climatic, space, and soil variables related to quality site classes of *Nothofagus antarctica* forests in southern Patagonia. SC is the site class where each stand is growing; S and T before the number of each site determine if the stand is located in Santa Cruz or Tierra del Fuego, respectively; BIO2 (maximal monthly temperature − minimal monthly temperature); BIO3 (isothermality ((BIO2/BIO7) × 100)); BIO4 (temperature seasonality (standard deviation × 100)); BIO5 (maximal temperature of the warmest month); BIO6 (minimal temperature of the coldest month); BIO7 (temperature annual range (BIO5–BIO6)); BIO9 (mean temperature of the driest quarter); BIO10 (mean temperature of the warmest quarter); Alt, altitude; C, soil carbon concentration; C:N, soil carbon:nitrogen ratio; EVPT, evapotranspiration; N, soil nitrogen concentration.

Comparing mainland and archipelago sites, the Andean mountains play an important role in the different climatic conditions between them, as well as the soil formation history. Such as, in the mainland, the Andes intersect the westerly winds, generating a noticeable climatic contrast between the Pacific (windward side) and the Atlantic slopes (where the forests are located) with a strong west-east rainfall gradient (Coronato et al. 2008). However, in the Tierra del Fuego archipelago, the Andes mountains are less high and loose continuity, shifting to a W-E orientation, which implies a decrease in the magnitude of the west-east precipitation gradient (Coronato et al. 2008). Thus, rain is more uniformly distributed in the stands occurring in the central area of the biggest island of Tierra del Fuego. Temperatures in the archipelago are more uniform due to the ameliorating effect of the surrounding seawater (Strahler and Strahler 2000). This has been corroborated in Patagonia in general, where the mean annual thermal amplitude varies from 16 °C in the north (on the mainland) to 8 °C in the south, or even down to 4 °C on the outermost archipelago islands (Coronato et al. 2008). This could explain in part the separation of ñire stands between archipelago and mainland locations found with the PCA of our study. Also, differences in altitude and soil characteristics between continental and island sites may be related to their geological dissimilarities. Many of the mainland sites are located in the geological province called the South Patagonian Cordillera (Ramos 1999), which is characterized by having north-south orientation and high elevations; while the archipelago sites are located in the Fuegian Andes (Borrello 1972), where the mountains are the lowest Andean summits in Patagonia and the only portion of the Andes in Patagonia that have an west-east orientation (Coronato et al. 2008).

In this regard, the differences in bioclimatic variables between mainland and archipelago forests have been previously reported at a stand level. For example, Bahamonde et al. (2014) recorded higher monthly mean temperatures in ñire forests growing in Santa Cruz (mainland), compared to stands growing in Tierra del Fuego (archipelago), but also determined higher soil moisture values in island forests, which may be due to a lower evapotranspiration rate in the archipelago locations.

5 Final considerations

Identifying the most suitable combinations of climate and soil for obtaining higher productivities can be useful for improving management of *N. antarctica* forests in southern Patagonia, especially considering potential climate change scenarios. For instance, this knowledge may be useful for choosing appropriate areas for planting *N. antarctica* according to the best combinations of climate and soil conditions. In addition, the results gathered will serve as basis for developing further trials assessing major aspects that may improve forest productivity. Finally, the information gathered provides knowledge on carbon sequestration modeling in these forests and contributes to improve our understanding of the ecology of this austral species.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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