




Article

Trends in ANPP Response to Temperature in Wetland Meadows across a Subcontinental Gradient in Patagonia

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Abstract: Due to ongoing global warming, seasonal patterns of aboveground net primary production (ANPP) may be altered by temperature trends. Of particular interest is the seasonal association between ANPP and temperature at the beginning of the growing season (the period encompassing minimum to maximum ANPP), where two contrasting mechanisms are in tension. On the one hand, the restrictions exerted by low temperatures in winter may be relaxed, increasing the slope of seasonal association between ANPP and temperature over the years. On the other hand, increases in temperature may increase water demand, reducing the slope over time. Across 543 wetland meadow areas in Patagonia, we estimated ANPP and obtained temperature records on a monthly basis from 2001 to 2019. The seasonal association between ANPP and temperature, tested through linear regression, was statistically significant in 96% of the cases (9921/10317 (543 wetland areas × 19 growing seasons)). The fitted linear models explained, on average, 84% of ANPP seasonal (June–December) variations. Through regression trees, we found out that the two tested mechanisms, the relaxation of temperature restriction and the increase in water demand, showed clear spatial patterns. The relaxation due to temperature increase took place at higher latitudes, but the water-limiting mechanism increased over mid-latitude areas.

Keywords: global warming; growing season; regression trees; MODIS; Google Earth Engine



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1. Introduction

The study of the temporal patterns of the growth rate of vegetation, aboveground net primary production (ANPP), and their association with environmental drivers is critical to understanding the impact of the ongoing global warming effects [1,2]. Across grassland ecosystems of the world, there is a good understanding of the spatial [3,4] and inter-annual [5–9] association between ANPP and precipitation. However, our understanding of ANPP seasonal variations and their association with temperature is less clear. This deficit of clarity is partially associated with the positive covariation of temperature and CO₂ [10], which increases ANPP, but is also due to the association between temperature and drought severity [11,12] which decreases it. Moreover, many of the studies addressing ANPP association with climate drivers are harvest-based, focusing on a single, peak biomass value. This prevents our understanding of how seasonal variations of ANPP are related to biophysical drivers, such as temperature.

ANPP seasonal patterns are governed by seasonality in terms of incoming radiation, temperature, and precipitation [13,14]. From mid to high latitudes, ANPP increases at the beginning of spring, reaches its maximum at the beginning of summer, and decreases during

autumn [15–17]. This pattern is compressed at even higher latitudes and altitudes [18]. Of particular interest is the start of the growing season, the period in which seasonal ANPP goes from minimum to maximum, since its variation is tightly associated with herbivores' reproductive behavior both in managed [19–21] and natural ecosystems [22,23], and is a key component of ecosystem functional types [17,24,25]. Recently, in a meadow area at a very high altitude, above 3000 m above sea level (m.a.s.l.), it was shown that under ongoing global warming, ANPP increased at the start of the growing season due to a warming-induced earlier onset [26]. This result highlights the constraint that temperature imposes on ANPP when other factors are not limited, mainly water availability. However, it remains unknown if this finding can be extrapolated to other meadow areas located at mid and high latitudes in other parts of the world.

In southern South America, in the ecological area of Patagonia, the largest semiarid area of the continent, wetland meadows are imbedded within the main matrix of arid and semiarid steppes [27]. These areas are key for rangeland sustainability [28] and act as biodiversity hot spots [29–32]. Even though they usually represent a small proportion of the landscape within any ranch, from 2% to 8% [33], its ANPP can be up to six times higher than the one of the surrounding steppe areas [15,34–36]. The mechanism for this pattern is associated with the fact that water availability in meadows relies on the depth of the water table, and not directly on the amount of rainfall [31]. Within these ecosystems, ANPP regional spatial variations have been partially studied. Mean ANPP is at its maximum towards the west, close to the Andes Mountains where mean annual precipitation is also maximum and mean temperature reaches its minimum. Additionally, ANPP relative interannual variation increases towards the north [15]. However, this study only covers a minor portion of wetland area distribution across Patagonia. Moreover, regarding the seasonal variation of ANPP, no study has addressed the seasonal association of ANPP and temperature at the start of the growing season in meadow areas.

In the central basin of Patagonia, July's temperature governs the starting date of the growing season [19], influencing the reproductive performance of sheep herds [33]. Within this area, there is a delay in the start of the growing season if the temperature in July decreases [19]. Moreover, in many areas of Patagonia, the average minimum temperature has increased over the last twenty years [37]. These two patterns suggest that, in rangeland areas of Patagonia, the association between ANPP seasonal variations at the start of the growing season and temperature should be changing. There are, at least, two opposite predictions on the seasonal association between ANPP and temperature. On the one hand, as the restrictions exerted by low temperatures in winter are relaxed, due to temperature increases, the positive association between ANPP and temperature could become steeper. In other words, the slope of seasonal association between ANPP and temperature could increase through the years. However, on the other hand, increases in temperature also represent increases in water demand, which may impose a new restriction on ANPP, reducing the positive slope of the association between ANPP and temperature through the years.

Our main objective was to analyze the spatial variation, across an 18° latitude range, of the association between ANPP and temperature within meadow areas. To do so, and for a set of 543 meadow areas embedded in the semiarid Patagonian steppes, we proposed two specific objectives. The first one was to describe the spatial variation in the association between ANPP at the beginning of the growing season and temperature. The second objective was to describe if the association between ANPP and temperature changed over time. Additionally, if it did, we aimed to understand which mechanism prevailed: the relaxation of temperature restriction or, on the contrary, a negative trend suggesting an increase in water demand. To do so, we performed linear models associating ANPP seasonal variations and temperature per year from 2001 to 2019, and then we used the estimated parameters of the models to describe the possible temporal trends with regression trees. Through this approach, we evaluated which of the two alternatives regarding temperature effect on ANPP prevailed.

2. Materials and Methods

2.1. Site Description

Sampling sites were entirely located within the phytogeographic region of Patagonia at the southern end of South America (Figure 1). The climate of this wide region is cold temperate, with a pattern that denotes the influence of the Andes mountain range and latitude [38]. Moreover, altitude also plays a key role in shaping temperature variations [39]. Mean annual temperature ranges from 3 °C in the south to 12 °C in the north, with absolute minimum temperatures below −20 °C. The thermal amplitude varies from 5 °C in the extreme south of the region to 16 °C in the north [38]. Mean annual precipitation decreases from the Andes Mountains towards the east, from more than 1000 mm of annual precipitation towards the Andes to less than 150 mm towards the central basin of Patagonia, while its variability increases, in this sense, for the vast majority of the area [38,40]. The precipitation is concentrated in the autumn–winter period with a consequent marked summer water deficit [16,40]. However, the extreme south of the region has a more uniform seasonal distribution of rainfall, showing some additional rains, especially in the summer, in a narrow eastern strip [16,38]. This decrease in rainfall from west to east determines a gradient of vegetation types: from forests through grass steppes, to shrub steppes and semideserts [41,42]. Imbedded in the semiarid matrix of Patagonia are wetland meadows, locally named “mallines” or “vegas”. Mallines present seasonal periods of flooding due to large fluctuations in the water table [31,32], which determines that their vegetation is generally characterized by containing hygrophytic species [29,30,43]. Within these areas, water distribution determines different physiognomies, with species better adapted to drought conditions at the borders and species better adapted to flooding in the center [43,44]

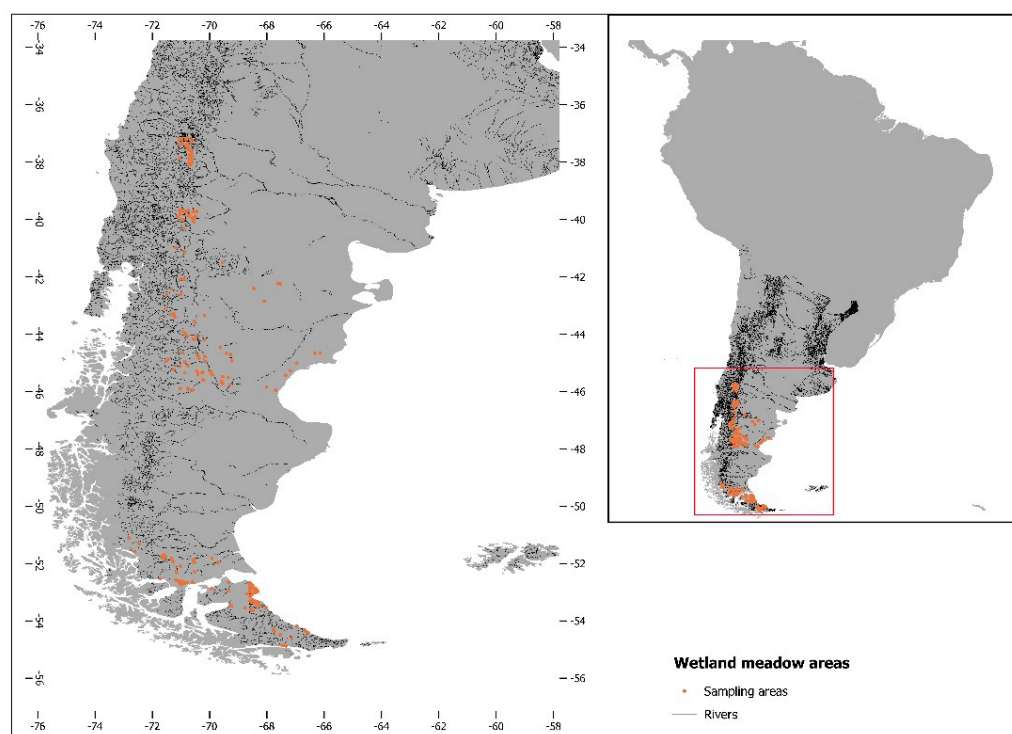


Figure 1. Left panel: Location of the wetland meadow areas in South America. Right panel: Wetland meadows area location across Patagonia. Each dot represents a sampling area of 5.3 ha. The total number of areas is 543.

2.2. ANPP Monthly Association with Temperature

Wetland meadow locations across Patagonia are not easily reached [27]. For example, there is no land cover classification able to identify their location over the entire region,

even though some subregional studies have been able to identify their location [36,45]. Moreover, wetland meadow areas exhibit contrasting cover ranges associated with the depth of the water table, and/or grazing history [34–36]. To surpass this location limitation, we took advantage of a recent compilation of 543 wetland meadows' botanical surveys carried out by local experts across the entire region of Patagonia. All the botanical surveys were carried out to describe botanical heterogeneity. This gave us the advantage of securing the location of wetland meadow areas. However, in these areas, studies were carried out on different vegetation physiognomies associated with the depth of the water table and/or grazing history.

Across these 543 wetland meadow areas, located from -54° to -37° latitude and from -72° to -66° longitude (Figure 1), we, on the one hand, estimated ANPP on a monthly basis based on locally calibrated remote sensing data [15] and, on the other, obtained from a world database monthly maximum and minimum temperature [46] to finally study the association between them. ANPP, expressed in kg/ha·day with monthly values from 2001 to 2019, was estimated as the triple product of incoming photosynthetic radiation (PAR, in MJ/m² day), the proportion of it absorbed by green active vegetation (*f*PAR), and by the conversion of the absorbed radiation into biomass, i.e., the radiation use efficiency (RUE, in g/MJ) [14]. Monthly PAR values were obtained from ERA5-Land monthly averaged data [47] through the Google Earth Engine (GEE) platform [48]. This worldwide database has a pixel resolution of 11,132 m. *f*PAR values were obtained from the MODIS satellite mission, specifically using NDVI values from product MOD13Q1 [48] with a pixel resolution of 250 m. NDVI values were non-linearly converted to *f*PAR following a local protocol developed for meadow areas of Patagonia [15]. Finally, ANPP was estimated as the product between APAR (PAR × *f*PAR) and RUE; the latter was also obtained from local estimations [15]. Maximum and minimum temperature were averaged to generate an estimator of mean monthly temperature. Both maximum and minimum temperature values were obtained from the TerraClimate database, also through the GEE [48]. This worldwide database has a pixel resolution of 4638.3 m. For each area and growing season from 2001 to 2019, we estimated the linear association between monthly ANPP and the standardized temperature considering the period between June and December ($n = 7$ months). Because of the analysis, we obtained a total of 10,317 estimators of the Y-intercept and the same number of estimators of the slope (543 meadow areas × 19 analyzed periods, from 2001 to 2019) and their statistical significance (alpha level of 0.05).

2.3. Spatial and Inter-Annual Variation in the Slope

Two approaches were taken to analyze the spatial and inter-annual variations and their association with geographical coordinates. First, and to analyze the spatial variation, we compared two statistical techniques: linear multiple regression and regression trees. For both analyses, the dependent variable was the slope of the seasonal association between ANPP and temperature, and the independent variable was the geographical coordinates (LAT and LONG). The use of multiple linear regression and regression trees allowed us to compare the complexity of the spatial pattern. While the former only allowed linear associations, the latter allowed non-linear ones. Specifically, due to the absence of wetland meadow areas towards the northeast portion of Patagonia (Figure 1), this was particularly important for the linear multiple regression approach. However, the regression tree was more flexible on this end. In a nutshell, regression trees describe the variation of a dependent variable (i.e., slope estimator) by applying a recursive partitioning procedure based on an iterative search for the best binary splits of data into more homogeneous groups, using geographical coordinates in our case as explanatory variables. The method searches for a single explanatory variable which splits the data into two homogeneous subgroups to minimize an impurity or diversity measure in the subgroups, e.g., the Gini coefficient, information index, etc. To do so, explanatory variables as well as their thresholds are compared to choose those minimizing the risk of misclassifying errors for each split. Then, data are divided, and this process is applied separately to each subgroup, and so on,

recursively, until the subgroups either reach a minimum size or until no improvement can be made. Default values finalize the tree construction based on a complexity parameter to avoid overfitting ($cp = 0.01$). In addition, we established 50 as the minimum number of cases (wetland meadow areas) in each terminal node. Multiple regression analysis was constructed using the nlme R package [49]. The evaluated model considered the independent variables in a full polynomial degree of two. Regression trees were constructed using the rpart R package [50] which is based on the original ideas of Breiman [51].

Second, and to understand the inter-annual variation, we took a two-step approach. In the first step, we looked at the temporal trend of the slope of the linear association between ANPP and temperature. We used the Pearson correlation coefficient as an estimator of the temporal trend. Positive correlations of the slope over time would support the restriction relaxation exerted by temperature. On the contrary, negative ones would support the increases in water demand which impose new restrictions on ANPP. In the second step, we took advantage of the regression tree. In this case, we used the Pearson correlation coefficient of the slope through the years as the dependent variable and the geographical coordinates as the independent variable. All statistical analyses were carried in an R environment (R Core Team 2021).

3. Results

3.1. ANPP Monthly Association with Temperature

Overall, the linear association between monthly ANPP and temperature was highly significant across wetland meadow areas and growing seasons. The tested association was statistically significant in 96% of the cases (9921/10,317) and was always positive. Moreover, the fitted models explained, from a minimum of 50% to a maximum of 90%, with an average of 84%, the ANPP monthly variations, indicating that there is a tight and positive association between variations in ANPP and temperature during the growing season (June–December). However, the mean estimated slope (b_1) exhibited a 210-fold variation (Figure 2) where ANPP increased from a minimum of 0.037 to a maximum of 7.8 kg/ha-day per one degree of increase in mean temperature during the growing season. Moreover, the variation in the slope did not exhibit a straight relation with either latitude or longitude (Figure 2).

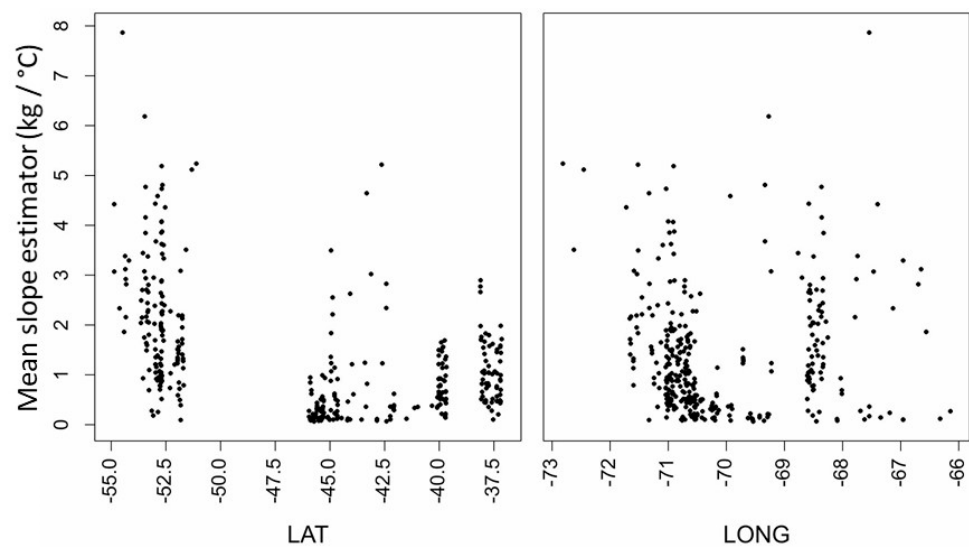


Figure 2. Association between the slope of the seasonal pattern between aboveground net primary production (ANPP) and temperature across the geographical range for latitude (LAT) (left panel) and longitude (LONG) (right panel).

The complexity of the association between the slope and the geographical coordinates was better captured by regression trees than by multiple linear regression. On the one

hand, the proposed multiple regression analysis explained 37% of the spatial variation in the slope with the following adjusted model: $b_1 = 979 - 3.01LAT + 0.01LAT^2 + 30.7LONG + 0.24LONG^2 - 0.05LATLONG$ (Adjusted R-squared: 0.3672, p -value: $<2.2 \times 10^{-16}$). The regression tree (Figure 3), on the other hand, explained 64% of the spatial variation in the slope up to the sixth split (Figure 3; Table S1 in Supplementary Materials). According to the regression tree, the first main split was associated with sites located east or west of -71° LONG, and accounted for 27% of the variability in b (Table S1). Those west of -71° LONG represented 10% of the sites while those east of it represented the remaining 90%. Moreover, b_1 was 3.5-fold higher in sites towards the west when compared to those east of -71° LONG. The second and third splits were associated with the location of the sites either north or south of -52° LAT, and east of -71° LONG (Figure 3). These three splits accounted for 56% of the variability in b_1 (Table S1). Within these two groups, the ones north of -52° LAT represented most of the sites (68%), and on average had a slope almost four-fold lower than those south of -52° LAT (Figure 3). Up to the sixth split, the model accounted for 64% of the variability in b_1 (Figure 3, Table S1). At these levels, divisions were associated with portions north or south of -40° LAT, -53° LAT, and -52° LAT.

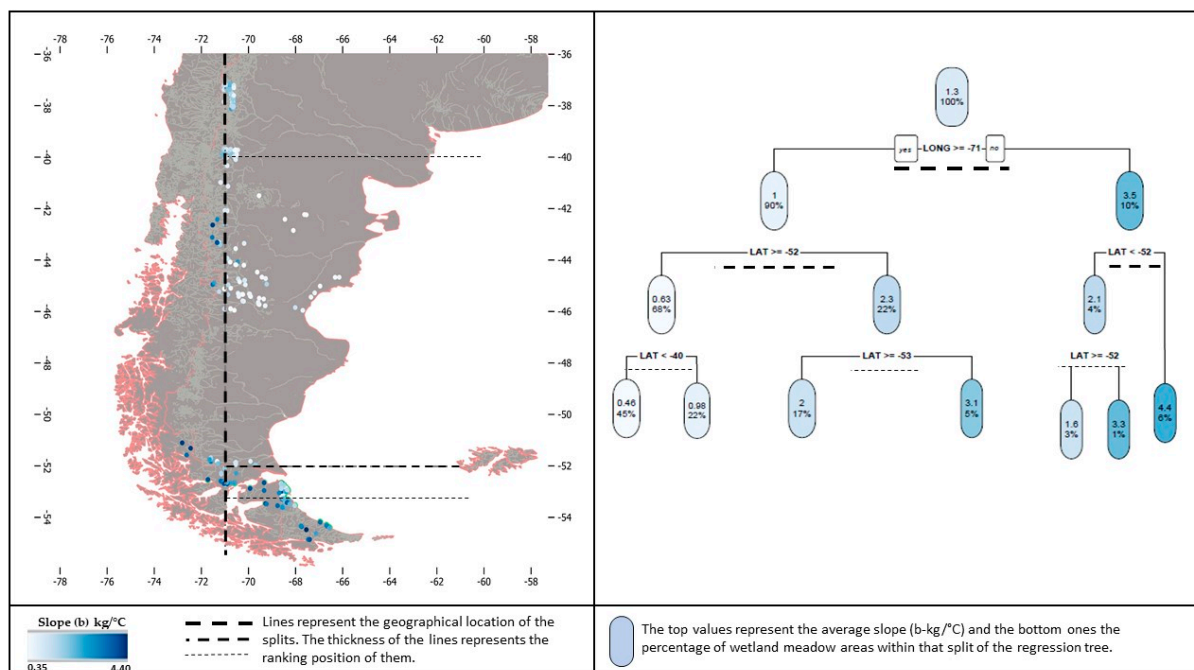


Figure 3. Left Panel: Geographic distribution of the average aboveground net primary production (ANPP) response to temperature for each wetland meadow area. Right panel: Regression tree analysis of the spatial variation for the ANPP response to temperature (slope of the linear regression analysis) with geographical coordinates. The dashed lines on the map from the left panel correspond to splits in the regression tree (right panel).

3.2. Temporal Trends of ANPP Response to Temperature

In 18% ($n = 99$) of the 543 meadow areas, there were significant (p -value < 0.05) temporal trends in the slope of linear regression between ANPP and temperature. Within the areas with significant trends, negative ones prevailed (67% of the sites with significant trends were negative). The complexity of the association between the slope of temporal trends and the geographical coordinates was, as with the spatial variation, better captured by regression trees than by multiple linear regression. However, both analyses explained a vast proportion of the spatial variability in the temporal trend of the slope. The multiple regression analysis explained 62% of the spatial variation in the trend with the following adjusted model: $Trend\ b_1 = 563 - 0.77LAT + 0.002LAT^2 + 17LONG + 0.12LONG^2 - 0.01LATLONG$ (Adjusted R-squared: 0.6229, p -value: $<2.2 \times 10^{-16}$). The regression tree (Figure 4) ex-

plained 89% of the spatial variation in the temporal trend with only four splits (Table S1). According to the regression tree, the first main split was associated with sites located north or south of -49° LAT. Those to the south of it exhibited positive trends of b_1 and represented 20% of the areas. North of -49° LAT, there were both positive and negative trends (Figure 4). Positive trends, however, were west of -71° LONG but negative to the east of it (Figure 4). Finally, east of -71° , there was another split across -39° LAT with smaller differences among both terminal nodes.

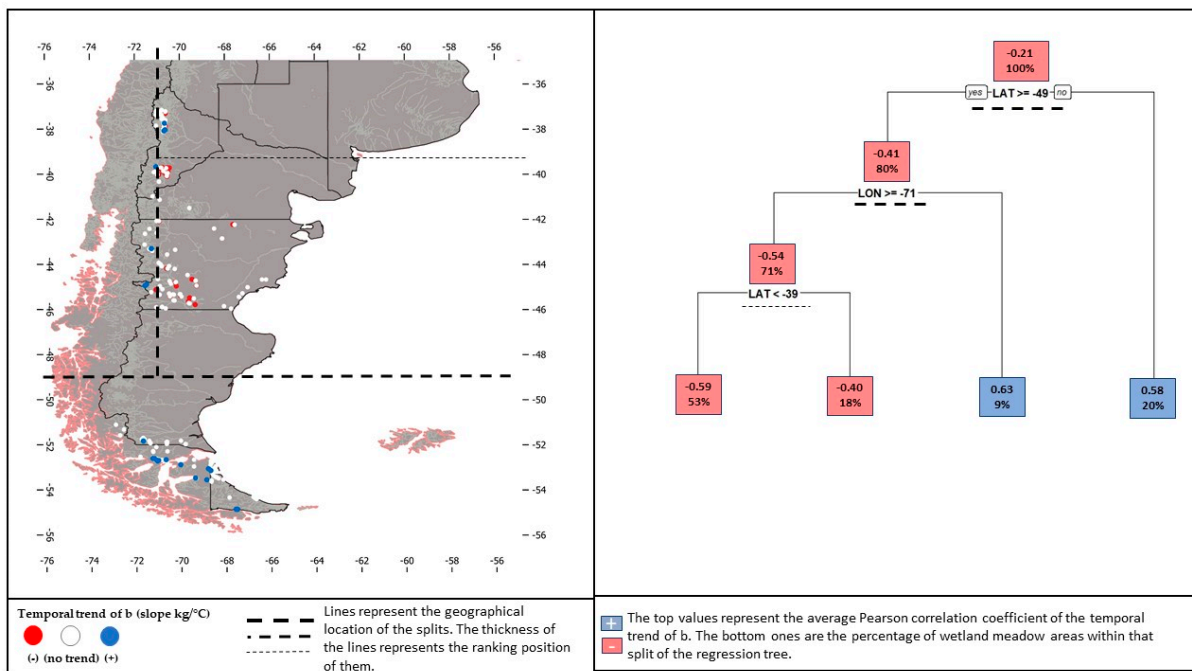


Figure 4. Left Panel: Geographic distribution of the wetland meadow areas describing the temporal trends of the slope of the linear regression between aboveground net primary production (ANPP) and temperature. Right panel: Regression tree analysis of the spatial variation in the temporal trend with geographical coordinates. The dashed lines on the map from the left panel correspond to splits in the regression tree (right panel). In the regression tree diagram (right panel), red boxes represent negative trends and blue boxes positive ones.

4. Discussion

Our results confirmed that, across wetland meadows, there is a strong positive and linear association between ANPP and temperature at the start of the growing season. However, the slope of this association showed a 210-fold variation (from 0.037 to 7.8 kg/ha-day per one degree of increase in mean temperature) and significant temporal trends. Regarding the two tested mechanisms, the relaxation of temperature restriction and the increase in water demand, both mechanisms showed clear spatial patterns. The relaxation due to temperature increases took place at higher latitudes, but the water-limiting mechanism increased over mid-latitude sites.

The 210-fold variation in the slope of the association between ANPP and temperature highlights, on the one hand, the heterogeneity of the vegetation across these wetlands and, on the other, its variation over time within each area. Many authors have described across different wetland meadows differences in physiognomy and vegetation cover [29,35,42,43,52,53]. The consensus is that, within wetland meadows, there are at least three main physiognomies [54] strongly associated with the landscape distance from the center to the periphery of the main water stream [43]. Across these different physiognomies, ANPP can vary up to two-fold, from 5000 kg/ha-yr to 9000 kg/ha-yr [15]. Our analysis partially suggests that ANPP response to temperature was restricted by these different

physiognomies. The response over time seems to be very novel, and as far as we are aware there are no descriptions of the temporal patterns described here.

The temporal trends in the slope of the association between ANPP and temperature highlight at least three possible mechanisms. Regarding the positive trends, and as proposed previously, increases in the average minimum temperature in the last twenty years [37] have driven increases in the response of ANPP to it. This was particularly true towards the western and southern ends of the study area. These findings support the constraint reduction in ANPP by temperature when other factors are not limited, mainly water availability, as observed in similar areas of the world [26]. For these sites, global warming predictions should enhance conditions for both primary and secondary production [55,56].

Regarding the negative trends, there were two overlapped sources of variation for the observed pattern. On the one hand, our results support the second proposed mechanism: the increase in water demand given the increase in temperature. This is particularly true for sites located towards the center of the study area, where hyperarid conditions exist [11,57]. However, on the other hand, rangeland areas of Patagonia have been long described as overgrazed since the sheep introduction at the end of the 19th century [28,39,58–61]. In this context, wetland meadow areas are current “hotspots” of degradation given that, within Patagonia, the vast majority of these areas are outside the international union for conservation of nature levels I to III [27]. Consequently, in most ranches, these lowland areas are mixed with the surrounding steppes [15,28,35,53], preventing a differential grazing management to preserve them. Future studies should address which mechanism exerts more pressure: global warming or overgrazing. To do so, the use of techniques such as RESTREND analysis appear as a potential paths to disentangle the relative importance of climate from grazing within these areas [62–66].

5. Conclusions

Overall, we were able to quantify the main role that temperature plays in ANPP dynamics at the beginning of the growing season in wetland meadow areas of Patagonia. Our results showed a tight and positive association between ANPP and temperature. This seasonal association exhibited strong regional spatial patterns and, in some cases, temporal trends. The two tested mechanisms, the relaxation of temperature restriction and the increase in water demand, both showed clear spatial patterns. The relaxation due to temperature increases took place at higher latitudes, but the water-limiting mechanism increased in mid-latitude areas.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/meteorology1020015/s1>. Table S1. Proportion of variation explained by tree regression.

Author Contributions: Conceptualization, J.G.N.I., P.A.C. and M.T.; methodology, J.G.N.I. and P.A.C.; data curation, M.H.C. and J.G.N.I.; writing—original draft preparation, J.G.N.I.; writing—review and editing, P.A.C., M.T. and M.H.C. All authors have read and agreed to the published version of the manuscript.

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Conflicts of Interest: The authors declare no conflict of interest.

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