



# Effects of Temperature and Water Availability on Northern European Boreal Forests

Guiomar Ruiz-Pérez\* and Giulia Vico

Department of Crop Production Ecology, Swedish University of Agricultural Sciences, Uppsala, Sweden

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### \*Correspondence:

Guiomar Ruiz-Pérez  
guiomar.ruiz.perez@slu.se

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Boreal forests are warming faster than the rest of the planet. Do the benefits of higher temperatures and longer growing seasons for forest productivity exceed the negative effects of more frequent dry spells and heat waves, shifting precipitation patterns, and higher evaporative demands? And are the effects uniformly distributed geographically? To answer to these questions, the relationship between climatic variables and NDVI—a proxy of forest productivity at regional scale—was explored via Partial Least Square (PLS) regression analyses. We focused on Northern Europe, where contrasting findings on the effects of warming have been reported and that has so far been overlooked by systematic large-scale explorations of the linkages between boreal forest productivity and climatic conditions. The results show that the effects of warmer temperatures on boreal forest productivity are not uniformly positive and that water stress is already negatively affecting these forests. Indeed, increased temperatures appear beneficial in northern and wetter regions, while warmer temperatures mostly reduce forest productivity in southern and drier areas. These results are suggestive of already existing limitations due to water availability and warm temperatures, even in mesic regions like Northern Europe. These conditions are expected to become more frequent and intense in the future, potentially reducing the ability of boreal forests to provide their essential ecosystem services unless forest management practices are adapted to the new conditions.

**Keywords:** boreal forest, temperature, precipitation, water stress, NDVI, Northern Europe

## INTRODUCTION

Global warming is more pronounced in boreal forests than elsewhere, with temperatures increasing twice as fast as the rest of the planet (Intergovernmental Panel on Climate Change, 2014). They are considered largely unaffected by or even benefitting from climate change (Boisvenue and Running, 2006), particularly if compared to ecosystems experiencing drier or more variable conditions (Allen et al., 2010; Anderegg et al., 2013). So far, rising temperatures have mostly enhanced boreal forest productivity and some forests might still be able to cope with further temperature increases (Myneni et al., 1997; Kauppi et al., 2014). Nevertheless, there is increasing evidence that boreal ecosystems are also negatively affected by climate change (Martin-Benito and Pederson, 2015), suggesting that their vulnerability to future conditions is currently severely underestimated (Allen et al., 2015). Indeed, future climates can lead to more frequent stress events, including longer periods without precipitation (hereafter “dry spells”) and potentially damaging high temperatures, which can cause widespread reduction in productivity and enhance mortality (Anderegg et al., 2013; Buermann et al., 2014). Dry spells can also cancel out the beneficial effects of higher temperatures (Belyazid and Zanchi, 2019).

Based on remotely sensed data, a prolonged and extensive regional decline in forest productivity [termed “browning trend” by Goetz et al. (2005), Lloyd and Bunn (2007)] has already been observed in eastern Alaska and western Canada (Beck and Goetz, 2011), western central Eurasia and western North America (Buermann et al., 2014). Additionally, tree rings and wood density measurements suggest that in recent decades there has been a divergence between warming and tree growth, with localized shifts to a negative correlation between temperature and growth (D’Arrigo et al., 2008; Porter and Pisaric, 2011). Moreover, boreal forests appear increasingly vulnerable to indirect effects of rising temperatures, including temperature-induced drought stress (Barber et al., 2000; Beck and Goetz, 2011), increased frequency of fires (Kasischke and Turetsky, 2006; Rubtsov et al., 2011), increased risk of insect outbreaks (Kurz et al., 2008) and more frequent climate extremes (Mulder et al., 2019). Nevertheless, in Northern Europe, the effects of rising temperatures are still largely unclear and partially contrasting. For example, positive correlations emerged between tree growth and monthly mean temperature in June and July of the year prior to the ring formation at latitudes higher than  $\sim 65^\circ\text{N}$ , whereas correlations were negative at lower latitudes (Babst et al., 2012). Reports of forest growing stocks showed that forest productivity has been increasing in the region (Gauthier et al., 2015), whereas analysis based on remotely-sensed variables found mostly stable productivity in boreal forests (Bjerke et al., 2014). Northern Europe is also not exempt from indirect damaging effects of rising temperatures, with recent reports of detrimental effects of dry spells and high temperatures on forest productivity in southern Sweden, symptoms of drought-induced top dieback in southern Norway, several drought-affected sites over Finland, and reductions in the carbon (C) sequestration potential of forests (Muukkonen et al., 2015; Rosner et al., 2018; Belyazid and Zanchi, 2019).

These partially contrasting observations regarding the effects of changing climatic conditions on Northern European forests can be due to differences in the proxy of forest productivity being used in each study—from remotely sensed vegetation indices such as NDVI (Olofsson et al., 2008) to *in-situ* measures such as tree-rings (Babst et al., 2012); the extent and diversity of the study site(s)—from specific species (Rosner et al., 2018) to mixed forests (Piao et al., 2017); the spatial resolution and coverage—from images at different spatial resolutions (Olofsson et al., 2008 and Sulla-Menashe et al., 2018) to experimental plots (Rosner et al., 2018); the temporal resolution of observations and the length of the period analyzed—from analyses based on monthly averages (Babst et al., 2012) to seasonal and annual averages (Beck and Goetz, 2011). These discrepancies call for an updated analysis extending over the entire region, in order to elucidate the key drivers of forest productivity and hence how future conditions can affect these forests and where management should focus on climate adaptation. Ensuring continued forest productivity in Northern Europe in the future is key for European climate mitigation actions and economy. Indeed, one of the pathways toward the reduction of  $\text{CO}_2$  stipulated in the Paris Agreement of the United Nations Framework Convention on Climate Change (UNFCCC) is the use of harvested biomass

to substitute fossil fuel (Kallio et al., 2013; Smyth et al., 2017). Northern European forests are the main source of biomass in Europe and hence they are necessary for the achievement of the European targets for  $\text{CO}_2$  emission reduction in energy and climate policies (Rytter et al., 2015, 2016). Already today, 40% of energy used in the Nordic countries is obtained from renewable sources, mostly from forest biomass ( $\sim 60\%$  of the total renewable energy; Nordic Statistics, 2017). In Sweden and Finland, the consumption of wood-based energy by the rural population is more than five times the European average (Köhl et al., 2011). Northern European forests act as a C sink in the global C cycle, with an estimated annual C gain around 20,000 Gg [the highest proportion of European forests; United Nations Framework Convention on Climate Change (2011)]. Moreover, Northern European forests are also a key economic resource, especially in Finland and Sweden, constituting around 5.5 and 3.5% of national GDP, respectively. The pressure to produce biomass already clashes with the provision of other ecosystem services, such as those linked to soil and water quality (Koskiaho et al., 2003), mental and physical health (Grahn and Stigsdotter, 2003), and opportunities for recreational activities and tourism (Hall et al., 2009; Tangeland et al., 2013). Aside from their importance for climate actions and economy, investigating the effects of Northern European forests is interesting because of the intrinsic differences between these forests and other boreal regions. From the management standpoint, Northern European forests differ from other boreal forests in species composition and use. Scots pine, Norway spruce, mountain birch and downy birch dominate the boreal forest of Europe, with a minor component of European aspen (Boonstra et al., 2016 #128). Furthermore, forests in Northern European have been harvested for longer periods and more intensively than in North America and Russia, so that there is considerably less primary forest left (Ruckstuhl et al., 2008; Elbakidze et al., 2013). Climatically, Northern Europe is subject generally to milder and wetter conditions when compared to similar latitudes in Asia and North America (mostly characterized by continental climates). These conspicuous differences prevent the direct extrapolation of results and conclusions obtained elsewhere (Kong et al., 2017).

Because of the importance of boreal forests in Northern Europe for the delivery of the aforementioned ecosystem services, there is the need to quantify the forest sensitivity to climatic conditions at regional scale and identify which climatic conditions are beneficial and which are detrimental for these forests. Future climates are expected to result in a substantial increase in temperatures, in particular at high latitudes. The projected changes in precipitation are less clear, but an increase in winter precipitation and a decrease during the summers is expected (Ruosteenoja et al., 2018). Even if the amount of precipitation remained unaltered, the expected increase in temperature will enhance losses via evapotranspiration and result in more frequent periods of low water availability (Ruosteenoja et al., 2018). As such, extreme conditions in terms of heat and drought like the ones observed in summer 2018 are expected to become common in the next few decades (Toreti et al., 2019). Therefore, the importance of water availability for forest productivity on Northern Europe is expected to increase;

and management approaches should consider this aspect in increasing detail at least in more vulnerable regions. With a focus on the interplay between warmer temperatures and water availability, the following hypotheses were tested:

- Even though classified as temperature- and light-limited, the productivity of Northern European forests is also affected by water availability;
- The effects of warmer temperature on forest productivity are not homogeneously positive over Northern Europe;
- The correlation between temperature and forest productivity is positive in cold and moist locations while shifting to negative in warm and dry ones;
- By driving vegetation water availability, the timing of precipitation plays a more important role than the total precipitation amount.

To this aim, we explore the relationship between the MODIS-derived Normalized Difference Vegetation Index (NDVI)—a measure of vegetation activity and a proxy of forest productivity—and high-resolution gridded meteorological data (E-OBS) across Northern Europe for the period 2000–2015. Such large-scale study allows going beyond site-specific observations, potentially providing explanations for existing conflicting findings on Northern European forest responses to climate change. In particular, the response of forests to variations in climatic drivers within this period is examined and regions where forest productivity is positively and negatively affected by warming are identified. The potential mechanisms behind different responses are discussed, with special focus on the joint role of temperatures and water availability. The results have implications in the face of climate change because boreal regions are predicted to shift from short, cool summers toward longer, warmer summers. It will also serve to identify the most problematic hotspots where specific management strategies—species choices, planting density, rules of thinning and final felling, harvest intensities (e.g., Baul et al., 2017)—should be implemented.

## DATA AND METHODS

### Study Area

Northern Europe has a heterogeneous landscape, characterized by extensive forests, agricultural lands mostly in the southernmost regions and sparsely vegetated areas at higher elevations and in the northernmost areas. Here the focus is forested areas extending from latitude 55° to 70°N in Norway, Sweden and Finland (**Figure 1**—Denmark and Baltic countries were not included).

The forested areas were identified based on the CORINE land cover dataset (version 2012, 100 × 100 m of resolution, provided by the European Environment Agency). CORINE land cover is widely used for environmental modeling and land cover/land use change analyses in Europe (Büttner, 2014). CORINE land cover is widely used for environmental modeling and land cover/land use change analyses in Europe (Büttner, 2014). Two European validation studies have shown that the achieved accuracy is above the 85%, lending

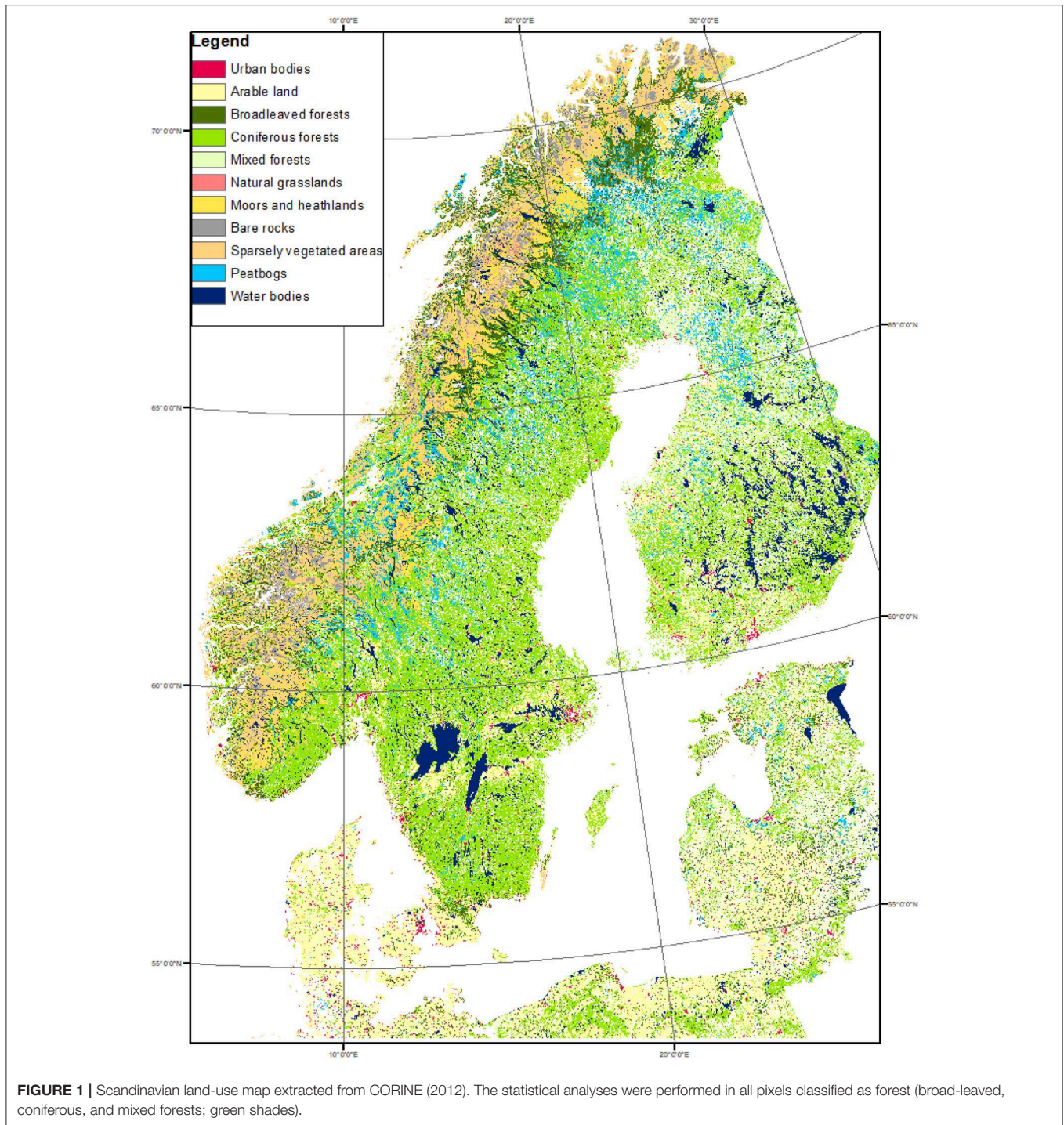
support to the use of this product (Soukup et al., 2016). The analyses were extended to all pixels identified in CORINE as dominated by coniferous, broadleaf or mixed forests. More than 90% of those pixels were classified as coniferous. This approach allowed excluding the non-vegetated or sparsely vegetated areas, grasslands, croplands, water bodies and urban areas.

### Source of Data

#### Moderate Resolution Imaging Spectroradiometer (MODIS)—Normalized Difference Vegetation Index (NDVI)

To explore the entire study area, the Normalized Difference Vegetation Index (NDVI) was used as a proxy of forest productivity. NDVI is a radiometric measure of the amount of photosynthetically active radiation (~400–700 nm) absorbed by vegetation and provides an indirect measure of vegetation photosynthetic activity, among other ecosystems, also in boreal forests (Park et al., 2016). Even though some aspects of productivity are not well-captured by this index (Fernández-Martínez et al., 2019; Tei et al., 2019), NDVI is often used as proxy of forest productivity (Olofsson et al., 2008; Sulla-Menashe et al., 2018) because it is well-correlated with tree growth, according to several independent validations against tree rings (Beck and Goetz, 2011; Berner et al., 2011). Further, NDVI has some advantages with respect to other remotely-sensed products. For example, Enhanced Vegetation Index (EVI) is often more sensitive than NDVI to variations in the viewing geometry, surface albedo, and sun elevation angle across variable terrain (Matsushita et al., 2007; Sestie et al., 2012). These factors are particularly relevant at middle-to-high latitudes (Walther et al., 2016). Similarly, even though promising, other recent products such as the Solar Induced Fluorescence (SIF) and/or the Photochemical Reflectance Index (PRI) appear to be negatively affected by atmospheric effects and random noises (Walther et al., 2016). On these bases, and similar to other recent studies (Sulla-Menashe et al., 2018; Mulder et al., 2019), NDVI was selected as the most suitable variable to perform a regional analysis of how boreal forest is affected by climate conditions.

NDVI data for the period 2000–2015 were extracted from tiles h18v02, h18v03, and h19v03 of the level 3 MOD13Q1 and MYD13Q1 provided by the Terra and Aqua satellites, respectively (NASA Land Processes Distributed Active Archive Center), at 16 day temporal resolution and 250 × 250 m spatial resolution. In these products, NDVI is retrieved from daily, atmosphere-corrected, bidirectional surface reflectance, via a MODIS-specific compositing procedure that discards low quality pixels. This product provides the maximum NDVI observed over the 16-day period, so that most of the effects of clouds and other atmospheric noises are effectively removed [see Didan (2015) for details]. Because the MODIS sensors aboard Terra and Aqua satellites are identical and, for each one, the maximum NDVI observed over the 16-day period is computed 8 days apart from one another, we combined both products so that, in practical terms, the temporal resolution of the NDVI dataset used here was 8 days.



### Meteorological Data: The E-OBS Dataset

Meteorological data for the study region for the period 2000–2015 were obtained from the E-OBS dataset. E-OBS is a high-resolution gridded dataset providing daily precipitation, minimum, maximum, and mean temperatures from 1950 (Haylock et al., 2008). This dataset was generated via innovative interpolation techniques combined with an accurate

pre-processing of the raw data retrieved from meteorological stations [see Haylock et al. (2008) for details]. The accuracy of E-OBS meteorological data depends on the number of meteorological stations and their spatial distribution. The station list updated to November 2016 reported more than 11,000 stations, of which over 1,900 were located in the region of interest.

This particular product was selected mainly because of its high spatial resolution ( $0.25^\circ \times 0.25^\circ$ )—higher than most of the current available gridded dataset of climatic variables. To our knowledge, there are only two precipitation products with finer resolution (CHIRPS and GSMAP-MVK with  $0.05^\circ$  and  $0.10^\circ$ , respectively), but they do not cover high latitudes. E-OBS has been previously used with satisfactory results (Kysely and Plavcova, 2010; Nikulin et al., 2011) and recently tested explicitly for Sweden (Ledesma and Futter, 2017).

## Data Preparation

### NDVI Data

The NDVI data were prepared for the analyses following a three-step approach. First, NDVI data were filtered based on their quality, exploiting the pixel reliability map included in each MOD13 file. This layer contains a flag describing the overall pixel quality at each time step [−1: No data; 0: Good data, 1: Marginal data (useful); 2: Snow/Ice and 3: Cloudy]. For each pixel, only NDVI values with reliability level of 0 or 1 were considered. The NDVI values with reliability 1 were further contrasted against the previous and subsequent value. Differences between the current NDVI and previous or subsequent values higher than the long-term mean NDVI in each pixel were considered as indicative of potential inconsistencies and the corresponding value discarded. Areas with sparse vegetation were masked out, by completely excluding pixels with long-term mean NDVI below 0.12, as recommended by Bjerke et al. (2014). Indeed, according to NASA providers, NDVI values between −0 and 0.12 correspond to scarce vegetation cover or bare soil.

Second, for each pixel, NDVI values were averaged over the growing season (see definition of growing season in the following sub-section). Finally, following Buermann et al. (2014), the data were aggregated to a  $0.25^\circ \times 0.25^\circ$  spatial grid to match the spatial resolution of the gridded meteorological data (details on the resampling approach can be found in section Spatial resampling). In this way, we obtained a proxy of annual vegetation productivity, to be analyzed for its interannual variability and linked to observed meteorological conditions. These spatial aggregation and seasonal averaging have also the advantage of decreasing the effect of low quality pixels, mostly caused by long cloudy periods.

### Definition of the Climatic Variables of Interest

To capture different mechanisms, we considered six climatic variables, and their values relative to both the whole year and the growing season only (subscript A and GS, respectively). Among the basic meteorological variables, we selected the annual and seasonal precipitation totals ( $PPT_A$ ,  $PPT_{GS}$ ), daily average temperature ( $T$ ,  $T_{GS}$ ) and daily maximum temperature ( $T_{MAX,A}$ ,  $T_{MAX,GS}$ ). Totals of reference evapotranspiration ( $ET_{0,A}$  and  $ET_{0,GS}$ ) were used as a measure of the ecosystem water demand; they include the role of temperature and solar radiation (and hence, indirectly, day length). Further, two additional variables were considered: (1) the  $ET_{0,A}/PPT_A$  ratio ( $ET_{0,GS}/PPT_{GS}$  ratio) describing the potential for annual (seasonal) water imbalances; and (2) the maximum number of consecutive days without precipitation ( $DWP_A$ ,  $DWP_{GS}$ ), characterizing the length of dry

**TABLE 1** | Symbols, definitions, and units of the climatic variables considered in this research.

Climatic variables	Definition	Units
$PPT_A$	Annual mean daily precipitation	mm
$PPT_{GS}$	Mean daily precipitation within the growing season	mm
$T_A$	Annual mean daily temperature	$^\circ\text{C}$
$T_{GS}$	Mean daily temperature within the growing season	$^\circ\text{C}$
$T_{MAX}$	Annual mean of the maximum daily temperatures	$^\circ\text{C}$
$T_{MAX-GS}$	Mean of the maximum daily temperatures within the growing season	$^\circ\text{C}$
$ET_{0,A}$	Annual mean reference evapotranspiration	mm
$ET_{0,GS}$	Mean reference evapotranspiration within the growing season	mm
$ET_{0,A}/PPT_A$ ratio	Ratio of annual cumulative $ET_0$ to annual cumulative PPT	–
$ET_{0,GS}/PPT_{GS}$ ratio	Ratio of cumulative $ET_0$ within the growing season to cumulative PPT within the growing season	–
$DWP_A$	Maximum number of consecutive days without precipitation within the year	day
$DWP_{GS}$	Maximum number of consecutive days without precipitation within the growing season	day

Annual values are defined with reference to the period from November to October of the following year; the growing season is defined as the days with a mean daily temperature higher than  $5^\circ\text{C}$ .

spells. These additional indicators allow exploring the potential effects of water shortage. The  $ET_0/PPT$  ratios quantify the water available in comparison to the evapotranspiration demand, thus summarizing the combined effects of precipitation, temperature and day length (i.e., warm temperatures and long days lead to high  $ET_0$ ). The ratio  $ET_0/PPT$  allows distinguishing between water-limited and energy-limited ecosystems (Budyko, 1964). DWP was suggested by the World Meteorological Organization Expert Team of Climate Change Detection and Indices as one indicator of extremes in climate and also by the Swedish Commission on Climate and Vulnerability for similar purposes (Persson et al., 2007). DWP informs about the precipitation timing and an increase in DWP indicates that rainfall is clustering more strongly into wet and dry periods, which will affect soil moisture dynamics (Folwell et al., 2016). All the climatic variables are summarized in **Table 1**, along with their definitions, symbols, and units.

The climatic variables of interest were extracted from the meteorological data for every forested pixel in Northern Europe from  $55$  to  $70^\circ\text{N}$  and for each year over the period for which both NDVI and E-OBS data were available (2000–2015). Annual values (subscript A) are means or totals relative to the months from November of 1 year to October of the following year, i.e., they are relative to the period from the approximate beginning of winter dormancy to the end of the growing season during the following calendar year. Growing season values (subscript GS) refer to those observed within the thermal growing season (Ruosteenoja et al., 2016). Here, the thermal growing season was defined as the period with daily mean air temperature above  $5^\circ\text{C}$  for two or more consecutive days (Skaugen and Tveito, 2004; Kauppi et al., 2014; Peichl et al., 2014). The  $5^\circ\text{C}$  threshold

is commonly employed in temperate and boreal ecosystems; it emerged also by comparing the thermal growing season with the actual onset of the growing season as inferred from satellite observations in Fennoscandia (Karlsen et al., 2007).

$ET_{0,A}$  and  $ET_{0,GS}$  were determined as totals of daily reference evapotranspiration values determined according to the Hargreaves and Samani formula (Hargreaves, 1983). This approach has the advantage of requiring only the maximum, minimum and mean daily temperatures, and an estimate of the potential solar radiation.

### Spatial Resampling

The spatial resolution of the E-OBS meteorological data is  $0.25^\circ$ , whereas the CORINE land cover data and the NDVI data have spatial resolutions of 100 and 250 m, respectively. Therefore, both the land use and the NDVI data were resampled to the  $0.25^\circ$  spatial resolution for consistency. In the case of the discrete land use data from CORINE, the spatial aggregation scheme could affect the prevalence of the different classes and the spatial coherence of each land use class within the aggregated product. Here, to assign the prevailing land cover class, a majority approach was adopted, as proposed by de Jong et al. (2013), among others.

Conversely, NDVI data were aggregated to  $0.25^\circ$  using the cubic convolution method (ArcGis 10.4.2, ESRI, Redlands, CA, USA). This method was deemed more appropriate than bilinear interpolation when using satellite data because it reduces potential noises and it does not have the disjointed appearance of the nearest neighbor interpolation (Wu et al., 2008). It is important to note that the NDVI resampling was performed on the pre-processed maps (i.e., the steps detailed in section NDVI data were carried out at the original resolution).

Once all the datasets were resampled at the same spatial resolution, the pixels classified as forest were identified based on the resampled CORINE. These pixels—7,020 in total—were retained for the analyses detailed below.

### Data Analyses: Partial Least Square (PLS) Regression and Their Rationale

NDVI and meteorological data for all pixels classified as forest were analyzed by Partial Least Square (PLS) regression. The goal was to assess the role played by each climatic driver and whether such role varied with location (and hence climatic conditions). PLS is a generalization of the Principal Components Regression (PCR) analysis (Geladi and Kowalski, 1986; Wold et al., 2001). Similar to PCR, PLS is used to analyze the relationship between a set of dependent (y-variables: in our case,  $NDVI_{GS}$ ) and independent variables (x-variables: the climatic variables reported in **Table 1**). It extracts from the x-variables the set of new components with the best explanatory power of the y-variable. Different from simple regression techniques, both PCR and PLS can handle collinear predictors (Gunst and Mason, 1979), thus making these techniques suitable when considering multiple, potentially partially correlated, climatic indicators. This advantage makes PLS and/or PCR appropriate for our aims, since we expect that some of the climatic variables involved (**Table 2**) are correlated (Zscheischler and Seneviratne, 2017). The main

difference between PCR and PLS is that with PCR, the principal components are determined solely based on the data values of the x-variables, whereas with PLS the data values of both the x and y-variables influence the construction of the components. Thus, PLS is particularly useful when considering a high number of x-variables in comparison with the number of y-variables (Abdi, 2010)—as it is the case in this study. A similar approach was used by Peichl et al. (2014) to investigate the combined effect of temperature and water table level on the net  $CO_2$  exchange of a boreal fen. We apply the PLS analyses over a substantially larger area, i.e., Northern European forests within  $55$  and  $70^\circ N$ .

To better understand the role of the climatic variables, in each pixel, we performed nine different PLS analyses with different choices of climatic (explanatory) variables (**Table 2**). Each analysis considered five to six climatic variables, chosen as discussed next and listed in **Table 2**. In summary, this choice of climatic variables led to the six PLS analyses (referred to as 1–6) listed and justified below. Further analyses complemented this set, by considering the same set of climatic variables of analyses 1, 4 and 5, but by focusing just on the growing season (Analysis 1<sub>GS</sub>) or on the values of the climatic variables pertaining the previous year (Analyses 4 and 5 lag). The second-order Akaike Information Criterion (AIC) allowed the estimate of the relative quality of each statistical model. The AIC measures the relative model fit and it is proportional to the likelihood of the model and the number of parameters used to generate it (Burnham et al., 2011). A set of climatic variables with high explanatory power and low AIC value are suggestive of those variables being adequate to explain the changes in NDVI.

The explanatory variables were chosen as follows. The first two PLS analyses aimed at quantifying the explanatory power of the climatic variables when considering only their annual means [Analysis 1, as e.g., in Ichii et al. (2002) and Yuan et al. (2009)] or within growing season means (Analysis 1<sub>GS</sub>, as e.g., in Zhao et al., 2018).

Analysis 2 involved only the basic meteorological variables: PPT, T and  $T_{MAX}$  for the whole year and within the growing season. As such, Analysis 2 represents the baseline for comparison to other choices of the explanatory variables. Comparison of the results of Analysis 2 and those of Analyses 1 and 1<sub>GS</sub> shows whether annual and seasonal variables need to be combined to explain the observed patterns of NDVI.

Four additional sets of explanatory variables were considered, based on the following rationale. Since the maximum temperature is likely to occur during the growing season, we only considered  $T_{MAX}$  within the growing season ( $T_{MAX,GS}$ ), while keeping annual T ( $T_A$ ), while keeping annual T, including thus both climatic variables but computed over different periods. Further,  $ET_0$  and both the water stress indicators ( $ET_0/PPT$  ratio and DWP) likely have a higher explanatory power of forest productivity when computed within the growing season rather than over the whole year. Hence, the basic climatic variables were complemented by  $ET_{0,GS}$  in Analysis 3,  $ET_{0,GS}/PPT_{GS}$  ratio in Analysis 4, and  $DWP_{GS}$  in Analysis 5. Analysis 6 included a water stress index but it did not consider  $ET_{0,GS}$ . When compared to the results of Analysis 5, Analysis 6 allowed assessing the relative importance of including a water stress indicator in lieu of  $ET_{0,GS}$ .

**TABLE 2** | Combinations of climatic variables considered in each PLS analysis and median, maximum, and minimum AIC score attached to each combination of climatic variables over the study site.

Climatic variables	1	1 <sub>GS</sub>	2	3	4	5	6	4 lag	5 lag
PPT <sub>A</sub>	X		X	X	X	X	X	X	X
PPT <sub>GS</sub>		X	X	X	X	X	X	X	X
T <sub>A</sub>	X		X	X	X	X	X	X	X
T <sub>GS</sub>		X	X						
T <sub>MAX,A</sub>	X		X						
T <sub>MAX,GS</sub>		X	X	X	X	X	X	X	X
ET <sub>0,A</sub>	X								
ET <sub>0,GS</sub>		X		X	X	X		X	X
ET <sub>0,A</sub> /PPT <sub>A</sub> ratio	X								
ET <sub>0,GS</sub> /PPT <sub>GS</sub> ratio		X			X				
ET <sub>0,GS</sub> /PPT <sub>GS</sub> ratio (lag)								X	
DWP <sub>A</sub>	X								
DWP <sub>GS</sub>		X				X	X		
DWP <sub>GS</sub> (lag)									X
AIC	13.25 <sub>17.66</sub> 13.01	12.78 <sub>18.02</sub> 12.46	11.72 <sub>12.42</sub> 10.42	16.68 <sub>18.23</sub> 15.52	11.26 <sub>11.92</sub> 11.01	7.26 <sub>10.58</sub> 3.36	13.70 <sub>15.46</sub> 9.43	11.44 <sub>16.68</sub> 11.44	11.46 <sub>14.3</sub> 7.95
ΔAIC	5.99	5.52	4.46	9.46	4	0	6.44	4.18	4.2

ΔAIC is the difference between AIC of each analysis and the minimum AIC (corresponding to Analysis 5).

**TABLE 3** | Long-term and study-period annual average temperature, precipitation, and length of the growing season.

		LONG-TERM			STUDY PERIOD		
		Average	Period	Source	Average	Period	Source
TEMPERATURE (°C)	Norway	1.1	1960–2013	CRU	1.6	2000–2015	E-OBS
	Sweden	4.8	1960–2013	SMHI	5.3	2000–2015	E-OBS
	Finland	2.0	1960–2013	FMI	4.1	2000–2015	E-OBS
PRECIPITATION (mm)	Norway	960	1960–2013	CRU	1030	2000–2015	E-OBS
	Sweden	600	1960–2013	SMHI	620	2000–2015	E-OBS
	Finland	620	1960–2013	FMI	648	2000–2015	E-OBS

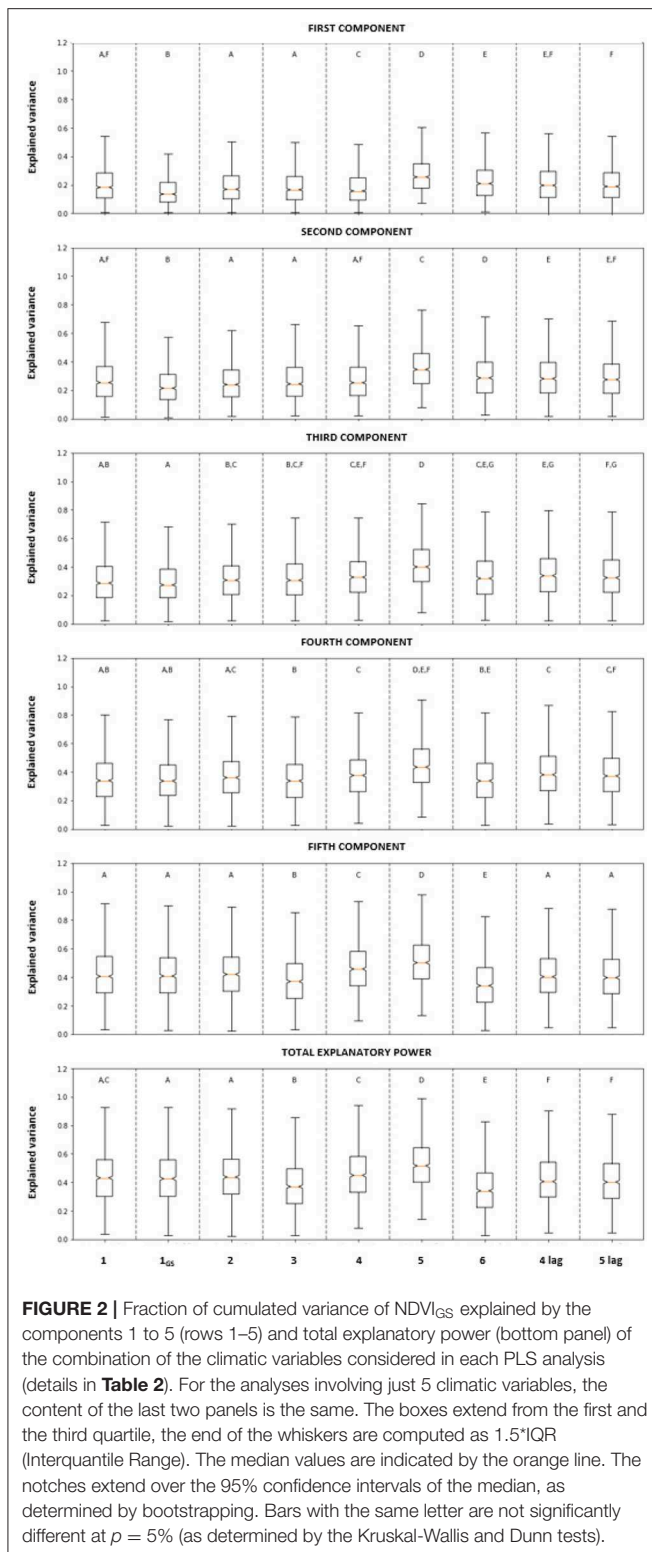
The sources of data are: CRU, Climatic Research Unit; UEA, University of East Anglia; SMHI, Swedish Meteorological and Hydrological Institute; FMI, Finnish Meteorological Institute.

All the analyses mentioned above were based on the climatic and vegetation data of the same year in which the NDVI was observed, as in Buermann et al. (2014). Indeed, no apparent lag effect longer than 1–2 months, i.e., no lag effect beyond the current year, emerged in previous analyses of NDVI data at higher northern latitudes (Wu et al., 2015). However, other studies showed that climatic conditions during the previous growing season can affect vegetation activities and NDVI in some locations over the northern high latitude region (<20% of Northern Europe) (Tei and Sugimoto, 2018). Moreover, a 1 year-long lag effect of droughts (or periods with low water availability) emerged in some regions located in northern latitudes (Vicente-Serrano et al., 2013). To explore the possibility of a lag effect of water scarcity, two additional PLS analyses were performed, with the same configuration as Analyses 4 and 5, but considering ET<sub>0,GS</sub>/PPT<sub>GS</sub> ratio and DWP<sub>GS</sub> relative to the previous growing season (Analyses 4 and 5 lag).

Moreover, the non-parametric Kruskal-Wallis test (Kruskal, 1952) was used to test whether the median cumulated

explanatory power of the PLS were significantly (at 5%) different among the nine analyses performed. When the Kruskal-Wallis test indicated that there were significant differences among the medians, multiple pairwise comparisons based on the Dunn's test (Dunn, 1964) allowed identifying which specific groups of analyses led to significantly different results from the others.

Finally, we computed the correlation coefficient between NDVI<sub>GS</sub> and each climatic variable (Table 2) in each pixel and we extracted the 90th and 10th percentile of those values. Aiming to focus on those locations where the response of NDVI<sub>GS</sub> to the climatic variables was the strongest, the pixels with the highest correlation (i.e., above the 90th percentile) and the lowest correlation (i.e., below the 10th percentile) were singled out. Then, the median and variability of the mean annual temperature and total precipitation for each group were compared. To ensure that values higher/lower than these extremes corresponded to highly positive/negative correlations between the variables and NDVI<sub>GS</sub>, we tested that both percentiles were significantly (at 5%) different from zero.



**FIGURE 2 |** Fraction of cumulated variance of NDVI<sub>GS</sub> explained by the components 1 to 5 (rows 1–5) and total explanatory power (bottom panel) of the combination of the climatic variables considered in each PLS analysis (details in **Table 2**). For the analyses involving just 5 climatic variables, the content of the last two panels is the same. The boxes extend from the first and the third quartile, the end of the whiskers are computed as 1.5\*IQR (Interquartile Range). The median values are indicated by the orange line. The notches extend over the 95% confidence intervals of the median, as determined by bootstrapping. Bars with the same letter are not significantly different at  $p = 5\%$  (as determined by the Kruskal-Wallis and Dunn tests).

## RESULTS

### Climatic Conditions

The long-term average annual temperature for the period 1960–2013 was 4.8°C in Sweden, 1°C in Norway, and 2°C in Finland.

Among the 15 study years (2000–2015), all years except 2010 were warmer than these long-term averages (**Table 3**). As expected, the average annual temperature decreased with latitude.

The length of the growing season decreased with latitude along with temperature. In the northernmost regions, the average growing season length over the period 1960–2013 was <170 days in all years, while it was around 210 days in southern Sweden. A substantial increase of the duration of the growing season has been observed from 1960 to 2014 in Sweden as a consequence of warming (Kauppi et al., 2014).

Regarding precipitation, the long-term average annual total for the period 1960–2013 was 960 mm in Norway, 600 mm in Sweden, and 620 mm in Finland. All the years within the study period had annual average precipitation similar to the long-term precipitation averages (**Table 3**).

In summary, over the period 2000–2015, the study region experienced warmer temperatures and longer growing seasons without significant changes in precipitation, when compared to the long-term averages (**Table 3**). This combination can lead to more frequent temperature-induced water stress.

### Abiotic Controls on NDVI<sub>GS</sub>: PLS Analysis

A PLS analysis was performed for each set of explanatory variables (**Table 2**) and pixel. For our purposes, the key outputs of the PLS analyses are (1) the variance explained by each component; and (2) the correlation coefficients, the sign of which allows distinguishing negative and positive correlations between the climatic conditions and the NDVI<sub>GS</sub> (x and y-variables, respectively). Due to the large area analyzed, the results of the PLS analyses can differ from pixel to pixel. The results are presented mostly in an aggregated form, i.e., as distributions of values across pixels, to facilitate the comparison among locations and the different combinations of explanatory variables.

### Variance Explained by the Components

**Figure 2** summarizes the distribution of the cumulated explanatory power for the component 1 to 5, and its variability across pixels, for the components 1–5. The bottom panel reports the total explanatory power for each set of predictor variables.

Analyses 1 and 1<sub>GS</sub> had a low median explanatory power (**Figure 2**; median total explanatory power of 43.7 and 42.5%, respectively), despite the inclusion of all the climatic variables for the whole year and the growing season, respectively. The variables included in Analysis 1 (i.e., variations within the whole year) provided a small but significantly (at 5%) higher explanatory power in the first two components than Analysis 1<sub>GS</sub> (top two plots) but there was no difference between these two analyses when considering their total explanatory power (bottom plot).

Analysis 2 combined the basic meteorological variables for both the whole year and the growing season ( $T_A$ ,  $T_{MAX,A}$  and  $PPT_A$  and  $T_{GS}$ ,  $T_{MAX,GS}$  and  $PPT_{GS}$ , **Table 2**). The median explanatory power of the first three components was 27.2%, while the median total explanatory power was 42.5%. There was no significant difference in the total explanatory power between Analysis 2 and those considering the annual and growing season variables in isolation (Analyses 1 and 1<sub>GS</sub>).



Analysis 3 was designed to quantify the importance of  $ET_{0,GS}$  (and hence, indirectly day-length and potential solar radiation) to explain the observed patterns in  $NDVI_{GS}$ . Thus, it considered the basic meteorological variables plus  $ET_{0,GS}$  (Table 2) but neglected  $T_{MAX,GS}$  and  $T_{GS}$ . The median explanatory power of the three first components was not significantly different from those of the previously discussed choices of explanatory variables (Figure 2, three first panels).

Analyses 4 and 5 were designed to better understand the effects of water availability on the observed NDVI. By including either the  $ET_{0,GS}/PPT_{GS}$  ratio or the days without precipitation ( $DWP_{GS}$ ), the total explained variance of  $NDVI_{GS}$  significantly (at 5%) increased with respect to the analyses not considering any proxy of water availability. Between the two water availability proxies, the explanatory power was significantly (at 5%) higher when considering  $DWP_{GS}$  (Analysis 5) than that including  $ET_{0,GS}/PPT_{GS}$  ratio (Analysis 4).

Analyses 3 and 6, which involved the same number of explanatory variables (5 in total), presented similar results regarding the first three components with a median explanatory power of 30.5 and 31.8%, respectively (Figure 2). However, the total explanatory power of Analysis 3 was significantly (at 5%) higher than Analysis 6 (Figure 2), pointing to the importance of including  $ET_{0,GS}$  as predictor of the  $NDVI_{GS}$ .

Finally, Analyses 4-lag and 5-lag were designed to evaluate the potential lag effect of the climatic conditions on plant productivity. In both cases, considering the climatic variables during the same growing season in which  $NDVI_{GS}$  was measured (i.e., Analyses 4 and 5) resulted in a significantly (at 5%) higher explanatory power than those based on lagged climatic variables.

In summary, despite having the same number of climatic variables as Analysis 1, 1<sub>GS</sub>, 2, and 4, Analysis 5 (which included  $PPT_A$ ,  $PPT_{GS}$ ,  $T_A$ ,  $T_{MAX,GS}$ ,  $ET_{0,GS}$ , and  $DWP_{GS}$ ) had a significantly higher explanatory power than any other choice of climatic variables investigated here, both in each component and in total. Analysis 5 emerged as the best fitting model also based on the AIC (Table 2). It should be noted that, in practical terms, models with AIC differing from the minimum AIC (corresponding to the best fitting model) of <2 all have plausible support, i.e., no differences between models (Burnham and Anderson, 2002). The differences obtained in our analyses were higher than that threshold in all cases, showing that there were significant differences between the models and Analysis 5 had the highest performance (Table 2).

### Correlation Coefficients

Focusing on the set of climatic variables with the highest explanatory power (Analysis 5), we considered the sign of the correlation coefficients between the climatic (x-)variables and  $NDVI_{GS}$  (y-variable), and whether positive or negative correlations were co-occurring with specific mean annual temperature and precipitation total. Positive correlations imply that higher values of the climatic variable result in higher values of  $NDVI_{GS}$ ; and, *vice versa*, negative correlations imply that higher values of the variable results in lower  $NDVI_{GS}$ .

To focus on the locations where the response of  $NDVI_{GS}$  to the climatic conditions was strongest, the pixels with the

**TABLE 4** | Values of the percentile 90th and 10th of the correlation coefficient between  $NDVI_{GS}$  and each climatic variable included in Analysis 5.

Climatic variables	Percentile 90th	Percentile 10th
$PPT_A$	0.487	-0.347
$PPT_{GS}$	0.481	-0.418
$T_A$	0.521	-0.315
$T_{MAX,GS}$	0.462	-0.493
$ET_{0,GS}$	0.483	-0.115
$DWR_{GS}$	0.419	-0.372

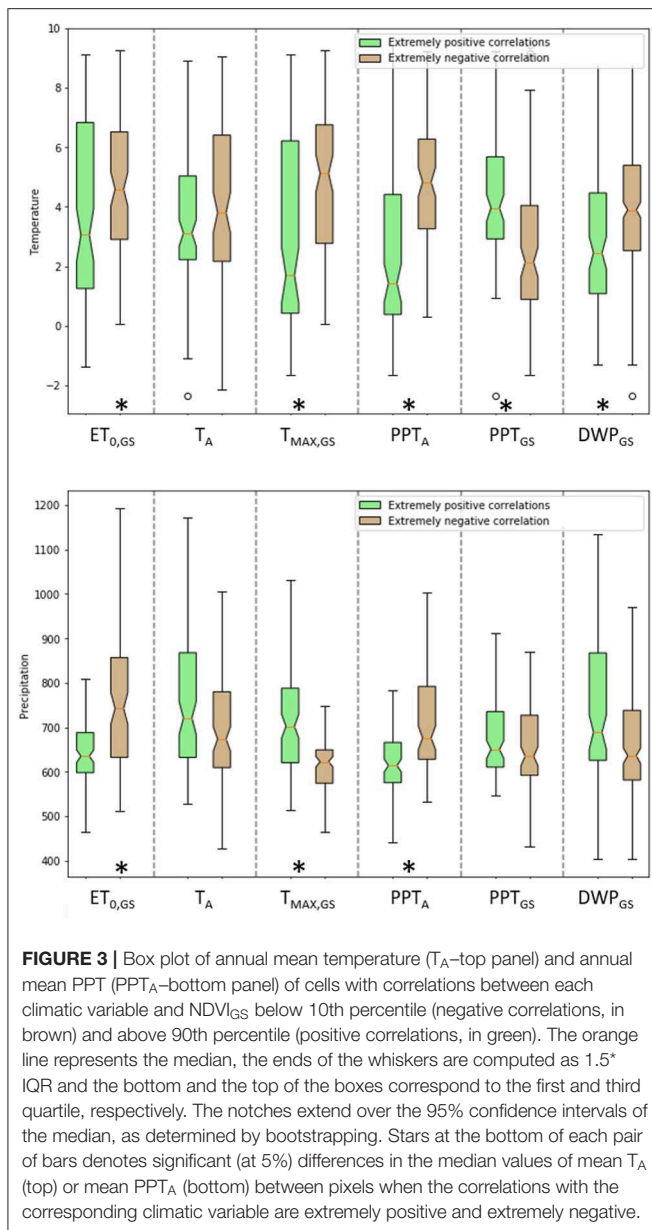
highest (above the 90th percentile) and lowest (below the 10th percentile) correlation coefficients between  $NDVI_{GS}$  and each climatic variable were singled out. All the correlation coefficients above the 90th percentile were positive, while all the ones below the 10th percentile were negative. The values of these percentiles for each climatic variable are reported in Table 4. Both percentiles for all climatic variables are significantly (at 5%) different from zero, indicating that values higher/lower than these extremes correspond to high correlations between the variables and  $NDVI_{GS}$ . Figure 3 summarizes the median and variability of mean annual temperature (top panel) and precipitation (bottom panel) of the pixels with the highest (green) and lowest (brown) correlation coefficients between  $NDVI_{GS}$  and each climatic variable.

The highest (and positive) and lowest (and negative) correlation coefficients were found in a wide range of thermal regimes (Figure 3, top panel). However, focusing on the medians, pixels with extremely negative correlation coefficients between  $NDVI_{GS}$  and any of the climatic variables (except  $PPT_{GS}$  and  $T_A$ ) were located in significantly (at 5%) warmer regions (Figure 3 top panel and Figure 4). The same pattern holds also for  $T_A$ , but the difference between the median correlation coefficients is not significant at 5%. This general pattern is suggestive that higher  $ET_{0,GS}$ ,  $T_A$ ,  $T_{MAX,GS}$ ,  $PPT_A$ , and  $DWP_{GS}$  result in lower values of  $NDVI_{GS}$  in warmer places. Regarding mean annual PPT (Figure 3, bottom panel), median correlations between  $T_{MAX,GS}$  and  $NDVI_{GS}$  were significantly (at 5%) higher in wetter than drier pixels. Also extremely positive correlations between  $T_A$  and  $DWP_{GS}$  with  $NDVI_{GS}$  were more common in wetter pixels. Hence, higher temperatures and higher number of days without precipitation appear more beneficial when precipitation totals are higher. Conversely, extremely positive correlations between  $NDVI_{GS}$  and  $PPT_A$  and  $ET_{0,GS}$  occurs significantly (at 5%) more in pixels with lower mean  $PPT_A$ .

## DISCUSSION

### Drivers of Boreal Forest Productivity in Northern Europe: the Key Role of Water Availability

A set of PLS analyses was performed to identify the main drivers of boreal forest productivity. While statistical analyses such as the one presented here cannot reveal the mechanistic cause of the observed patterns, the comparison of different choices of



explanatory variables allows identifying the key drivers and is suggestive of the mechanisms at play. Our pairwise comparison of the seven analyses without time lags highlighted that considering proxies of water availability markedly increases the explanatory power of the climatic variables. Indeed, even though Analyses 1, 1<sub>GS</sub>, 2, 4, and 5 included the same number of climatic variables (Table 2), the total explanatory power of Analysis 5 was significantly higher than that of the other analyses (Figure 2). Analysis 5 is also ranked as the best model based on AIC, followed by Analysis 4 (Table 2). Altogether, these findings support our first hypothesis, suggesting that water availability can limit plant productivity also across boreal forests in Northern Europe—an ecosystem so far considered as light- and temperature-limited, but not water-limited (Allen et al., 2010).

It has long been recognized that water availability can affect plant photosynthetic capacity, growth, and physiological stress responses (Hsiao, 1973). Nevertheless, so far the response of boreal forests to reduced soil water availability has been seldom considered (Solberg, 2004; Grossiord et al., 2014). A decrease in aboveground growth rates as a consequence of water limitation and a clear interaction between biodiversity and water availability emerged in a boreal forest stand located in Finland (Grossiord et al., 2014). In southeastern Norway, dry and warm summers led to defoliation, yellowing, scarce cone formation and high mortality in Norway spruce (Solberg, 2004; Andreassen et al., 2006). However, these results are based on specific sites and conditions, while our analyses show that the sensitivity of boreal forest to water limitations is common in most of Northern Europe.

Finally, the potential lag effect of water scarcity on forest productivity was explored by Analysis 4-lag and 5-lag. Regional dendroclimatological studies have shown that tree growth is better correlated to the conditions during the previous growing season than those of the current one (Carrer et al., 2010; Babst et al., 2012). Nevertheless, while lag effects in tree-rings and autocorrelation in ring width measurements are well-established (Berner et al., 2011), lag effects in NDVI measurements have not been widely examined. Further, a high correlation between tree rings and NDVI does not imply that tree rings adjust immediately to changes in NDVI (Kaufmann et al., 2008). As such, even though a lagged effect of growing conditions on tree ring formation has been observed, a similar delay might not emerge when considering NDVI (Wu et al., 2015; Tei and Sugimoto, 2018). Indeed, our results show that current year conditions have a higher explanatory power than those of the previous year, suggesting that  $NDVI_{GS}$  mostly responds to current conditions. This result is consistent with previous analyses showing that conditions of the previous year are dominant in <20% of high latitude study sites in Europe (Wu et al., 2015; Tei and Sugimoto, 2018).

## Effects of Temperature on Boreal Forest Productivity: From Positive to Negative

To disentangle the role of different climatic variables on  $NDVI_{GS}$ , we considered the combination of climatic variables with the highest explanatory power (Analysis 5) and explored the sign and level of correlation between the different climatic variables and  $NDVI_{GS}$  across locations and climatic conditions. Special attention was devoted to temperature in an attempt to unravel the potentially opposite effects of the predicted increase in temperatures on boreal forest productivity. On the one hand, warmer temperatures reduce the constraints on productivity imposed by low temperature and growing season length typical of higher latitudes; on the other hand, warmer temperatures can lead to more frequent and severe heat stress but also to water stress, even if not associated to reductions in precipitation (Ruiz-Pérez et al., 2019). Temperature was included in Analysis 5, directly through  $T_A$  and  $T_{MAX,GS}$ , indirectly through  $ET_{0,GS}$ . Temperature plays a key role on boreal forest productivity regardless of latitude—a conclusion consistent with

previous results on boreal ecosystems and their dependency on temperatures (e.g., Bonan and Shugart, 1989). Nevertheless, our results show that the correlations between  $T_A$  (and  $T_{MAX,GS}$ ) and  $NDVI_{GS}$  were far from uniformly positive across the study region (Figure 4). In other words, the expectation that an increase in temperatures is beneficial for boreal forests does not always hold.

Patterns emerged when comparing the climatic conditions under which the extremely negative (below the 10th percentile) and the extremely positive (above the 90th percentile) correlations occurred (Figures 3, 4). Regardless of the temperature-related climatic variable considered, extremely positive correlations occurred mostly in locations with lower annual mean temperature. A similar divergence between increased temperatures and tree-ring formation was observed in the southernmost regions of Scandinavia [Babst et al. (2012) and Trahan and Schubert (2016)]. Nevertheless, being based on satellite data and standard meteorological data, our approach permits analyses at regional scale, thus facilitating the identification of regions that are potentially more sensitive to specific climatic conditions.

Geographically, the effects of warming temperatures on forest productivity depend on the mean annual temperature (as apparent in Figure 3, top panel) and hence substantially on latitude. The majority of pixels with extremely positive correlation between temperature-related climatic variables and  $NDVI_{GS}$  are located in northern/colder regions. Conversely, the pixels with extremely negative correlation are mostly located at lower latitudes. An example of this geographical distribution is reported in Figure 4, which refers to the case of the correlation between  $T_{MAX,GS}$  and  $NDVI_{GS}$ .  $65^{\circ}N$  emerges as the latitudinal threshold at which the correlation between  $T_{MAX,GS}$  and  $NDVI_{GS}$  shifts from extremely positive at higher latitudes to extremely negative at lower ones. Only one pixel with extremely negative correlation is located north of  $65^{\circ}N$ , while 65.9% of those with extremely positive correlation are. This latitudinal threshold is consistent with the one emerging from analyses based on the European Tree Ring Width (TRW) network, suggesting that Northern Europe can be divided into two regions according to similarities in the annual growth variability (Babst et al., 2012). A similar threshold emerges also outside Northern Europe. In Eurasia, the correlation between summer temperatures and tree ring increments increases linearly with latitude from negative to positive values, with positive correlations at latitudes above  $65^{\circ}N$ , and negative elsewhere (Hellmann et al., 2016). Across the whole circumboreal region such emerging latitudinal threshold was  $67^{\circ}N$  (Tei and Sugimoto, 2018). Due to the clear link between temperature and latitude in these regions, the latitudinal threshold is most likely to be interpreted as a threshold in terms of temperature. In other words, at latitudes below  $65^{\circ}N$ , the air temperature might have already exceeded a limit above which boreal forests do not benefit from increases in air temperature. As apparent from Figure 4, this temperature threshold ranges from 14.5 to  $17.8^{\circ}C$  (average maximum air temperature within the growing season). Future warmer temperatures could shift this geographic boundary farther north.

Hence, these results confirm the hypothesis that the effects of warmer temperature of forest productivity are not

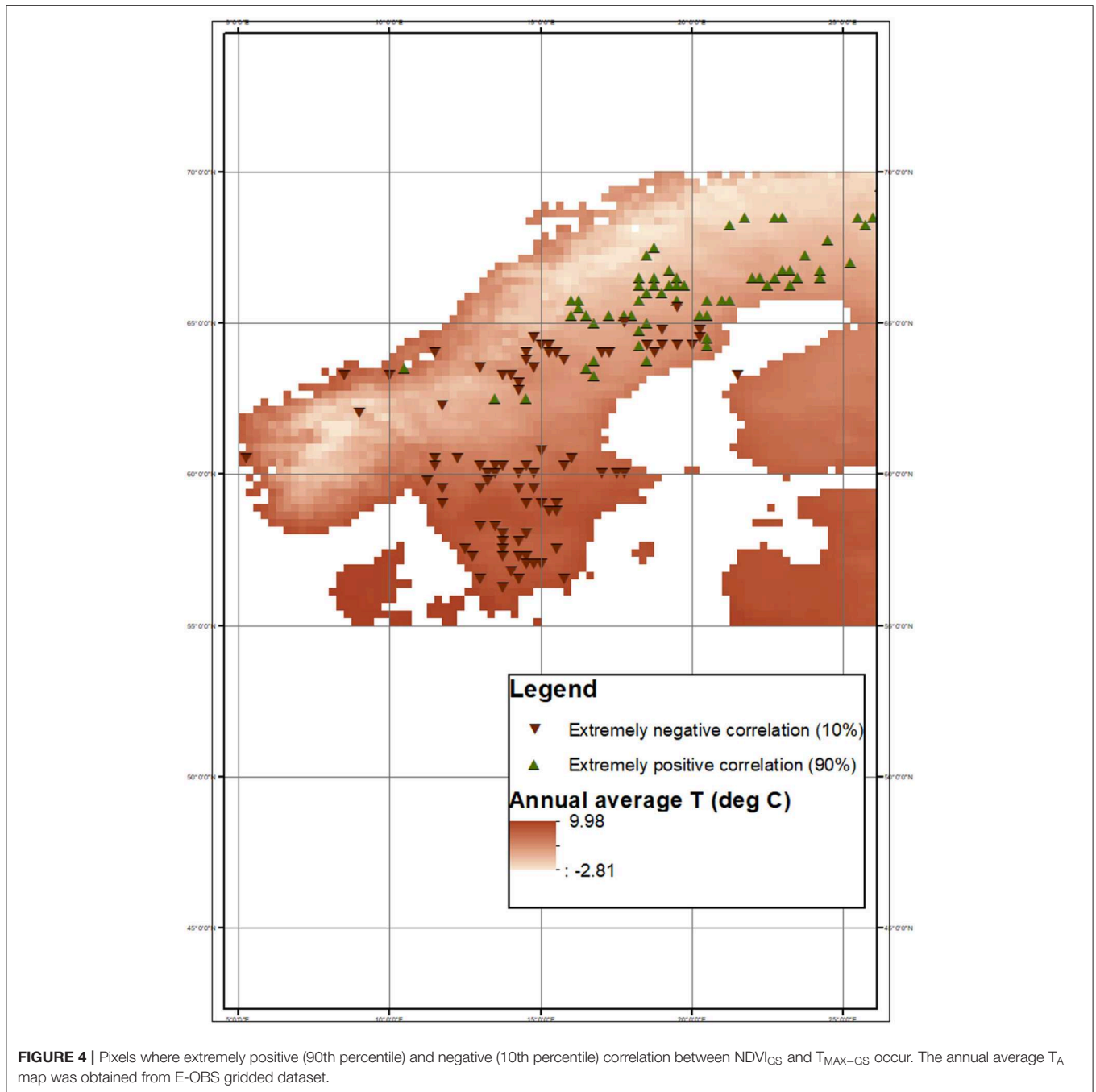
uniformly positive over Northern Europe. Rather, an increase in temperature is currently beneficial (as indicated by a positive correlation) mainly in the coldest (i.e., northernmost) regions, while negative correlations were observed in warmer regions (i.e., southernmost regions). Further, the emerging patterns are suggestive of a threshold-like pattern in the correlation between temperature and forest productivity. However, some exceptions emerged, i.e., some pixels with extremely positive correlations were located in southern regions and *vice versa*. These exceptions might be driven by local features such as soil properties or wind patterns. In particular, deeper soils and higher water retention capacity can reduce the effects of low precipitation amount in general and dry spells in particular, buffering dry, and warm periods.

## Interplay Between Temperature and Water Availability

In most circumstances, plants are able to cope well with high temperatures for short periods as long as they have access to sufficient water resources. Under well-watered conditions, plants can maintain their stomata fully open, ensuring not only a high net  $CO_2$  uptake, but also leaf evaporative cooling. Conversely, low soil water availability reduces not only stomatal aperture,  $CO_2$  uptake via photosynthesis and thus potentially plant growth (Hsiao, 1973), but also evaporative cooling, so that water limitations can exacerbate the negative effects of warm temperatures. If air temperature and solar radiation are high, then leaf temperature can become such that net  $CO_2$  assimilation rate is reduced (Yamori et al., 2014) and permanent damage could occur (O'Sullivan et al., 2017).

This role of the water availability on the response of tree growth to warmer temperatures has already been observed also in boreal regions. Indeed, one key consequence of global warming in boreal North America has been regional drought stress leading to reduced tree growth (Verbyla, 2015) and even enhanced tree mortality [(e.g., Williams et al. (2013)]. In Norway, tree-ring formation of Norway spruce was shown to respond negatively to warm summers in dry locations, while the response was positive in moist regions Solberg, 2004; Andreassen et al., 2006. Our results point to a similar pattern, but over a larger region and species set: most of the pixels with extremely negative correlations between  $NDVI_{GS}$  and  $T_A$  and  $T_{MAX,GS}$  are located in places with lower annual mean precipitation (Figure 3, bottom panel). These findings support our initial hypothesis, suggesting that the correlation between temperature and forest productivity varies not only according to a thermal gradient but also according to a moisture one, being positive in cold and moist regions and negative in warm and dry ones.

The analysis of the correlation coefficients between  $NDVI_{GS}$  and  $DWP_{GS}$  also shows the influence of water availability on boreal forest productivity. Extremely negative correlations between  $NDVI_{GS}$  and  $DWP_{GS}$  coefficients were more common in drier and warmer conditions, while extremely positive correlation coefficients occurred mostly in well-watered and cooler pixels (Figure 3). These results suggest that the effect of temperature is mediated by water availability and its timing.



**FIGURE 4 |** Pixels where extremely positive (90th percentile) and negative (10th percentile) correlation between  $NDVI_{GS}$  and  $T_{MAX-GS}$  occur. The annual average  $T_A$  map was obtained from E-OBS gridded dataset.

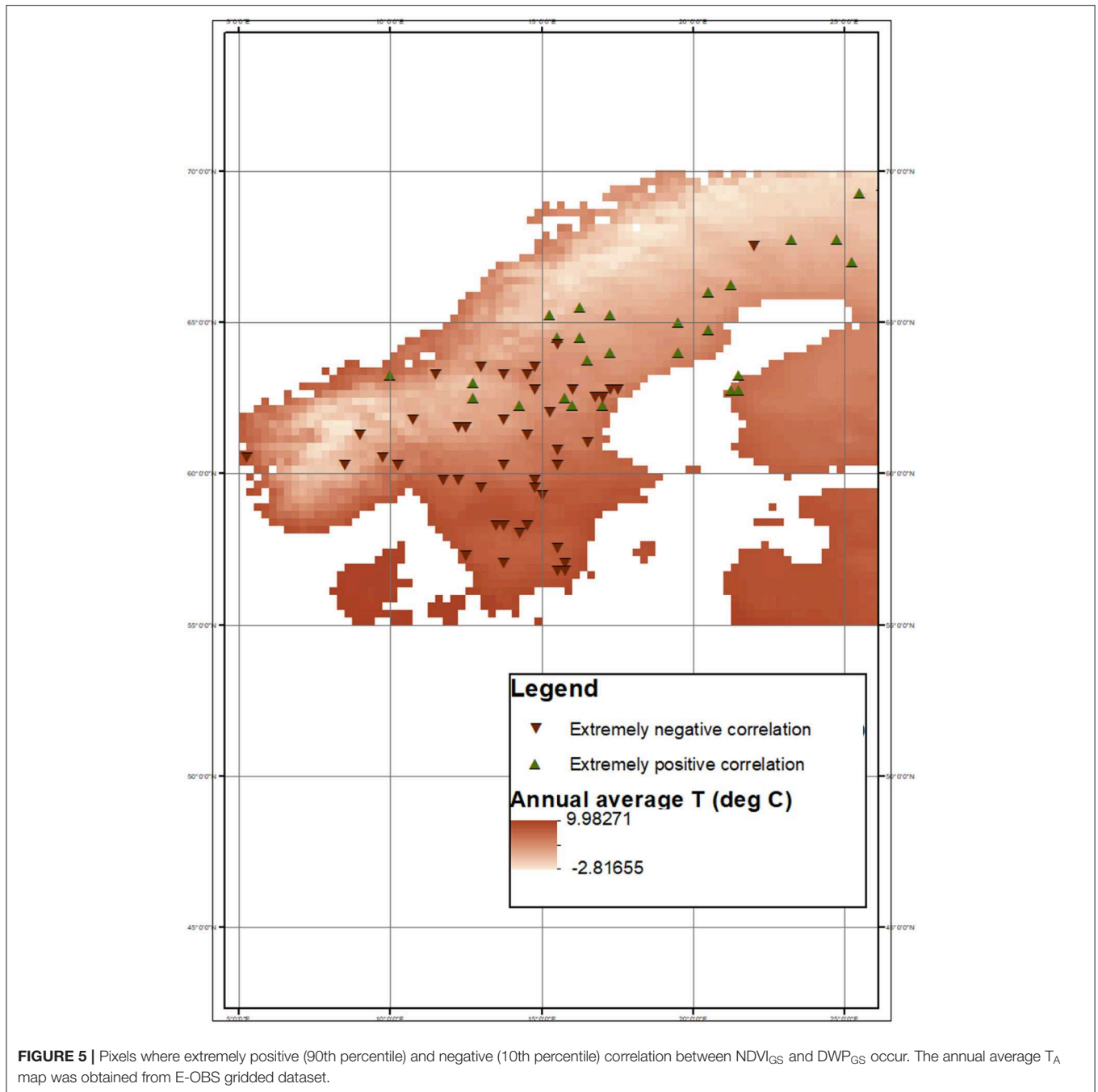
Hence, a (direct or indirect) role of water stress is to be expected not only in dry regions (Anderegg et al., 2013), but also in the relatively mesic Northern European boreal forests. Furthermore, most of the extremely negative correlations between  $T_{MAX,GS}$  and  $NDVI_{GS}$  are located over southern Sweden.

Geographically, similarly to temperature-related climatic variables, most pixels with extremely positive correlation between  $DWP_{GS}$  and  $NDVI_{GS}$  are located in northern/colder regions, whereas the pixels with extremely negative correlation are at lower latitudes (Figure 5). Moreover, even though less evident,

this dichotomy between north and south was also observed when comparing “less extreme” correlation coefficients (corresponding to the 80th–20th and 70th–30th percentiles) as shown in the **Supplementary Material**.

### Importance of Precipitation Timing

As shown by the Kruskal-Wallis and Dunnett’s tests, significant differences in the explanatory power emerged between the two proxies of water stress explored here (the  $ET_{0,GS}/PPT_{GS}$  ratio and  $DWP_{GS}$ ). The inclusion of  $DWP_{GS}$  (i.e., Analysis 5) led



**FIGURE 5 |** Pixels where extremely positive (90th percentile) and negative (10th percentile) correlation between  $NDVI_{GS}$  and  $DWP_{GS}$  occur. The annual average  $T_A$  map was obtained from E-OBS gridded dataset.

to the highest total explanatory power (Figure 2).  $PPT$  and  $ET_0$  are the key drivers of the water balance. Their ratio,  $ET_0/PPT$ , represents the water available for evapotranspiration and allows distinguishing between water-limited and energy-limited ecosystems (Budyko, 1964). This ratio is based on the precipitation and transpiration totals over the growing season or whole year. Cumulative values can mask fluctuations, so that wet periods can compensate dry periods. Conversely, the maximum number of consecutive days without precipitation,  $DWP$ , does not depend on the total amount of the precipitation but on

its timing. The higher explanatory power of  $DWP_{GS}$  supports our hypothesis that changes in the distribution in time of the precipitation have a larger effect on the inter-annual variability of  $NDVI_{GS}$  than variations in precipitation totals. Indeed, several previous studies showed that  $DWP$  is well-correlated with ecosystem functions in different pedoclimatic conditions. For example, the radial growth of six deciduous species in southern Appalachia (Eastern USA) were more sensitive to the number of storms and the number of dry days than to the total precipitation (Elliott et al., 2015). Moreover, in the Northern

Hemisphere forests, DWP correlates well with the C turnover rate—a measure of the net effect of several ecosystem processes, including background mortality, mortality by disturbances, and forest management (Thurner et al., 2016). These results have potential implications under future climates. Predictions of no change or even increase in the annual mean precipitation do not imply that Northern European forest productivity will not be affected by such changes, as the timing of precipitation will be critical.

DWP highlights periods when soil water availability could become low, as a result of an extended lack of precipitation. While the actual water stress level during a dry spell also depends on the soil water availability at the beginning of the dry period and the evapotranspiration rate during the period, periods without precipitation are often associated with high solar irradiance and potentially high temperature and low air humidity, i.e., conditions that enhance losses via evapotranspiration. It follows that even relatively short precipitation-free periods can lead to marked water losses (Folwell et al., 2016). A simple model representing the land surface energy and water balance applied over Europe showed that evapotranspiration rates decline (i.e., the surface shifts to a water-limited regime) after only four consecutive days without precipitation, given initial soil moisture conditions  $\sim 20\%$  above the minimum soil water conditions that do not limit transpiration rates (i.e., well-watered conditions) (Folwell et al., 2016). This estimated length of the period before the decline in evapotranspiration rates study is shorter or comparable to the DWP<sub>GS</sub> observed over Northern Europe during our study period (12 days average length; range 5–20 days). Hence, even though the effects of a period without precipitation depend on the actual properties of the system and the atmospheric conditions, the DWP<sub>GS</sub> occurring in Northern Europe are already long enough to be associated with reduced evapotranspiration rates, suggesting the occurrence of water stressed conditions. Thus, the explanatory power of DWP emerging from our analyses is suggestive of an effect of water stress in Northern European boreal forests—an ecosystem generally considered light- or energy-limited.

The analysis of the correlation coefficients of the combination of climatic variables with the highest explanatory power (Analysis 5) allows assessing the effects on NDVI<sub>GS</sub> of precipitation and its timing in further detail. As apparent in **Figure 3**, higher PPT<sub>A</sub> and PPT<sub>GS</sub> (i.e., annual and seasonal daily mean precipitation, respectively) have opposite effects on NDVI<sub>GS</sub>. In other words, the response of the Northern European forests to variations in precipitation totals depends on whether precipitation increases within the growing season or during the rest of the year. Extremely positive correlations between NDVI<sub>GS</sub> and PPT<sub>GS</sub> are apparent in warmer locations. There, higher temperatures enhance soil water depletion via evapotranspiration, so that higher precipitation amounts might be key to maintain well-watered conditions. In colder places, where the evaporative atmospheric demand is lower, the correlation between NDVI<sub>GS</sub> and PPT<sub>GS</sub> was negative. This is likely the result of reduced solar radiation with increasing precipitation, which could exceed the benefits of increasing water availability (Churkina and Running, 1998; Mulder et al., 2019). Conversely, extremely

positive correlations between NDVI<sub>GS</sub> and PPT<sub>A</sub> were found in colder and drier locations, while they were negative in warmer and wetter ones. Unlike precipitation within the growing season, precipitation outside the growing season can occur as snow in Northern Europe. Winter snow accumulation affects forest productivity in different and potentially opposite ways. On the one hand, reduced winter snow accumulation is generally related to earlier complete snowmelt, in turn leading to earlier leaf onset (Körner, 2003; Inouye, 2008; Ernakovich et al., 2014). As such, reduced snow accumulation could be beneficial for forest productivity by extending the growing season (Piao et al., 2017). On the other hand, larger snow accumulation can have positive effects on soil water availability during a large part of the growing season. Moreover, an earlier onset of the spring could also lead to drier soils later in the growing season, unless the larger water losses due to extended periods with non-negligible evapotranspiration are compensated by larger precipitation amounts (Buermann et al., 2013). Which of these opposite effects of snow is dominant depends on the location and climate. A multivariate analyses based on remotely-sensed snow water equivalent and NDVI showed that in Northern Europe snow accumulation primarily affects the date of leaf onset rather than soil water availability during the growing season (Wang et al., 2018). Nevertheless, in the northernmost regions, spring leaf onset did not prove to be well-synchronized with snowmelt date, due to other environmental constraints preventing trees from taking full advantage of earlier snowmelt (e.g., insufficient heat accumulation after snowmelt and light limitation) (Basler and Körner, 2012; Zohner and Renner, 2015). Therefore, in this region, reduced snow accumulation was not related to earlier spring onset, while it still affected soil water availability. This might explain why in our analyses extremely positive correlation between PPT<sub>A</sub> and NDVI<sub>GS</sub> emerged in cold and dry places. Conversely, in the southernmost regions, earlier snowmelt allows earlier spring onset, longer growing seasons and potentially higher average NDVI<sub>GS</sub>, when the growing season precipitation ensures well-watered conditions, leading to extremely negative correlations between PPT<sub>A</sub> and NDVI<sub>GS</sub> in warm and wet locations.

## CONCLUSIONS

Understanding the links between climatic variables and boreal forest productivity is considered one of the grand challenges for global change scientists (Williams et al., 2011). This is a stepping stone for robust projections of the response of boreal forests to shifts in climatic conditions, their role in the global C balance, and their ability to provide a number of ecosystem and socioeconomic services. Yet, systematic large-scale studies that explore the linkages between vegetation dynamics and climatic variability in the boreal region are still limited (Buermann et al., 2014) and have provided contradictory results for Northern Europe (Babst et al., 2012; Bjerke et al., 2014; Gauthier et al., 2015). It is thus still unknown whether the negative effects of global warming on forest productivity

will exceed the positive ones and whether such effects are uniformly distributed in this region. To address this knowledge gap, we used high-resolution gridded meteorological data and satellite NDVI data—a proxy of forest productivity—to explore how boreal forests in Northern Europe respond to variation in climatic drivers.

Our results are suggestive of the main drivers of boreal forest productivity and they provide essential and innovative information about the general response of the Northern European forest. Indeed, while only few studies have focused on the response of boreal forests to water availability, our results show that soil water availability does play a key role in boreal forest productivity, even in a relatively mesic region as Northern Europe. Further exploration of the correlation coefficients between NDVI<sub>GS</sub> and several climatic variables highlighted that boreal forests may indeed be negatively affected by water stress, in particular in southern and warmer regions. Further, the correlation between forest productivity and temperature is not uniformly positive over the region, rather it varies according to a thermal and moisture gradient. Indeed, warmer temperatures appears beneficial mainly in the northernmost (cooler) and wetter locations, whereas their effects appear negative in the southern (warmer) and drier ones. These different responses can partially explain the conflicting findings reported so far regarding the effects of increasing temperatures. Moreover, the timing of precipitation has a higher explanatory power for boreal forest productivity than precipitation totals, because of its role on the occurrence of water stress. These results and their interpretation are suggestive of likely mechanisms driving the interplay between climatic conditions and forest productivity in Northern Europe. We acknowledge that statistical analyses as the one performed here do not inform about the actual processes and depend on the temporal and spatial resolution of both meteorological and forest productivity data. As such, further testing via specific experiments is needed.

Our results have implications in the face of climate change and management for climate adaptation. Boreal regions are predicted to shift from short, cool summers to longer, warmer summers (Jylha et al., 2010). Even under unaltered precipitation patterns, warmer and longer summers can result in more frequent occurrence of periods with low water availability, potentially transitioning Northern Europe forests from “greening” to “browning,” as already observed in North America. Regarding climate adaptation, our large scale analysis supports the identifications of regions where the projected future conditions will most likely have negative rather than positive effects, thus allowing the prioritization of management actions. Furthermore, unequivocal scientific evidence of the already occurring effects of climatic conditions on boreal forests can facilitate management decisions toward better adapted ecosystems, now currently mostly based on subjective factors (Vulturius et al., 2018).

This large scale analysis shows that the expected benefits of rising temperatures are reduced or even reversed by water shortage and that there are regions or hot spots

over Northern Europe particularly vulnerable to the projected changes in climatic conditions. Synergetic efforts via *in-situ* experiments and the implementation of physically-based models should thus focus on those likely most vulnerable regions, in order to understand the actual mechanisms, make predictions under a changing climate, and potentially even identify suitable management approaches to reduce the vulnerability.

## DATA AVAILABILITY STATEMENT

The datasets generated for this study are available on request to the corresponding author.

## AUTHOR CONTRIBUTIONS

GR-P and GV have contributed equally to the conception and design of the work and the interpretation of the data. GR-P acquired and performed the data analysis and led the drafting of the manuscript. GV revised it critically and guided all the analysis process and design.

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## SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/ffgc.2020.00034/full#supplementary-material>

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**Conflict of Interest:** The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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