University of Zurich^UZH

Relating ecosystem functioning to fire severity in tundra ecosystems using community weighted means of plant traits

ESS 511 Master's Thesis

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Abstract

The severe wildfires in the Arctic tundra are increasing. The Anaktuvuk River fire occurred in northern Alaska in the year 2007 and burned 1,039 km^2 of tundra. Almost 50% of the fire had an intensity ranging from high to extreme severity. Fires can cause changes in biodiversity and in the expression of plant functional traits, altering both the structure and composition of vegetation, as well as ecosystem processes. Plant traits define how the primary producers, which carry out photosynthesis, change as environmental factors change. Variation in plant trait expression (e.g. in the case of a disturbance), is often calculated using community-weighted means (CWMs), which are useful for assessing the dynamics between community traits and ecosystem functioning and for representing trends in trait values over time.

Through statistical analysis (lm and ANODEV) of the independent variables (fire severity, year and their interaction) and the dependent variables (CWM of SLA, of plant height, of nitrogen and carbon content in leaves, for the vascular plants), it can be concluded that, in this study, fire severity appears to have no impact on the analyzed CWMs, neither in the short nor in the long term. Even just the years after fire have not had an impact, except for CWM of plant height. This is probably since, with the fire, almost all lower and less performing vegetation was burned, until it disappeared; thus, the average height values increased, but this does not mean that the plants, on average, were taller. By analyzing the SEM between the variables: CWM of SLA; CWM of Plant height; Ellenberg Indicator Value F; Year; Active layer depth; Fire severity; it was instead concluded that fire severity and year seem to have no impact on the other variables. On the contrary, the active layer depth influences the CWMs of SLA and of plant height, which in turn impact the Ellenberg Indicator Value F for soil moisture. Fire severity does not seem to be significant for vegetation structure. On the other hand, vegetation structure seems to have an influence on ecosystem functions.

Contents

1 Introduction

1.1 Fires in the Arctic tundra

The world is currently experiencing climate change, which has resulted in a rise in the frequency of extreme events, posing significant challenges to ecosystems worldwide, especially those situated at high latitudes (Walsh et al. 2020). These regions are most affected by climate change, and an increase in temperatures and precipitation is predicted (Treharne et al. 2020; Enright et al. 2014). At high latitudes, the Arctic tundra ecosystem is found, which, due to rising temperatures, this ecosystem is experiencing an increase in shrub cover (Rocha and Shaver 2011b; Hu et al. 2010). Consequently to the shrub cover increase, a warming of the atmosphere is expected, with serious repercussions for sea ice and permafrost (Rocha and Shaver 2011b; Hu et al. 2010; Narita et al. 2015; Noguer et al. 2001; Swann et al. 2010; Walker et al. 2006). Furthermore, a significant change is that the Arctic tundra is increasingly affected by severe wildfires (Hu et al. 2015; Heim et al. 2021b; Rocha and Shaver 2011b). These wildfires induce alterations in soil cover, a substantial decrease in biomass, and a shift in processes and patterns within ecosystems (Hu et al. 2015; Heim et al. 2021b; Rocha and Shaver 2011b; Amiro et al. 2006), both in the short and long term (Rocha et al. 2012).

Several studies have demonstrated that wildfires have side effects, mainly on the soil. As soil cover decreases, thermokarst can potentially be caused, which exposes deep soils rich in ancient carbon to the environment, leading to photosynthetic and microbial degradation, resulting in significant greenhouse gas emissions (Hu et al. 2015). This decrease in soil cover also leads to a reduction in albedo (Heim et al. 2021b; Jones et al. 2013). Consequently, more energy is transferred to the ground, raising its temperature by up to 1-4°C (Hu et al. 2015). Moreover, the active layer of permafrost is at least 15 cm thicker compared to control zones (Heim et al. 2021b; Jones et al. 2013; Rocha and Shaver 2011b; Jiang et al. 2015b). Additionally, the moisture content of the surface soil increases (Jiang et al. 2015b; Rocha and Shaver 2011b). This increase is primarily due to greater water pooling on the surface, permafrost thawing, and the destruction of the surface organic layer that typically absorbs water (Jiang et al. 2015b; Rocha and Shaver 2011b; Wein and MacLean 1983; Liljedahl et al. 2007).

From 1950 to 2007, on the northern slope of the Brooks Range of the Arctic tundra, in Alaska, approximately 1,500 km^2 were burned by fires, with ˜ 1,000 km^2 consumed solely by the Anaktuvuk River Fire (ARF) (Figure 2), accounting for 68% of the total burned area (Hu et al. 2015; Jones et al. 2009). This fire played a crucial role in shaping the vegetation of the tundra. Furthermore, it is predicted that the annual probability of large fires ($>$ 1,000 km^2) will increase from 6.7%, over the last 60 years, to 13% - 23% for the rest of the 21^{st} century (Hu et al. 2015).

The ARF occurred in 2007 and burned 1,039 km^2 of tundra (Hu et al. 2010). It took place from July 16^{th} to early October (around the 10^{th}). The data suggests that not only were the precipitation levels extremely low, but evaporation was also higher than normal (Hu et al. 2010; Jones et al. 2009). The cause of the fire, therefore, was exacerbated by the low precipitation and the increased temperature, which, by raising the likelihood of lightning, favored the occurrence of the fire (Hurteau et al. 2014; Romps et al. 2014). In addition to temperature and precipitation variations, other crucial factors, including extremely dry soil conditions, south winds, and a late-season anticyclone over the Beaufort Sea, favored a fire of this magnitude (Jones et al. 2009).

The ARF is also known for the strong severity of burn it caused (Figure 1). Nearly 47% of the area experienced burns ranging from high to extreme severity, while over 35% suffered burns from moderate to high severity (Jones et al. 2009). Only 18% had burns of low to moderate severity (Jones et al. 2009). For comparison, in the same year and area, another fire near the Kuparuk River has started; approximately 80% of the Kuparuk River fire burned with low severity, while only 20% had moderate severity burns, and less than 1% experienced high severity burns (Jones et al. 2009). Low severity was defined as "sites with mixed burned, unburned, and regenerating patches of vegetation"; moderate as "severity as sites mostly burned but with some vegetation remnants and minimal tussock regeneration", and high to extreme severity as "sites with complete vegetation and partial soil consumption" (Jones et al. 2009). These high severity fires can significantly alter soil properties and nutrient cycling, leading to long-term changes in the vegetation community (Heim et al. 2021b; Bouskill et al. 2022; Heim et al. 2021a).

The severity of burning serves as an indicator used to assess the extent of damage inflicted on vegetation during fires (Rocha and Shaver 2011b; Keeley 2009). In this study, the severity is measured through differenced Normalized Burn Ratio (dNBR) values before and after the fire (Hu et al. 2010; Jones et al. 2009).

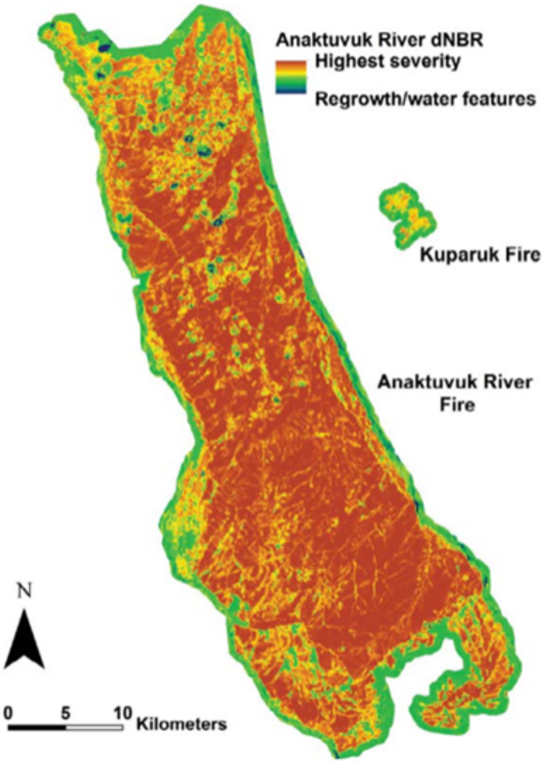


Figure 1: Map of the ARF and the Kuparuk River Fire with colors indicating the severity of burns through dNBR (Kolden and Rogan 2013). The range of the dNBR pixel value is between -30, in blue-green, and 827, in red.

Fires also release a significant amount of carbon into the atmosphere. It was found that the ARF released approximately 2.1 Tg of carbon, which is equivalent to all the carbon absorbed, on average, in one year in the Arctic (Jones et al. 2013; Mack et al. 2011; Hu et al. 2015).

It is predicted that the extent, frequency, and severity of fires will rise, and that the biome may become highly flammable, also due to the decrease in wetland areas, which would facilitate the spread of fires (Jones et al. 2009; Hu et al. 2010; Hu et al. 2015). Climate change affects the distribution, abundance, and diversity of vegetation, and it is estimated that in Arctic tundra regions, the summer period will become drier and the length of the vegetative growth cycle will increase (Hudson et al. 2011; Heim et al. 2021b).

1.2 Ecosystem functioning and plant traits

The plant traits encompass various characteristics of plants, such as anatomical, morphological, phenological, physiological, and biochemical ones; they thus determine how primary producers, performing photosynthesis, change with varying environmental factors (Kattge et al. 2011; Díaz et al. 2004; Lavorel and Garnier 2002; Aerts and Chapin III 1999; Garnier and Navas 2012; Grime 2006a; Grime 2006b). Plant traits reflect evolutionary and assembly processes that occur after a biotic or abiotic change; thus, they influence ecosystem processes (Valladares et al. 2007; Bjorkman et al. 2018). Their change enables vegetation to survive or, in the case of disturbance, adapt to the change of various environments (Kattge et al. 2011; Valladares et al. 2007). Therefore plant characteristics can serve as predictors for how species will react to environmental and climatic change (Bjorkman et al. 2018; Fridley et al. 2016; Soudzilovskaia et al. 2013). Plant traits impact the configuration and functioning of ecosystems, for example, by regulating: primary production, the decomposition process of organic matter, allocation of resources, nutrient cycling, and biological diversity (Kattge et al. 2011; Díaz et al. 2004; Lavorel and Garnier 2002; Aerts and Chapin III 1999; Garnier and Navas 2012; Grime 2006a; Grime 2006b; Bjorkman et al. 2018).

Variation in plant trait expression is often calculated using community-weighted means (CWMs), which are useful for assessing dynamics between community traits and ecosystem functioning and representing trait value trends over time (Garnier et al. 2004; De Bello et al. 2005; Louault et al. 2005; Quétier et al. 2007). CWMs are the weighted average of community traits, representing the mean value of traits within a weighted community, calculated considering the relative abundance of different species exhibiting those traits (De Bello et al. 2013; Bashirzadeh et al. 2023; Garnier et al. 2004; Díaz et al. 2007; Lepš et al. 2011; De Bello et al. 2005; Louault et al. 2005; Quétier et al. 2007; Pescador et al. 2015). Plant traits, namely morphological, structural, or physiological characteristics influencing the overall fitness of individual biological units, are significant drivers of ecosystem behaviour and are utilized for determining the ecological roles of species within an environment (Beest et al. 2021; Díaz and Cabido 2001).

1.2.1 Disturbance mechanisms on plant functional traits

The relevance of functional traits in demonstrating responses and impacts on ecosystems following altered disturbance regimes is widely recognized (Velbert et al. 2017). It is anticipated that intense environmental disturbances, such as: increased soil nutrient availability, increased biodiversity, extensive grazing, drought, various soil management treatments, human or natural interventions on grasslands, and frequent fires; will cause differences in the responses of functional traits, potentially reducing their variation (Czortek et al. 2021; Niu et al. 2016; Jung et al. 2014).

Fertilization has positive effects on certain vegetation traits, such as plant height or leaf area, while it does not significantly increase others, such as Specific Leaf Area (SLA) or Leaf Dry Matter Content (LDMC) (Siefert and Ritchie 2016). Conversely, increasing biodiversity through seed distribution has not led to a significant increase in any of the analyzed community functional traits (Siefert and Ritchie 2016). Drought has shown that, depending on the species, the response of functional traits differs, but overall, a decrease in SLA value and an increase in leaf carbon content and LDMC are observed (Jung et al. 2014). Grazing, as a disturbance, has caused significant variations in plant functional traits: significantly increasing the weighted mean values of carbon, nitrogen, and phosphorus in leaves and SLA, while decreasing the weighted mean value of leaf dry matter content (Niu et al. 2016). The changes, in this specific case, have also favored a shift in dominant species, increasing the presence of species with longer-lived and shorter leaves (Niu et al. 2016). Regarding different soil management treatments, such as aboveground biomass removal, plant functional traits have shown temporal changes, with evident differences between treatments in canopy heights, leaf attributes, and flowering behaviors (Velbert et al. 2017). Human or natural interventions in grasslands, like soil removal and mowing, have reduced functional diversity but increased species with characteristics such as canopy height, seed mass, and high SLA over time in soil removal grasslands (Czortek et al. 2021). There has been a significant increase in CWM values of functional traits over the years, showing significant variation among different historical disturbance treatments (Czortek et al. 2021). Finally, fire has significantly influenced plant trait CWMs, increasing SLA values and decreasing LDMC values, while leaf thickness

CWM has not undergone significant variations (Abedi et al. 2022). Fire has favored the abundance of fast-growing, small-statured species, thereby enhancing photosynthesis and growth rates (Abedi et al. 2022). In general, all disturbances have a more or less significant impact on plant functional traits, depending on the type of disturbance and its intensity; indeed, disturbances also have a long-term impact, especially on species turnover within communities (Jung et al. 2014; Theurillat and Guisan 2001; Helmuth et al. 2005; Jump and Peñuelas 2005).

Focusing more on the disturbance of fire in the Arctic tundra and its effects on plant traits, fires both destroy the vegetation canopy and char the soil surface (Jiang et al. 2015b). Vegetation canopy and soil surface have an influence on regulating the vegetation of the Arctic tundra (Jones et al. 2013; Qu et al. 2023). Fires can cause significant changes in biodiversity and the expression of plant functional traits, altering both the structure and composition of vegetation, as well as ecosystem processes (Ames et al. 2016; Kumordzi et al. 2019; Heim et al. 2021b; Debouk et al. 2015).

High-intensity fires can alter the type and functioning of ecosystems through changes in: community composition, functional traits and nutrient cycling processes; they can also alter soil physical properties and carbon reserves (Taber and Mitchell 2023; Rocha and Shaver 2011b; Rocha and Shaver 2011a; Dyrness and Norum 1983; Johnstone and Chapin 2006; Meigs et al. 2009). Interactions between fire severity and increasing temperatures can influence post-fire recovery and vegetation community succession, leading to changes in species composition and expressed traits (Liang and Hurteau 2023; Poulos et al. 2020; Taber and Mitchell 2023). It is demonstrated that higher fire intensity reduces species richness and diversity (Venn et al. 2016), homogenizing vegetation functional traits, thus posing challenges to ecosystem diversity, which will have lower turnover (Taber and Mitchell 2023; Ames et al. 2016; Díaz et al. 2007; Bond and Keeley 2005). Moreover, only a few species are capable of immediately adapting to environmental change; thus, the better-adapted vegetation will be selected as post-fire recovery vegetation (Li and Waller 2017; Taber and Mitchell 2023). Species adaptation to fire may, in some cases, modify species traits without significantly influencing the vegetation composition in the area (Mitchell et al. 2021). Understanding the impact of fire severity on vegetation after fire disturbance and how ecosystem plant functions will change, is important (Taber and Mitchell 2023).

1.3 Thesis purpose and research questions

In Arctic regions, tundra ecosystems represent one of the most vulnerable and crucial landscapes for comprehending the impacts of global climate change. Of the numerous threats that these ecosystems face, wildfires are a significant disturbance agent. The relationship between ecosystem functioning and fire severity in the Arctic tundra remains a relatively understudied field. However, other ecosystems are more extensively studied: fires can have a deep impact on several key aspects of material and energy flows (Marcos et al. 2021). These include: ecosystem functioning related to energy balances (albedo, latent heat, sensible heat); biogeochemical cycles of carbon (primary productivity, biomass, decrease of plant diversity and richness) or water (vegetation water content, soil moisture) (Marcos et al. 2021; Fernández-Guisuraga et al. 2023; Keeley et al. 2005; Fernandez-Garcia et al. 2020; Huerta et al. 2022; Grau-Andrés et al. 2019; Safford and Harrison 2004; Bret-Harte et al. 2013).

This study aims to explore the connection between ecosystem functioning and fire severity in Arctic tundra. It focuses on using CWMs of plant traits, which regulate primary production, organic matter decomposition, nutrient cycling, and biodiversity within ecosystems (Kattge et al. 2011; Díaz et al. 2004; Lavorel and Garnier 2002; Aerts and Chapin III 1999; Garnier and Navas 2012; Grime 2006a; Grime 2006b). The objective of this thesis is to understand if and how fire severity impacts ecosystem functioning, as measured through CWMs of functional traits of vascular plants, during post-fire recovery. To complete this objective, the research questions are as follows:

- Is fire severity impacting the Community Weighted Means of plant traits?
  - And how does the impact of fire severity on the CWMs change over time after a fire?
- How is vegetation structure linked to ecosystem functioning and fire?

Answering these questions could be useful and innovative in predicting the change in Arctic tundra ecosystems following a fire, whether the fire is more or less severe. Understanding how plant characteristics influence the response of Arctic ecosystems to fires is crucial for developing effective management strategies and predicting the impacts of climate change on Arctic tundras.

2 Methods

2.1 Study area

The study area of the Anaktuvuk River fire scar is located along the Anaktuvuk River in northern Alaska (Figure 2). It extends between the northern slopes of the Brooks Range Foothills towards the north, where a coastal plain is situated (Jandt et al. 2021). The fire originated at coordinates 69.047°N and 150.837°W, with elevation in the affected area ranging from 500 meters above sea level (masl) in the south to 100 masl in the north (Jandt et al. 2021).

Before the fire, the soil was described as acidic tundra (pH < 5.5) for 54%, non-acidic (pH > 5.5) for 15%, and shrubland for 30% (Jandt et al. 2012). The ecosystem is categorised as "shrub tussock mountain tundra, with gently sloping slopes and ridges in loess and colluvium" (Jandt et al. 2021).

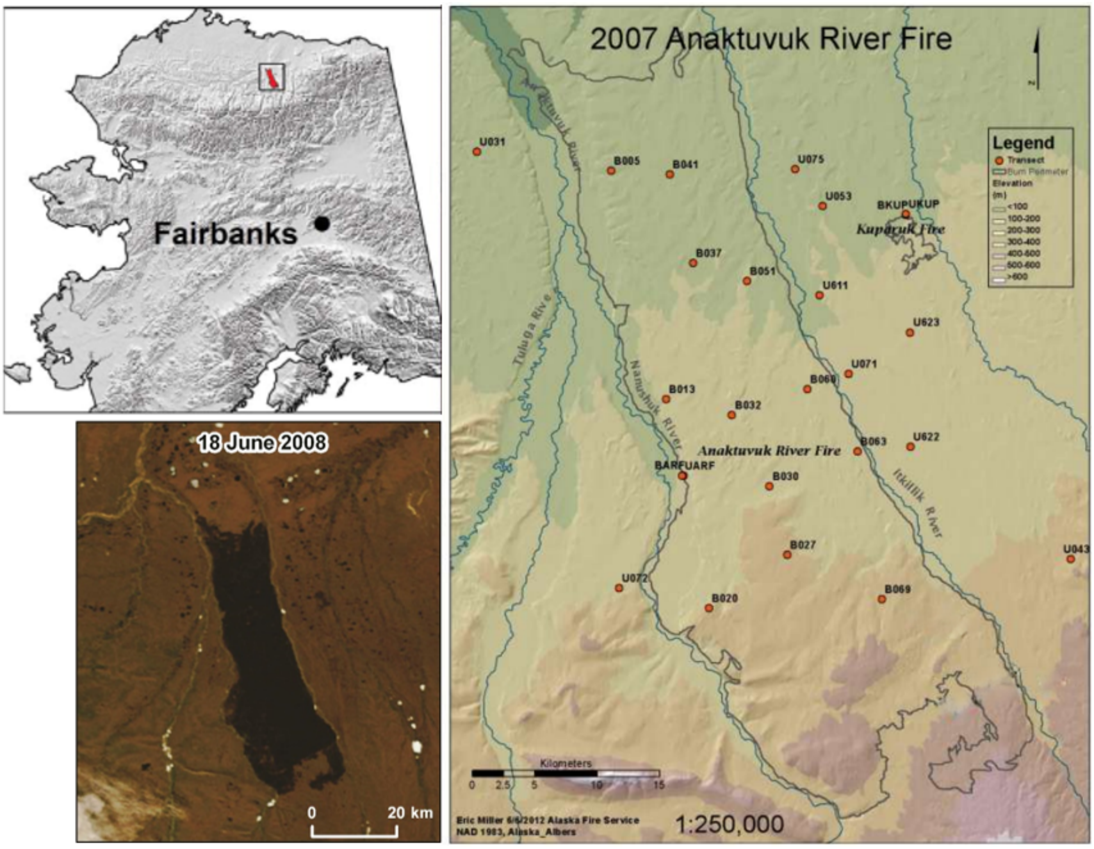


Figure 2: Left: Location of the ARF and Kuparuk River fires (upper) with a satellite image of the area in June 2008 (lower)(Kolden and Rogan 2013; Jones et al. 2009). Right: map of the study area showing all the permanent transects used in this study with the reference ID (Jandt et al. 2021).

In this area, winters are typically cold (-25°C) and summers are cool (20°C) (Jandt et al. 2021). Annual precipitation amounts to approximately 15 cm, with 11 cm falling between June and September (Jandt et al. 2012; Jandt et al. 2021).

The map (Figure 2) and the dataset also encompass the Kuparuk River fire, which occurred concurrently with the ARF in 2007 but burned a smaller area, 7.25 km^2, and lasted only for two weeks (Jandt et al. 2012; Jandt et al. 2021; Jones et al. 2009). This area is included to provide values for low-severity fires, so some transects were placed nearby this scar. These two fires are often considered together due to their similar ecosystems, climates, and burning conditions.

2.2 Experimental design and data calculations

The data are provided by the Bureau of Land Management mission and encompass 14 burned areas and 11 unburned areas (Miller et al. 2022). Each area is a transect, and within each transect, 100 measurements were recorded every 50 cm, out of a total 50 m length. In every transect, documentation was made of the active layer depth and of the types of plants present at each point, identified by their scientific species names based on Viereck's (Viereck 1992) vegetation classification. Data collection occurred over five different years: 2008, 2009, 2010, 2011, and 2017.

2.2.1 Fire severity

To determine fire severity, the differenced Normalized Burn Ratio (dNBR) pixel values for each burnt transect are provided (Miller et al. 2022). These values are obtained by subtracting the post-fire Normalized Burn Ratio (NBR) value from the pre-fire value to define the degree and extent of burned areas (Lutes et al. 2006). The NBR values are derived from Landsat 7 signals. Firstly, the with the help of the reflectance ratio of Near Infrared (NIR) band (band 4) and Shortwave Infrared (SWIR) band (band 7), the NBR value is calculated for two different scenes (pre and post-fire) using the formula described by Lutes et al. (2006):

$$NBR = (B4 - B7)/(B4 + B7) \tag{1}$$

Then, the post-fire NBR value (2008) is subtracted from the pre-fire NBR value (2007) to obtain dNBR values (dNBR = NBRprefire − NBRpostfire) (Keeley et al. 2008; Keeley 2009; Lutes et al. 2006). These values remain the same across all years (2008, 2009, 2010, 2011, 2017), varying only among transects, because the interest is only in the severity measured shortly before and after the fire. Values of 0 or lower are defined as "Unburnt," while all other values are maintained as continuous variables. Higher dNBR values indicate greater severity, thus indicating a more significant impact on the ecosystem and environment after the fire (Keeley 2009; Lutes et al. 2006).

2.2.2 Community Weighted Means (CWMs)

In the dataset data are categorized by transect and by year. For each plant, specie and genus name has been defined, allowing vascular plants to be isolated from other types of vegetation such as moss, liverwort or lichen. This categorization process utilized the *European and Mediterranean Plant Protection Organization* (2024) (EPPO) global database. For the vegetation not found in the EPPO database, specific articles were consulted to determine their classification.

Data were utilized to determine the percentage cover of each species for each transect across different years, adding the same vascular plant together and dividing by the total number of vascular plants found in the transect. Using the Tundra Trait Team (TTT) database (Bjorkman et al. 2018), which focuses on plant functional traits, the trait values for the species were determined by averaging the available values of the same vascular plant present in the table of TTT, calculating also the standard deviation. These traits include Specific Leaf Area (SLA) $[mm^2/mg]$, vegetation height $[cm]$, Nitrogen content in leaves $[mg/g]$, and Carbon content in leaves $[mg/g]$. Not all vascular plants found in the transect had a functional trait value in the database, they were therefore not considered.

By multiplying the trait value with the percentage cover, the Weighted Mean (WM) for each species in each transect for each year was calculated, with their own standard deviation. Subsequently, these results were aggregated for the same transect and year to obtain the total trait value per transect and per year, with their standard deviation. Finally, the total trait value was divided by the total abundance of all vascular plant species in the transect to derive the Community Weighted Mean (CWM) for each transect and each year, along with the standard deviation. At the end, despite the lack of functional trait data for each initial species, each transect and each year have a value for all four considered CWMs. These calculations were performed using R-Studio.

Below are described the four functional traits analyzed for the thesis project. The four selected CWMs are all positively correlated with each other, so if the value of one CWM increases, the values of the other CWMs also increase, as far as the Arctic tundra zones are concerned.

Specific leaf area The Specific Leaf Area (SLA) is defined as the ratio of one-sided leaf area to dry leaf mass (Ames et al. 2016; Venn et al. 2016). High SLA values are directly linked to higher growth rates and increased photosynthesis, thus also associated with higher nutrient uptake rates, lower values, on the other hand, are correlated with slower growth and a strategy focused on conserving resources, potentially in environments where resources are limited (Abedi et al. 2022; Mitchell et al. 2021; Anacker et al. 2011; Wright et al. 2004; Westoby et al. 2002). Therefore, SLA serves as a good indicator for plant health in terms of growth, photosynthesis, and soil nutrient resources.

Plant height The height of plants is correlated with their competitiveness for capturing sunlight (Hudson et al. 2011; Westoby et al. 2002). Plant height demands investments in stem construction and upkeep, which may become overly costly when stress factors are present and hinder photosynthesis (Velbert et al. 2017; Falster and Westoby 2003). Generally, in herbaceous vegetation, the taller the plants, the higher the SLA will also be, thus reducing the leaf area value per biomass out of the ground (Westoby et al. 2002).

Nitrogen content in leaves In photosynthesis proteins, nitrogen plays a crucial role, especially in the Rubisco protein (Wright et al. 2004). Therefore, it serves as an indicator of: the photosynthesis rate, concerning CO_2 absorption (Wright et al. 2004); plant growth and status, as well as leaf growth and development; and nutrient availability (Hudson et al. 2011; Jia et al. 2021; Crawford 1992). Higher SLA allows more efficient utilisation of supplementary nitrogen for photosynthesis (Abedi et al. 2022; Díaz et al. 2016; Wright et al. 2004; Poorter and Evans 1998). Furthermore, it has been demonstrated that plants with a higher content of nitrogen in leaves develop a better response to environmental stresses (Querejeta et al. 2022).

Carbon content in leaves Generally, leaves with a high SLA value require less leaf carbon investment, whereas those with a lower SLA require more carbon to make the leaves more durable (Sakschewski et al. 2015). However, in environments with drought or cold conditions, a higher SLA value is more advantageous for plants, because it allows them to store more carbon during the short growth period (Sakschewski et al. 2015). Vascular plants with higher carbon content in their leaves have been shown to be thicker compared to those with lower values (Happonen et al. 2022). This thickening alters the ratio between leaf mass and surface area, which primarily impacts the plant's photosynthesis, leading to an increase (Gagnon et al. 2019; Lafleur and Humphreys 2018). On the other hand, in recent studies, it has been demonstrated that photosynthesis is positively correlated with rapid leaf economy, having more photosynthetic machinery, and thus with a higher average SLA value (Wright et al. 2004; Sørensen et al. 2019; Shipley et al. 2006). Leaf carbon content is also an indicator of photosynthesis rate, plant growth, soil nutrient availability (Hudson et al. 2011; Crawford 1992).

2.2.3 Ellenberg Indicator Value F for soil moisture (EIV F)

The Ellenberg Indicator Value (EIV) F of the plant preferences for soil moisture has been defined for all the vascular plants, from different databases (*Lady Bird Johnson Wildflower Center* 2024; *Zeigerwerte der Pflanzen Mitteleuropas nach Ellenberg* 2024; Hill et al. 2004; Sekretareva 1999) and included in the table as an indicator of soil moisture. Each plant exhibits a distinct preference for soil moisture levels, thereby serving as an indicator of soil moisture conditions at a given location. The values are directly related to the plants, so they are potentially not as accurate as direct on-site measurements, concluding that therefore, these values will almost certainly correlate significantly with the CWMs values due to the fact that they come from the same source of analysis. The values range from a minimum of 3 to a maximum of 10, thus, following Ellenberg's categorisation, the soil in which the plants grow varies from "dry-site indicator" to "shallow-water-size indicator", thus providing an approximate description of the soil in which the vascular plants are found (Hill et al. 2004). The values were then averaged across species from the same transect and year, summing them per transect and year and dividing the value by the number of species present, providing an average value of the EIV F for each year and transect.

2.2.4 Active Layer Depth (ALD)

The average thaw depth of the active layer for all the transects and all years was also included in the table of the dataset. The unit of measurement is cm. This value indicates the thickness of the soil layer present in the permafrost, i.e. the layer close to the surface that can thaw in summer (higher value, more positive) and remains frozen in winter (lower value, more negative) (Dobiński 2020; Subcommittee, Permafrost 1988; Van Everdingen 2005).

2.3 Statistical analysis

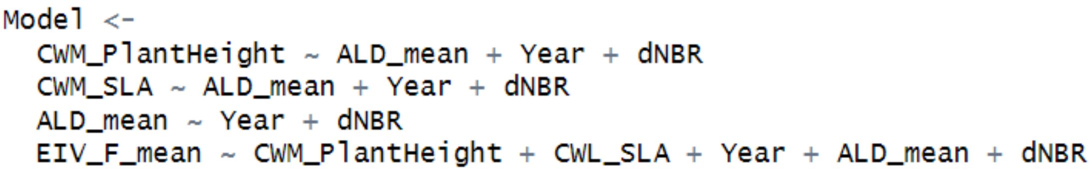
The linear model (lm) and analysis of deviance (ANODEV) were used to determine the influence of fire severity, years and their interaction (dNBR:year) on CWMs. The dependent variables are thus the four CWMs described above, abbreviated as: SLA (specific leaf area), $PlantHeight$ (height of the vegetation), $N\_content$ (nitrogen content in leaves) and $C\_content$ (carbon content in leaves), while the independent variables are fire severity (dNBR); years (2008, 2009, 2010, 2011, 2017) and their interaction (dNBR:year). The analysis was carried out for each dependent variable individually and no random effects were included in the study, so, the unconsidered factors do not significantly influence the results. The survey was conducted with R-studio mainly with the R-package 'dplyr'.

The linear model performs a linear regression analysis, examining the relationship between a dependent variable and independent ones. Consequently, the result displays, with a straight line and as accurately as possible, the model of the relationship between the dependent variable and the independent ones (*Linear Regression Model* 2024). The primary goal of linear regression analysis is to understand and quantify the correlation between variables, as well as to make predictions based on this relationship (*Linear Regression Model* 2024).

With ANODEV, two models were compared to determine if there are significant differences between them (*Analysis of Deviance* 2023). The two models differ by one independent variable, and if the p-value, of the independent variable, in the table is statistically significant, it means that the independent variable that has been added respectively, removed, has a remarkable effect on the dependent variable, compared to the other model (*Analysis of Deviance* 2023).

Subsequently, to answer the last research question, with the variables: CWM of SLA; CWM of Plant height; Ellenberg Indicator Value F; Year; Active layer depth; Fire severity; a Structural Equation Model (SEM) was carried out. This model involves the use of multiple equations to test and develop models to evaluate different relationships between the variables (Soliveres et al. 2014; Grace et al. 2010; Grace and Keeley 2006; Bollen 1989; Grace 2006). SEM can divide causal influences between multiple variables, direct and non-direct, by means of a simultaneous analysis (Soliveres et al. 2014; Grace et al. 2010; Grace and Keeley 2006; Bollen 1989; Grace 2006). This is why the model was essential, in this research, in order to study a hypothesis by means of several variables operating in the system.

This analysis was also conducted with R-studio but with the R-package ’lavaan’. The variables were scaled and centred, with the R-package ’scale’, in order to make a comparison between the estimated values, so to better understand the relationships and their abundance. The resulting values have a range from -1 to 1, negative values represent an indirect correlation between variables, while positive ones indicate a direct correlation (*Structural Equation Modeling* 2021). The estimated value reflects the intensity of the relationship and represents how many units the dependent variable changes when the independent variable changes by one unit (*Structural Equation Modeling* 2021). The significance is demonstrated by the associated p-value (*Structural Equation Modeling* 2021).



```
Model <-
  CWM_PlantHeight ~ ALD_mean + Year + dNBR
  CWM_SLA ~ ALD_mean + Year + dNBR
  ALD_mean ~ Year + dNBR
  EIV_F_mean ~ CWM_PlantHeight + CWL_SLA + Year + ALD_mean + dNBR
```

Figure 3: Model of SEM diagram used for the analysis of the relationships among: Year; fire severity (dNBR); Ellenberg Indicator Value F of soil moisture (EIV F); CWM of plant height; CWM of SLA; and Active Layer Depth (ALD). The structure of the model is: dependent variable ˜ independent variables.

3 Results

3.1 Impact of tundra fire severity on CWMs of plant traits

Through the values obtained from the statistical analysis of the research, the following conclusions and arrange figures were drawn. The study highlighted a significant interaction between the CWM of plant height and the independent variable years.

Via the linear model, it can be understood how the dependent variable (the four CWMs) evolves in relation to the independent variables (Year, dNBR, and dNBR:Year), thus representing how close the model estimates that the average of the real values of the dependent variable is, to those calculated using the model line. In general, thanks to the linear model (Table 1), it can observed that all models have a very low multiple R^2 value, indicating that only a small portion of the variation in the value of a CWM can be explained by the two independent variables and their interaction. This could therefore indicate that the model should be more complex or that there is no strong linear interaction between the variables.

Table 1: Linear model results for the relationship between independent variable (first column vertically) and dependent variable (first column horizontally). The table shows calculated multiple R^2 values and estimate value of each CWM.

	SLA	Plant Height	Leaf N Content	Leaf C Content
Multiple R^2	0.16	0.27	0.15	0.11
Intercept	1.36e+01	-2.54	17.92	430.57
dNBR	-3.77e-03	0.03	-0.002	-0.03
2009	-2.19e-01	19.88	-1.61	-55.69
2010	-2.42e-01	19.38	-2.53	-38.26
2011	4.62e-01	18.67	-2.89	-62.37
2017	-3.57	16.63	-7.61	-95.47
dNBR:2009	-5.4e-04	-0.04	-0.003	-0.05
dNBR:2010	-4.83e-05	-0.04	-0.003	-0.09
dNBR:2011	-1.58e-05	-0.03	-0.001	-0.04
dNBR:2017	2.89e-03	-0.03	0.007	0.02

It was discovered, through ANODEV (Table 2), that fire severity is not a significant continuous variable for any of the four CWMs considered, therefore, as illustrated in figures, data around the model lines are always scattered randomly, without a specific pattern. The independent variable years was found to be significant for CWM of plant height, thus indicating that, at least, one year has a significantly different value of average from the others. For the other three dependent variables, the independent variables years do not yield a significant p-value. Furthermore, the interaction between dNBR and year (dNBR:Year) has also resulted in a non-significant value for any of the CWMs, which is demonstrated, in the figures below, by the fact that the lines of the linear model are mainly parallel to each other.

Table 2: Results of the ANODEV for the comparison of the independent variables among the four CWMs. The table displays the F-value and associated p-value indicating the significance of the differences observed.

	SLA		Plant Height		Leaf N Content		Leaf C Content	
	F Value	P Value	F Value	P Value	F Value	P Value	F Value	P Value
dNBR	2.86	0.096	0.12	0.74	0.13	0.72	0.31	0.58
Year	2.15	0.09	3.75	0.008	2.5	0.051	1.93	0.12
dNBR:Year	0.094	0.98	1.7	0.16	0.15	0.97	0.021	1

3.1.1 CWM of Specific Leaf Area (SLA)

Despite the fire that occurred in 2007, until 2011, the slope of the line for CWM of SLA remained consistent, showcasing high CWM for SLA values at moderate burn severity values, compared to the reference values. However, in 2017, there was a noticeable decline in values of CWMs for SLA and a flattening of the line (although not statistically significant). This suggests less disparity between burnt and unburnt areas and a CWM of SLA value constant for all fire severity values (Figure 4).

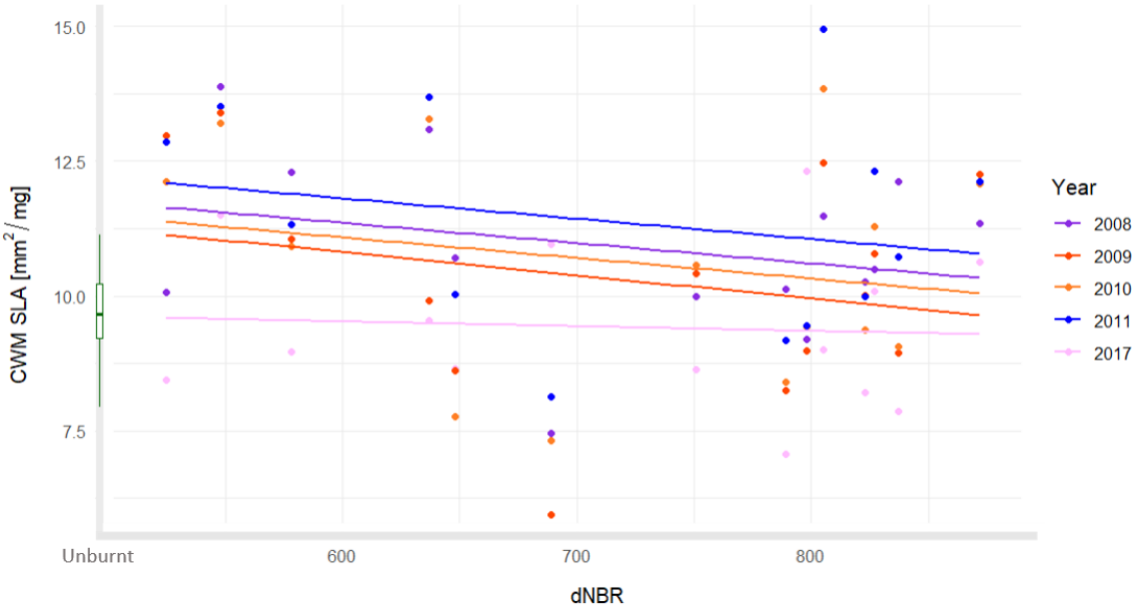


Figure 4: Effect of fire severity (dNBR) on the community weighted means for SLA across different years post fire (colors). In green are the reference values of the unburnt areas.

3.1.2 CWM of plant height

An observable change in slope of the values of CWM for plant height in relation to the fire severity can be noted between 2008 and subsequent years (Figure 5), leading to an average of values different from other years. This contributes to the significance found in the ANODEV Table 2 (p-value year = 0.008), which means that the variable year has a significant effect on the value of CWM for plant height. The CWM of plant height value is noticeably higher when the fire severity is very high; subsequently, in the following years, it decreases at the same value as dNBR. Even a decade after the fire, the CWM for plant height of the vascular plants value remained relatively consistent with that of moderate burn severity in 2008 and is comparable to that of unburnt areas.

3.1.3 CWM of leaf Nitrogen content

In 2008, the CWM for nitrogen content in leaves value was higher compared to other years, and almost equal to the reference value (Figure 6). The slope of the linear model remained consistent until 2011, but the value of the CWM for nitrogen content in leaves declined. After 10 years post-fire, there is a change in slope indicating higher CWMs for nitrogen content in leaves values in the more severely burned sites (even if not statistically significant), although the values are not yet equivalent to the photosynthesis rates in the unburnt areas.

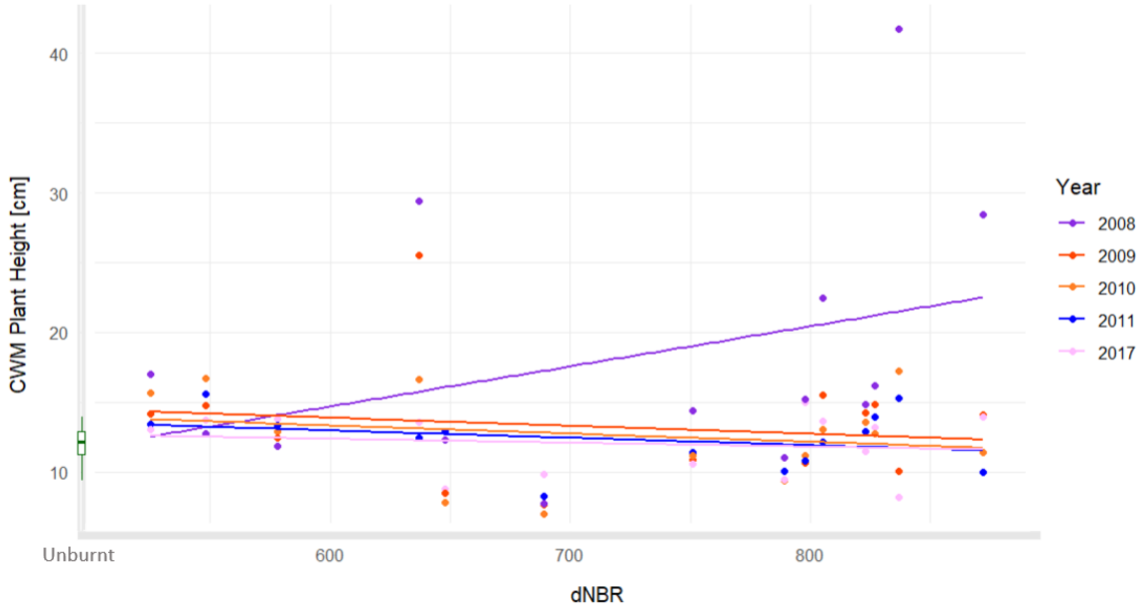


Figure 5: Effect of fire severity (dNBR) on the community weighted means for plant height across different years post fire (colors). In green are the reference values of the unburnt areas.

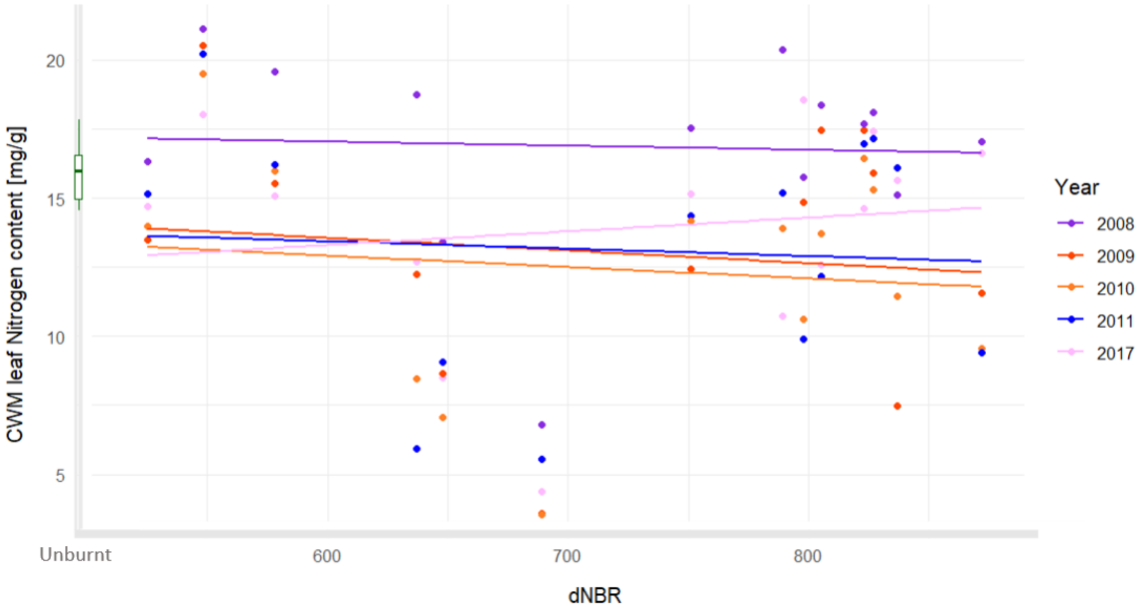


Figure 6: Effect of fire severity (dNBR) on the community weighted means for nitrogen content in leaves across different years post fire (colors). In green are the reference values of the unburnt areas.

3.1.4 CWM of leaf Carbon content

This metric provides insight, albeit on a broad scale, into how carbon storage in vegetation changes in plants. In 2008 the value of CWM of the carbon content in leaves was much higher compared to the other years, but it remains notably low compared to the average of the value of unburnt areas (Figure 7). However, the values remain almost costly for the different fire intensities.

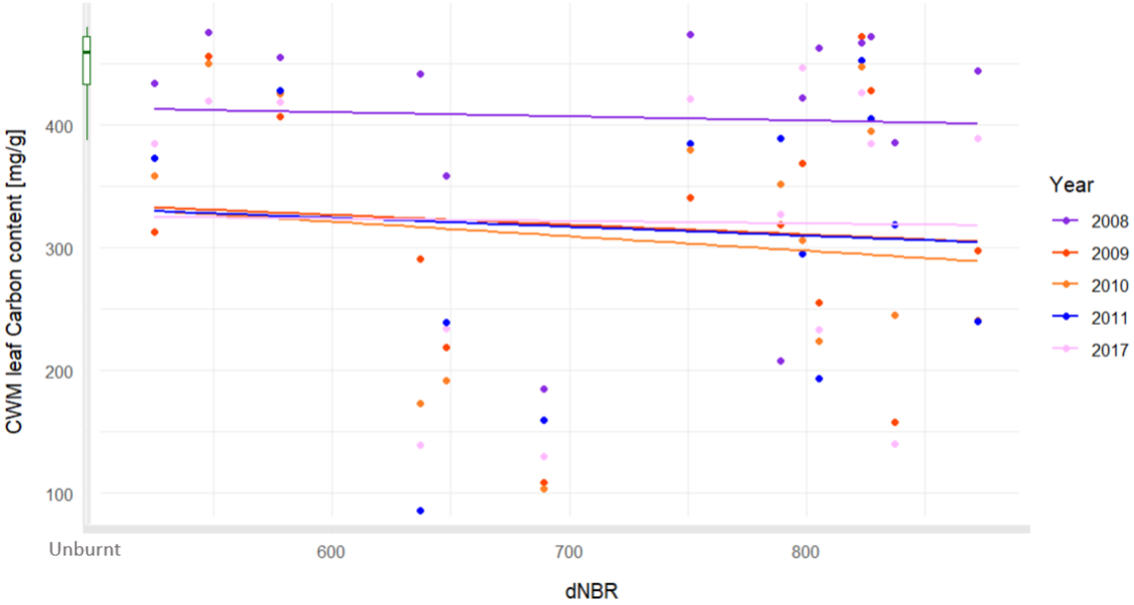


Figure 7: Effect of fire severity (dNBR) on the community weighted means for carbon content in leaves across different years post fire (colors). In green are the reference values of the unburnt areas.

3.2 Ecosystem functioning and fire linked to vegetation structure

The model used for analysis through SEM has a complex network of interactions. The values show the estimated effect of each independent variable on the dependent variable. Significant interactions are shown with solid lines and no-significant interactions are represented with dashed lines, the present number indicates their estimated values of the influence (Table 3 in A). The significant relationships are few, all of which are inversely proportional relationships (negative values) between the active layer depth and the CWM of SLA and CWM of plant height, as well as the value of soil moisture. It can be observed that the variables fire severity and years have no significant influence on the other variables (Figure 8).

Exposing the significant relationships, there are two scenarios:

1. In the first case, as the active layer depth decreases of one unit, CWM of plant height and CWM of SLA of plants increase respectively by 0.343 and 0.248 units. Moreover, if their value increases by one unit, the value for soil moisture decreases by respectively -0.560 and -0.495 units, indicating drier soil.
2. In the second case, as the active layer increases (becomes more negative) by one unit, it causes a decrease in CWM of plant height and CWM of SLA respectively by -0.343 and -0.248 units. And the decrease of them of one unit, leads to an increase in soil moisture of respectively 0.560 and 0.495 units.

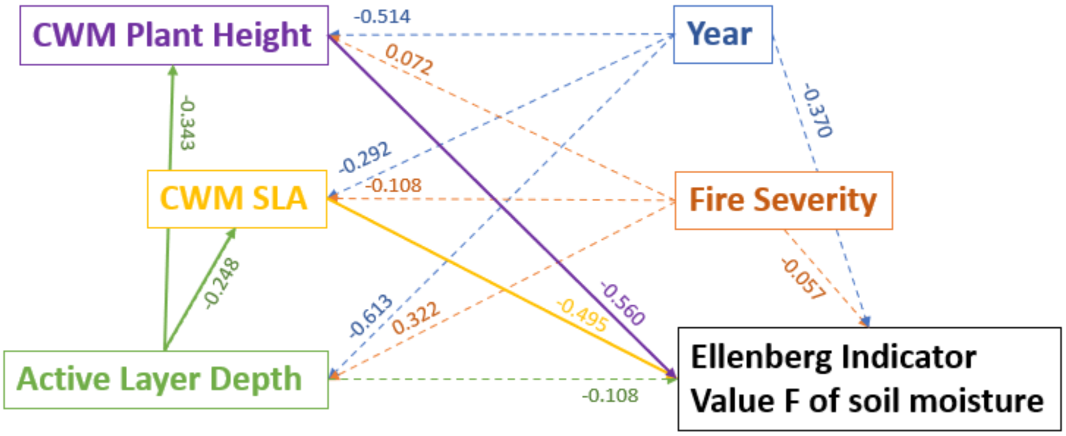


Figure 8: Structural Equation Model (SEM) exploring the relationships among: Year; fire severity (dNBR); Ellenberg Indicator Value F of soil moisture; CWM of plant height; CWM of SLA; and Active Layer Depth. Arrows indicate the direction of the relationships expected between latent and observed variables in the model, accompanied by their estimated values. The solid lines indicate significance, while the dashed lines represent non-significant relationships (Table 3 in A).

In general, the active layer depth has a greater influence on the value of CWM of plant height than on the CWM of SLA. However, the CWM of plant height has a greater influence on soil moisture value compared to the CWM of SLA.

4 Discussion

The Arctic tundra fires and their severity are crucial to consider for ecology and phenology (Rocha et al. 2012). They are rare, but it is predicted that their frequency and extent could strongly influence ecosystem properties (Heim et al. 2021b; Hu et al. 2015; Flannigan et al. 2009; Keeley et al. 2008). The responses to fire are manifold, including the re-establishment of vegetative communities and their regeneration (Keeley 2009).

4.1 Impact of tundra fire severity on CWMs of plant traits

Various factors influence the extent of fires, including abiotic elements such as weather conditions (Rocha et al. 2012), slope and orientation of the terrain, and biotic factors such as the presence of combustible material, hence the composition and age of vegetation (Keeley et al. 2008; Keeley et al. 2005; Rocha et al. 2012).

Little studied and less clear is the consideration of fire severity, which is, however, asserted to be correlated with the residual plant cover and soil thermal properties (Rocha and Shaver 2011b; Wein and Bliss 1973; Keeley 2009). Fire severity influences ecosystem responses (Keeley et al. 2008), but not significantly, according to the linear model (Table 1), even though, as previously stated, the model is only able to explain a small portion of the variation in the CWMs through the selected independent variables. Fire severity depends, in addition to abiotic factors, also by vegetation characteristics: such as its net primary production (Rocha et al. 2012; Jones et al. 2013; Keeley 2009), density, continuity, and flammability; but also on species survival characteristics (He et al. 2019). It is also closely related to the quantity and composition of combustible material accumulated in the shrub canopy (Keeley et al. 2008; Bond and Van Wilgen 2012; Schwilk 2003). Standard age of the vegetation also plays a crucial role, as biomass accumulates over time and decomposition rates are moderate (Keeley et al. 2008; Keeley and Fotheringham 2003); it is presumed that fire severity increases with vegetation standard age (Keeley et al. 2008; Minnich 1995).

As mentioned, changes in vegetation and soil properties are influenced by surface energy dynamics and nutrient availability (Keuper et al. 2012; Loranty et al. 2018). The functional traits analyzed (specific leaf area; plant height; and leaf nitrogen content) are good indicators to understand this change (Hobbie et al. 2002; Bjorkman et al. 2018). Through the CWM value of these functional traits, the changes can be measured, allowing us to better understand how environmental changes after a fire, more or less severe, affect vegetation (Heim et al. 2021b).

Post-fire CWM values are often higher than reference values because with the fire, less-performing vegetation, which potentially has dried out more due to hot and dry periods, is burned first. Thus, it will lead to an increase in the mean values of various CWMs of the still living vegetation. In the long time, plant regeneration can occur, which may lead to a decrease in the mean values or prevalence of certain species over others. These two considerations are to be taken into account; thus, they indicate that a change in CWM values does not necessarily imply a change in vegetation functional traits.

4.1.1 Individual discussion of each CWM of plant trait

From Figure 4, it can be observed that the CWMs of SLA values for the 4 years following the fire are higher compared to the values 10 years after it. They also have a different slope, suggesting that when the fire severity is higher, CWMs of SLA values are lower, although not statistically significant. In 2011, the average CWMs of SLA values were higher compared to other years, indicating that vegetation may begin to recover already after 4 years from the fire. The vegetation is characterized by the regeneration of grass tufts with low seed germination, thus the average values remain relatively high (Rocha and Shaver 2011a; Wein and Bliss 1973). In 2017, the values are lower and more similar to reference values, as after 10 years, new vegetation with greater germination is regrowing, thus reducing the average CWM of SLA values. In 2017, this disparity between the various severity levels seems to no longer exist. It is stated that after a fire, the prevalence of annual plants, which have a higher CWM of SLA value, increases, and it is associated with post-fire regeneration (Abedi et al. 2022; Keeley et al. 2011; Anacker et al. 2011; Sakschewski et al. 2015).

Regarding CWM of plant height, 2008 is the year that makes the p-value year significant, as values of CWM of plant height for severe fire severity are much higher compared to other years. This is probably due to the fact that, with higher intensity, practically all lower and less performing vegetation was burned, until it disappeared; thus, the average height values increased. This leads to the conclusion that vegetation that is able to survive is more performing and taller. In the following years, the values stabilize near reference values for all fire severity levels, resulting in non-statistical significance, thus assuming the regrowth of new vascular plants. Additionally, it has been shown that stress influences vegetation height; hence, perhaps for this reason, the average values are lower (Sonnier et al. 2010; Cornwell and Ackerly 2009).

Looking at the values of CWMs of leaf nitrogen content, the following can be observed: the tendency of 2008 to have high values, probably due to the death of less-performing plants; the decrease in values for the years from 2009 to 2011; and then the recovery for the year 2017, with even higher average values (but still not statistical significant) for severely burned areas, thus promoting post-fire regeneration (Abedi et al. 2022; Anacker et al. 2011; Sakschewski et al. 2015; Bashirzadeh et al. 2023; Rahmanian et al. 2019). Nevertheless, there does not seem to be a great difference in CWM of leaf nitrogen content values between more and less severely burnt places. On the other hand, a difference can be noticed between the burned and unburned sites, suggesting that in fire-affected areas, the rate of photosynthesis is lower and that plants, in general, are less efficient in growth and CO_2 absorption. According to Hobbie et al. (2002), time should be waited so that nitrogen, released from permafrost thawing during the fire, can lead to increased plant productivity (Keuper et al. 2012). This is because it is necessary for soil reserves to be restored first (Hobbie et al. 2002).

The values of CWMs of leaf carbon content are consistently below reference values: for 2008, the explanation is similar to that for CWMs of leaf nitrogen; while for the subsequent years, it can be observed that they are very similar (thus not statistically significant). There seems to be a gradual decrease in the slope between the most severely and less burned sites, which could indicate, as in the case of leaf nitrogen, an increase in post-fire regrowth, although less performing, comparing the values with the reference ones (Bashirzadeh et al. 2023; Rahmanian et al. 2019; Anacker et al. 2011; Sakschewski et al. 2015). Carbon storage in leaves is a crucial metric to understand whether and to what extent vascular plants can absorb carbon, thus limiting its concentration increase in the atmosphere. From Figure 7, it can be observed that even after 10 years, the CWM value of the carbon in the leaves is not equal to that contained in the leaves of the reference vegetation. This observation raises that, after a fire, regardless of its severity, plants need much more time to re-establish a carbon value in their leaves at the same level as plants that have not suffered a fire. This indicates a lower photosynthetic rate performance and, since the carbon cycle is crucial for global warming, this long recovery time could cause serious consequences for the ecosystem. An increase increase in carbon in the soil or atmosphere can be expected, that may transform the biome into a carbon source (Veraverbeke et al. 2021).

The non statistical significance of the results may however be interesting for other studies and for future research. One possible explanation of the non significance is due to the limited sample size of the data; the total data points for each year were 14, which are not sufficient to represent the entire area of the fire and accurately capture the changes in functional traits of the vegetation. Additionally, it was not possible to find a value for the functional traits for every vascular plant; therefore, the CWM result is not an accurate mean for all transects. Moreover, the CWM value of functional traits is an average of other values from a database that, although it is specific for tundra ecosystem, may not always be accurate for the specific vegetation at that location. To overcome these issues, it would have been better to obtain the values of functional traits directly from the vegetation at each transect measurement. Furthermore, more variables could potentially be incorporated into the model, such as: soil moisture, soil nutrients, slope, light received by the vegetation, or other biotic and abiotic factors that may influence vegetation growth and thus its functional traits. Lastly, the methodology may not be the most suitable for detecting significance. It can be observed, from Figures (4, 5, 6, 7), a trend for all four CWMs concerning fire severity. It can be noticed that the values of each CWM of plant trait at about 550 pixels are higher compared to those for approximately 700 pixels, before increasing again when the fire severity increases (˜ 850 pixel). The trend diminishes over time and may suggest that the most appropriate methodology is the quadratic model, and not the linear model.

4.1.2 General discussion of fire severity and vegetation recovery

Despite the severity of the fire, within 4 years after the event, the net primary production of vascular plants, both in moderately burned tundra and severely affected ones, had returned to pre-fire levels (Bret-Harte et al. 2013). However, the biomass of vascular plants in burned areas remained lower than that of unburned areas (Bret-Harte et al. 2013). Although the biomass of graminoids was comparable between fire-affected and intact areas, complete regeneration of deciduous and evergreen shrub biomass had not yet occurred (Bret-Harte et al. 2013).

Fire promotes plant homogenization; therefore, it influences beta diversity, especially through different-aged fire scars (Abedi et al. 2022), with a consequent reduction in the ecosystem functions of dominant species (Heydari et al. 2020). The impact of fire on species diversity is thus negative (Keeley et al. 2008; Grace and Keeley 2006). Plant species diversity is lower immediately after the fire and increases over time afterward (Venn et al. 2016; Heim et al. 2022; Frost et al. 2020; Jandt and Meyers 2000). After the fire, species richness was also low, but it increased over the years (Figure 9 in A). Furthermore, high-severity fires have lower species richness and evenness values compared to low-severity fire areas (Heydari et al. 2020). However, it has been proven that, in low-intensity areas, species richness and uniformity decrease after fire, whereas in high-intensity areas they increase (Heydari et al. 2020). After a fire, therefore, multiple species with also different growth forms can coexist (Bashirzadeh et al. 2023; Bannister et al. 2020).

A relatively rapid recovery of the vegetation cover of the arctic tundra after a fire (within 10 years) is expected (Rocha et al. 2012), as indicated by this study as well. This is likely due to the rapid response of plants (such as *Eriophorum vaginatum* or *Vaccinium sp.*), which, taking advantage of the large carbon and nutrient reserves in the soil (left from the ash; thawed from the permafrost layer; or remained protected during combustion), are able to grow much faster (Rocha et al. 2012; Wein and Bliss 1973; Narita et al. 2015). *Eriophorum vaginatum*, in particular, is susceptible to fires; although burns can be severe enough to destroy all aboveground parts of the plant, new shoots are protected by the bases of the tussocks, moss mats, and peat, all of which favor this species as one of the first colonizers of a post-fire area, especially in the short term, as confirmed by data (Wein and Bliss 1973; Heim et al. 2022; Tsuyuzaki et al. 2018). Additionally, sedges (*Carex sp.*) can grow vigorously on post-fire soil, as tussock growth is resistant to the effects of fire (Jones et al. 2009). Another significant species both in various studies and in this data, is *Betula nana*; it is known to dominate shrub expansion in tundra regions, sprouting easily from rhizomes, especially in the long term (Jones et al. 2009; Heim et al. 2022; Bret-Harte et al. 2013; Mallen-Cooper et al. 2021; Deslippe and Simard 2011). Consequently, the ARF scar area was classified, following the fire, as "shrub-sedge mixed tundra, with shrub cover exceeding 25%", thus greater than a typical tussock tundra (Bret-Harte et al. 2013; Jandt et al. 2012; Viereck 1992). This determination indicates that, 10 years after the fire, species richness and the number of individuals of these fast-growing species, increased in fire-disturbed sites (Bashirzadeh et al. 2023) (Figure 9 in A). The vascular plants, after 10 years since the fire, are recovering, and with the change of predominant plants there may be a change in the CWMs values. This is potentially not yet observable in these results because the new plants are young and not yet fully developed.

Fire promotes the dominance of cover by ruderal plants, broadleaf herbs, and grasses; they have very high competitive ability and can occupy undisturbed and degraded ecosystems (Bashirzadeh et al. 2023; Abedi et al. 2022; Enright et al. 2007). Therefore, on average after the fire, annual plants outnumber perennial ones, affirming that disturbance promotes the establishment (secondary succession) of a large number of small-statured, fast-growing species (with an R-Strategy) (Abedi et al. 2022; Grime 1973; Venn et al. 2016; Keith et al. 2007; Kahmen and Poschlod 2004). According to Abedi et al. (2022), two years after the fire, the value of CWM of SLA is higher compared to control areas, confirming that fire can favor the appearance of fast-growing ruderal species (annual plants), which have higher CWM of SLA and of leaf nitrogen content (Abedi et al. 2022; Davies et al. 2009; Khaled et al. 2006; Rhodes et al. 2010; Bashirzadeh et al. 2023). This could also be inferred from this study by examining individual species and their values, but there do not appear to be significant differences for various fire severity values.

The initial regeneration of vegetation in the tundra was primarily limited by the photosynthetic capacity of plants, influenced more by the reduced leaf area of the remaining vegetation than by nutrient deficiency (Jiang et al. 2015b). The simulation made by Jiang et al. (2015b) revealed an excess of nutrients in the soil, both due to continuous mineralization and the abundance of organic nutrients in the ashes. The return of vegetation after the fire was mainly supported by the absorption of residual inorganic nitrogen present in the ashes, due to permafrost thawing and increased microbial activity (Heim et al. 2021b; Keuper et al. 2012) and by the transfer of nitrogen and phosphorus from soil organic matter to vegetation (Jiang et al. 2015b). Since nutrient reserves remaining after the fire were closely tied to the severity of the event, the importance of fire severity in modulating the allocation of carbon nutrients in post-fire tundra ecosystems was highlighted (Jiang et al. 2015b). Despite higher amounts of residual inorganic nutrients in cases of more severe fires, those of moderate severity showed faster recovery due to lower plant mortality and the consequent increase in photosynthetic capacity (higher value of CWM of SLA and of plant height (Bjorkman et al. 2018)) (Jiang et al. 2015b). Furthermore, Jiang et al. (2015b) state that, if the severity of burning is greater, the quantity of nitrogen and phosphorus in vegetation and soil organic matter (SOM) will be greater. However, if severity is too high, nutrients in vegetation and SOM will be lower, thus plant growth will be reduced (Jiang et al. 2015b), concluding that there should be a difference between more and less severely burned areas. However, the presence of residual inorganic nutrients allowed both severe and moderate fires to recover and surpass the unburned site in 5 years after the fire, both in terms of total surface biomass and productivity (Jiang et al. 2015b). The study of Jiang et al. (2015b), however, is based on a model, and it is likely that the time frame for recovery will be longer.

An increase in soil temperature (determined by changes in soil thermal properties due to burned material remaining on the surface (Santana et al. 2010)) encourages mineralization rates and thus also permafrost thawing, which leads to greater availability of nutrients primarily stored by shrubs, which have longer roots (Heim et al. 2022; Jansson and Hofmockel 2020; Oulehle et al. 2016; Salmon et al. 2016). The, relatively, rapid recovery of the vegetation cover will have implications for climate change and the regime of other fires (Rocha et al. 2012). It is expected that fire will change the tundra into an area dominated by graminoids, deciduous plants, and woody shrubs (Rocha et al. 2012; Rupp et al. 2000; Rocha and Shaver 2011a; Johnstone et al. 2010; Sturm et al. 2001; Tape et al. 2006; Hudson and Henry 2009). Therefore, the functional traits of plants, will reflect the fact that post-fire plant growth strategies are faster, maximizing soil resource acquisition (Taber and Mitchell 2023; Forero et al. 1999; Reich 2014; Wright et al. 2004). Although from this study the severity of the fire does not appear to have a statistically significant impact on the CWM of vascular plants in the short- and long-term, fire disturbance, depending on fire severity, creates spaces that favor shrub establishment and accelerate their proliferation (Heim et al. 2022; Lantz et al. 2010; Myers-Smith et al. 2011; Myers-Smith et al. 2019; Shevtsova et al. 2020). This can lead to significant changes in vegetation community structure during post-fire invasion (Myers-Smith et al. 2019). Consequently, the growth in shrub abundance is expected to result in a future increase in the frequency, severity and extent of fires, and in the change in plant species characteristics (Jones et al. 2013; Higuera et al. 2008).

4.2 Ecosystem functioning and fire linked to vegetation structure

Fires can alter the microenvironment by increasing soil temperature, thawing, and nutrient availability, as well as affecting soil moisture and hydrological processes (Rocha et al. 2012; Jiang et al. 2015b; Keeley et al. 2008). These changes can increase plant productivity and soil respiration for some time afterward the disturbance (Rocha et al. 2012; Wein and Bliss 1973; Vavrek et al. 1999; Fetcher et al. 1984). It has been demonstrated that broad-scale environmental factors, such as temperature, primarily shape the CWMs, while finer-scale factors, such as topography or soil characteristics, mainly influence functional diversity and trait distribution among dominant species (De Bello et al. 2013).

Analyzing the SEM results, it can be observed that the years after the fire are not significant when the model includes other variables. Therefore, the previously described significance between CWM of plant height and year is no longer relevant if other variables are considered to better explain the variation in CWM of plant height over time. This means that the significance is likely due, as mentioned earlier, solely to the loss of "low" vegetation (˜ 10 cm), not to the increase in "high" vegetation (˜ 20 cm), in the most burned sites.

The severity of the fire does not have a significant effect on any of the other variables, but this does not mean that the fire itself, apart from severity, does not impact the other variables. In fact, it is demonstrated that fire increases permafrost thaw depth in 75% of burned areas (Rocha et al. 2012), deepening the active layer depth and increasing soil temperature (Heim et al. 2021b; Rocha et al. 2012; Loranty et al. 2018). Contrary to our results, Rocha and Shaver

(2011b) state that thaw depth increases with fire severity, indicating that the active layer depth was deeper in severely burned sites. This result can also be seen from the data in this study, if an ANODEV is conducted between the dependent variable active layer depth (ALD) and the independent variable dNBR, disregarding the others (Table 4 in A). An increase in ALD thickness can lead to greater nutrient availability, especially nitrogen (Heim et al. 2021b), which promotes plant productivity (Rocha et al. 2012; Fetcher et al. 1984; Wein and Bliss 1973; Vavrek et al. 1999; Heim et al. 2022). Nevertheless, in the results of this study, an increase in the active layer does not directly cause an increase in the CWMs of SLA and plant height, despite them being often linked to vegetation productivity. This, however, could merely be due to the fact that the plants are still low and still developing, thus the effect of the increased nutrient availability is not yet visible. After a fire, permafrost restores itself, thus the active layer decreases, as vegetation and organic soils are reconstituted and, consequently, insulation from the atmosphere increases (Heim et al. 2021b; Michaelides et al. 2019; Bret-Harte et al. 2013; Racine et al. 1987; Jorgenson et al. 2010).

Areas characterized by drier ecosystems (i.e. more arid) experienced a higher percentage of fire damage compared to those with wetter ecosystems (i.e. more humid) (Rocha et al. 2012). After the fire, therefore, variations in soil moisture were heterogeneous among ecosystems: while some showed significant changes, others revealed mild fluctuations (Jiang et al. 2015a). Additionally, no significant variations in average soil moisture in the tundra were observed after the fire, despite a greater accumulation of surface water in burned sites due to the destruction of the organic layer, which normally absorbs water (Jiang et al. 2015a; Rocha and Shaver 2011b). It has also been demonstrated that vegetation responses to fire include a shift in vegetation community types, such as a change from dry tundra to wet tundra (Rocha and Shaver 2011b; Hinzman et al. 2005).

From this analysis, it can be observed that the statements in the result section (3.2) are confirmed. Immediately after the fire, CWM of SLA and of plant height values are lower, causing an increase in soil moisture, also due to the thawing of the permafrost and thus to the increase of the active layer depth (statement two (3.2)). However, it is not excluded that, with a decrease in the active layer thickness, the value of CWM of SLA and of plant height may increase, thereby causing a decrease in soil moisture. Therefore, as time passes after the fire, statement one (3.2) could be the most relevant. However, in the tundra, soil moisture is subject to a variety of influences, including summer precipitation, snow distribution, freeze-thaw cycles, permafrost status, soil characteristics, and topography (Myers-Smith et al. 2015). This variety of factors makes soil moisture assessment more complex than climatic variables, and it is evident that it is simplistic to derive a value solely from vegetation (as in this study case using the Ellenberg Indicator Value F for soil moisture) without considering other factors. Therefore, the significance resulting from the SEM analysis is relevant but should be interpreted with caution.

The limitations of this model are several. The data sample is not very large, 70 observations, which may not be sufficient to represent the entire area analysed and to detect significant differences. The model itself could be more comprehensive, for example: including other ecosystem functioning or disturbances. Furthermore, it is highly likely, that the significance of the interaction between the two CWMs and the soil moisture indicator is lower in reality than derived from this model. This because all values were calculated using the same vegetation classification and are averages of data, making it much more likely for an interaction to occur. Therefore, this model is acceptable but not perfect. Furthermore some plants the values of functional traits were not found in the database, so the calculation of CWMs is not an accurate mean, as in the case of the previous analysis. In addition, the utilization of the dNBR value for assessing fire severity may not be the most appropriate approach. The amalgamation of fire severity and ecosystem responses into a singular index might not offer the optimal means to fully comprehend the intricacies of the phenomena under consideration (Keeley et al. 2008). Consequently, fire severity may not be adequately captured by this index. Moreover, relying exclusively on vascular plants to detect vegetation differences could have been limiting; solely analyzing vascular plants may not serve as a universal indicator of vegetation change. The Arctic tundra, in addition to vascular plants, is characterized by various cryptogamic plants, which are likely more crucial for tundra ecosystems due to their higher abundance. Consequently, they are likely more pivotal for ecosystem functioning and may have undergone a more significant impact from fire. These reasons could potentially be linked to the variables failing to explain much of the variance and having an insignificant impact on other variables.

In general, the consequences of fires on organic layer depth and soil moisture result in increased soil temperature and deepening of thawing (Jiang et al. 2015b). However, the extent of this phenomenon depends on the response of soil thermal conductivity to soil moisture, changes in organic layer thickness, and vegetation (Jiang et al. 2015a; Yoshikawa et al. 2003; Liljedahl et al. 2007). Fires in the tundra have a significant effect on ecosystem functioning, involving both vegetation and watershed hydrological processes (Keeley et al. 2008). Consequently, the structure of vegetation should be also linked to fire and ecosystem functions, although many more variables play a crucial role in understanding the system.

5 Conclusion

Due to the ongoing climate change in the Arctic an increase in the frequency, extent and intensity of fires is predicted (Higuera et al. 2008; Hu et al. 2010). However, it is not yet fully clear how fire intensity influences vegetation. From these results, it can be concluded that fire severity does not appear to have an impact on the functional traits of vascular plants, for the four investigated CWMs (SLA, plant height, nitrogen and carbon content in leaves), both in the short term (< 5 years) and in the long term (10 years). Additionally, fire severity also does not seem to be significant for vegetation structure, which, however, seems to have an influence on ecosystem functions.

A rise in vegetation will lead to a change in the traditional Arctic tundra vegetation, causing an increase in shrubs, which would alter the values of plant functional types, the ecosystem functioning and also increase the amount of fuel for future fires (Higuera et al. 2008). Determining all factors leading to ecosystem change is essential for understanding the long-term effects of fire and its intensity, on both vegetation and ecosystem functioning, which, from this preliminary analysis, appears to be strongly influenced.

The feedbacks between tundra fires and climate are complex, but suggest possible short and long-term impacts (Higuera et al. 2008; Shaver et al. 2006; Oechel et al. 2000; Mack et al. 2004). The severity of fires could also be significant, especially in the short term, although the extent to which fire intensity determines ecosystem responses remains, for the moment, uncertain (Keeley et al. 2008). Impacts of fire include changes in vegetation, changes in soil moisture levels, alteration of microbial activity, and changes in the nitrogen and carbon cycles, as well as active layer thickness modification (Veraverbeke et al. 2021; Jiang et al. 2015a; Bret-Harte et al. 2013). Therefore the impact of fire on ecosystem functioning, involving both vegetation and watershed hydrological processes, is significant.

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References

Abedi, Mehdi et al. (2022). “Fire disturbance effects on plant taxonomic and functional β-diversity mediated by topographic exposure”. In: *Ecology and Evolution* 12.1, e8552. DOI: 10.1002/ece3.8552.

Aerts, Rien and F. Stuart Chapin III (1999). “The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns”. In: *Advances in ecological research.* Vol. 30. Elsevier, pp. 1–67. DOI: 10.1016/S0065-2504(08)60016-1.

Ames, Gregory M. et al. (2016). “Multiple environmental drivers structure plant traits at the community level in a pyrogenic ecosystem”. In: *Functional Ecology* 30.5, pp. 789–798. DOI: 10.1111/1365-2435.12536.

Amiro, B. D. et al. (Nov. 2006). “The effect of post-fire stand age on the boreal forest energy balance”. In: *Agricultural and Forest Meteorology* 140.1-4, pp. 41–50. DOI: 10.1016/J.AGRFORMET.2006.02.014.

Anacker, Brian et al. (2011). “Ecological strategies in California chaparral: interacting effects of soils, climate, and fire on specific leaf area”. In: *Plant Ecology & Diversity* 4.2-3, pp. 179–188. DOI: 10.1080/17550874.2011.633573.

Analysis of Deviance (2023). URL: https://online.stat.psu.edu/stat504/lesson/6/6.3/6.3.4.

Bannister, Jan R. et al. (2020). “Shrub influences on seedling performance when restoring the slow-growing conifer Pilgerodendron uviferum in southern bog forests”. In: *Restoration ecology* 28.2, pp. 396–407. DOI: 10.1111/rec.13090.

Bashirzadeh, Maral et al. (2023). “Post-Fire Recovery of Plant Biodiversity Changes Depending on Time Intervals since Last Fire in Semiarid Shrublands”. In: *Fire* 6.3, p. 103. DOI: 10.3390/fire6030103.

Beest, Mariska te et al. (2021). “Grass functional trait responses to experimental warming and fire in Afromontane grasslands”. In: *African Journal of Range & Forage Science* 38.1, pp. 88–101. DOI: 10.2989/10220119.2020.1843538.

Bjorkman, Anne D. et al. (2018). “Tundra Trait Team: A database of plant traits spanning the tundra biome”. In: *Global Ecology and Biogeography* 27.12, pp. 1402–1411. DOI: 10.1111/geb.12821.

Bollen, Kenneth A. (1989). *Structural equations with latent variables.* John Wiley & Sons.

Bond, William J. and Jon E. Keeley (July 2005). “Fire as a global ’herbivore’: The ecology and evolution of flammable ecosystems”. In: *Trends in Ecology and Evolution* 20.7, pp. 387–394. ISSN: 01695347. DOI: 10.1016/j.tree.2005.04.025.

Bond, William J. and Brian W. Van Wilgen (2012). *Fire and plants*. Vol. 14. Springer Science & Business Media.

Bouskill, Nicholas J. et al. (2022). "Microbial contribution to post-fire tundra ecosystem recovery over the 21st century". In: *Communications Earth & Environment* 3.1, p. 26. DOI: 10.1038/s43247-022-00356-2.

Bret-Harte, M. Syndonia et al. (Aug. 2013). "The response of Arctic vegetation and soils following an unusually severe tundra fire". In: *Philosophical Transactions of the Royal Society B: Biological Sciences* 368.1624. DOI: 10.1098/RSTB.2012.0490.

Cornwell, William K. and David D. Ackerly (2009). "Community assembly and shifts in plant trait distributions across an environmental gradient in coastal California". In: *Ecological monographs* 79.1, pp. 109–126. DOI: 10.1890/07-1134.1.

Crawford, R.M.M. (1992). *Arctic Ecosystems in a Changing Climate*. Academic Press.

Czortek, Patryk et al. (2021). "Long-term shifts in the functional diversity of abandoned wet meadows: Impacts of historical disturbance and successional pathways". In: *Ecology and Evolution* 11.21, pp. 15030–15046. DOI: 10.1002/ece3.8186.

Davies, K.W. et al. (2009). "Interaction of historical and nonhistorical disturbances maintains native plant communities". In: *Ecological Applications* 19.6, pp. 1536–1545. DOI: 10.1890/09-0111.1.

De Bello, Francesco et al. (Oct. 2005). "Predictive value of plant traits to grazing along a climatic gradient in the Mediterranean". In: *Journal of Applied Ecology* 42.5, pp. 824–833. DOI: 10.1111/J.1365-2664.2005.01079.X.

De Bello, Francesco et al. (2013). "Hierarchical effects of environmental filters on the functional structure of plant communities: a case study in the French Alps". In: *Ecography* 36.3, pp. 393–402. DOI: 10.1111/j.1600-0587.2012.07438.x.

Debouk, Haifa et al. (Oct. 2015). "Functional Trait Changes, Productivity Shifts and Vegetation Stability in Mountain Grasslands during a Short-Term Warming". In: *PLOS ONE* 10.10, e0141899. ISSN: 1932-6203. DOI: 10.1371/JOURNAL.PONE.0141899.

Deslippe, Julie R. and Suzanne W. Simard (2011). "Below-ground carbon transfer among Betula nana may increase with warming in Arctic tundra". In: *New Phytologist* 192.3, pp. 689–698. DOI: 10.1111/j.1469-8137.2011.03835.x.

Díaz, Sandra and Marcelo Cabido (2001). "Vive la différence: plant functional diversity matters to ecosystem processes". In: *Trends in ecology & evolution* 16.11, pp. 646–655. DOI: 10.1016/S0169-5347(01)02283-2.

Díaz, Sandra et al. (2004). “The plant traits that drive ecosystems: evidence from three continents”. In: *Journal of vegetation science* 15.3, pp. 295–304. DOI: 10.1111/j.1654-1103.2004.tb02266.x.

Díaz, Sandra et al. (Feb. 2007). “Plant trait responses to grazing – a global synthesis”. In: *Global Change Biology* 13.2, pp. 313–341. DOI: 10.1111/J.1365-2486.2006.01288.X.

Díaz, Sandra et al. (2016). “The global spectrum of plant form and function”. In: *Nature* 529.7585, pp. 167–171. DOI: 10.1038/nature16489.

Dobiński, Wojciech (2020). “Permafrost active layer”. In: *Earth-Science Reviews* 208, p. 103301. DOI: 10.1016/j.earscirev.2020.103301.

Dyrness, C.T. and R.A. Norum (1983). “The effects of experimental fires on black spruce forest floors in interior Alaska”. In: *Canadian Journal of Forest Research* 13.5, pp. 879–893. DOI: 10.1139/x83-118.

Enright, Neal J. et al. (Nov. 2014). “Resistance and resilience to changing climate and fire regime depend on plant functional traits”. In: *Journal of Ecology* 102.6, pp. 1572–1581. DOI: 10.1111/1365-2745.12306.

Enright, N.J. et al. (2007). “Soil vs. canopy seed storage and plant species coexistence in species-rich Australian shrublands”. In: *Ecology* 88.9, pp. 2292–2304. DOI: 10.1890/06-1343.1.

European and Mediterranean Plant Protection Organization (2024). URL: https://www.eppo.int/.

Falster, Daniel S. and Mark Westoby (2003). “Plant height and evolutionary games”. In: *Trends in ecology & evolution* 18.7, pp. 337–343. DOI: 10.1016/S0169-5347(03)00061-2.

Fernandez-Garcia, Victor et al. (2020). “Fire regimes shape diversity and traits of vegetation under different climatic conditions”. In: *Science of the Total Environment* 716, p. 137137. DOI: 10.1016/j.scitotenv.2020.137137.

Fernández-Guisuraga, José Manuel et al. (2023). “Short-term responses of ecosystem multifunctionality to fire severity are modulated by fire-induced impacts on plant and soil microbial communities”. In: *Science of The Total Environment* 898, p. 165477. DOI: 10.1016/j.scitotenv.2023.165477.

Fetcher, Ned et al. (1984). “Changes in arctic tussock tundra thirteen years after fire”. In: *Ecology* 65.4, pp. 1332–1333. DOI: 10.2307/1938338.

Flannigan, Mike D. et al. (2009). “Implications of changing climate for global wildland fire”. In: *International journal of wildland fire* 18.5, pp. 483–507. DOI: 10.1071/WF08187.

Forero, Manuela G. et al. (1999). “Causes and consequences of territory change and breeding dispersal distance in the black kite”. In: *Ecology* 80.4, pp. 1298–1310. DOI: `10.1890/0012-9658(1999)080[1298:CACOTC]2.0.CO;2`.

Fridley, Jason D et al. (2016). “Longer growing seasons shift grassland vegetation towards more-productive species”. In: *Nature Climate Change* 6.9, pp. 865–868. DOI: `10.1038/nclimate3032`.

Frost, Gerald V. et al. (2020). “Multi-decadal patterns of vegetation succession after tundra fire on the Yukon-Kuskokwim Delta, Alaska”. In: *Environmental Research Letters* 15.2, p. 025003. DOI: `10.1088/1748-9326/ab5f49`.

Gagnon, Mikael et al. (2019). “The carbon sink due to shrub growth on Arctic tundra: a case study in a carbon-poor soil in eastern Canada”. In: *Environmental Research Communications* 1.9, p. 091001. DOI: `10.1088/2515-7620/ab3cdd`.

Garnier, Eric and Marie-Laure Navas (2012). “A trait-based approach to comparative functional plant ecology: concepts, methods and applications for agroecology. A review”. In: *Agronomy for Sustainable Development* 32, pp. 365–399. DOI: `10.1007/s13593-011-0036-y`.

Garnier, Eric et al. (Sept. 2004). “Plant Funtional Markers capture ecosystem properties during Secondary Succession”. In: *Ecology* 85.9, pp. 2630–2637. DOI: `10.1890/03-0799`.

Grace, James B. (2006). *Structural equation modeling and natural systems.* Cambridge University Press.

Grace, James B. and Jon E. Keeley (2006). “A structural equation model analysis of postfire plant diversity in California shrublands”. In: *Ecological Applications* 16.2, pp. 503–514. DOI: `10.1890/1051-0761(2006)016[0503:ASEMAO]2.0.CO;2`.

Grace, James B. et al. (2010). “On the specification of structural equation models for ecological systems”. In: *Ecological monographs* 80.1, pp. 67–87. DOI: `10.1890/09-0464.1`.

Grau-Andrés, Roger et al. (2019). “Increased fire severity alters initial vegetation regeneration across Calluna-dominated ecosystems”. In: *Journal of Environmental Management* 231, pp. 1004–1011. DOI: `10.1016/j.jenvman.2018.10.113`.

Grime, J. Philip (2006a). *Plant strategies, vegetation processes, and ecosystem properties.* John Wiley & Sons.

— (2006b). “Trait convergence and trait divergence in herbaceous plant communities: mechanisms and consequences”. In: *Journal of vegetation science* 17.2, pp. 255–260. DOI: `10.1111/j.1654-1103.2006.tb02444.x`.

Grime, John Philip (1973). “Competitive exclusion in herbaceous vegetation”. In: *Nature* 242.5396, pp. 344–347. DOI: `10.1038/242344a0`.

Happonen, Konsta et al. (2022). “Relationships between above-ground plant traits and carbon cycling in tundra plant communities”. In: *Journal of Ecology* 110.3, pp. 700–716. DOI: `10.1111/1365-2745.13832`.

He, Tianhua et al. (2019). “Fire as a key driver of Earth’s biodiversity”. In: *Biological Reviews* 94.6, pp. 1983–2010. DOI: `10.1111/brv.12544`.

Heim, Ramona J. et al. (2021a). “Fire in lichen-rich subarctic tundra changes carbon and nitrogen cycling between ecosystem compartments but has minor effects on stocks”. In: *Biogeosciences Discussions* 2021, pp. 1–18. DOI: `10.5194/bg-19-2729-2022`.

Heim, Ramona J. et al. (Mar. 2021b). “Post-fire vegetation succession in the Siberian subarctic tundra over 45 years”. In: *Science of The Total Environment* 760, p. 143425. DOI: `10.1016/J.SCITOTENV.2020.143425`.

Heim, Ramona J. et al. (2022). “Fire disturbance promotes biodiversity of plants, lichens and birds in the Siberian subarctic tundra”. In: *Global Change Biology* 28.3, pp. 1048–1062. DOI: `10.1111/gcb.15963`.

Helmuth, Brian et al. (2005). “Biophysics, physiological ecology, and climate change: does mechanism matter?” In: *Annu. Rev. Physiol.* 67, pp. 177–201. DOI: `10.1146/annurev.physiol.67.040403.105027`.

Heydari, Mehdi et al. (2020). “Spatio-temporal changes in the understory heterogeneity, diversity, and composition after fires of different severities in a semiarid oak (Quercus brantii Lindl.) forest”. In: *Land Degradation & Development* 31.8, pp. 1039–1049. DOI: `10.1002/ldr.3518`.

Higuera, Philip E. et al. (2008). “Frequent fires in ancient shrub tundra: implications of paleorecords for arctic environmental change”. In: *PloS one* 3.3, e0001744. DOI: `10.1371/journal.pone.0001744`.

Hill, Mark O. et al. (2004). *PLANTATT-attributes of British and Irish plants: status, size, life history, geography and habitats.* Centre for Ecology & Hydrology.

Hinzman, Larry D. et al. (2005). “Evidence and implications of recent climate change in northern Alaska and other arctic regions”. In: *Climatic change* 72, pp. 251–298. DOI: `10.1007/s10584-005-5352-2`.

Hobbie, Sarah E. et al. (2002). “A synthesis: the role of nutrients as constraints on carbon balances in boreal and arctic regions”. In: *Plant and Soil* 242, pp. 163–170. DOI: `10.1023/A:1019670731128`.

Hu, Feng Sheng et al. (Dec. 2010). “Tundra burning in Alaska: Linkages to climatic change and sea ice retreat”. In: *Journal of Geophysical Research: Biogeosciences* 115.G4, p. 4002. DOI: `10.1029/2009JG001270`.

Hu, Feng Sheng et al. (Sept. 2015). “Arctic tundra fires: natural variability and responses to climate change”. In: *Frontiers in Ecology and the Environment* 13.7, pp. 369–377. ISSN: 1540-9309. DOI: `10.1890/150063`.

Hudson, James M.G. and G.H.R. Henry (2009). “Increased plant biomass in a High Arctic heath community from 1981 to 2008”. In: *Ecology* 90.10, pp. 2657–2663. DOI: `10.1890/09-0102.1`.

Hudson, J.M.G. et al. (2011). “Taller and larger: shifts in Arctic tundra leaf traits after 16 years of experimental warming”. In: *Global Change Biology* 17.2, pp. 1013–1021. DOI: `10.1111/j.1365-2486.2010.02294.x`.

Huerta, Sara et al. (2022). “Short-term effects of burn severity on ecosystem multifunctionality in the northwest Iberian Peninsula”. In: *Science of The Total Environment* 844, p. 157193. DOI: `10.1016/j.scitotenv.2022.157193`.

Hurteau, Matthew D. et al. (Sept. 2014). “Climate change, fire management, and ecological services in the southwestern US”. In: *Forest Ecology and Management* 327, pp. 280–289. ISSN: 0378-1127. DOI: `10.1016/J.FORECO.2013.08.007`.

Jandt, Randi R. and C. Randy Meyers (2000). *Recovery of lichen in tussock tundra following fire in northwestern Alaska.* US Department of the Interior, Bureau of Land Management, Alaska State Office.

Jandt, Randi R. et al. (2021). “Fire Effects 10 Years After the Anaktuvuk River Tundra Fires”. In: DOI: `10.13140/RG.2.2.20210.02243`.

Jandt, R.R. et al. (2012). *Findings of Anaktuvuk River Fire Recovery Study, 2007-2011, Bureau of Land Management, Fairbanks, AK.*

Jansson, Janet K. and Kirsten S. Hofmockel (2020). “Soil microbiomes and climate change”. In: *Nature Reviews Microbiology* 18.1, pp. 35–46. DOI: `10.1038/s41579-019-0265-7`.

Jia, Min et al. (2021). “Estimation of leaf nitrogen content and photosynthetic nitrogen use efficiency in wheat using sun-induced chlorophyll fluorescence at the leaf and canopy scales”. In: *European journal of Agronomy* 122, p. 126192. DOI: `10.1016/j.eja.2020.126192`.

Jiang, Yueyang et al. (2015a). “Contrasting soil thermal responses to fire in Alaskan tundra and boreal forest”. In: *Journal of Geophysical Research: Earth Surface* 120.2, pp. 363–378. DOI: `10.1002/2014JF003180`.

Jiang, Yueyang et al. (Sept. 2015b). “Modeling carbon–nutrient interactions during the early recovery of tundra after fire”. In: *Ecological Applications* 25.6, pp. 1640–1652. DOI: `10.1890/14-1921.1`.

Johnstone, Jill F. and F. Stuart Chapin (2006). “Effects of soil burn severity on post-fire tree recruitment in boreal forest”. In: *Ecosystems* 9, pp. 14–31. DOI: `10.1007/s10021-004-0042-x`.

Johnstone, Jill F. et al. (2010). “Changes in fire regime break the legacy lock on successional trajectories in Alaskan boreal forest”. In: *Global change biology* 16.4, pp. 1281–1295. DOI: `10.1111/j.1365-2486.2009.02051.x`.

Jones, Benjamin M. et al. (Aug. 2009). “Fire Behavior, Weather, and Burn Severity of the 2007 Anaktuvuk River Tundra Fire, North Slope, Alaska”. In: *Arctic, Antarctic, and Alpine Research* 41.3, pp. 309–316. ISSN: 15230430. DOI: `10.1657/1938-4246-41.3.309`.

Jones, Benjamin M. et al. (July 2013). “Identification of unrecognized tundra fire events on the north slope of Alaska”. In: *Journal of Geophysical Research: Biogeosciences* 118.3, pp. 1334–1344. DOI: `10.1002/jgrg.20113`.

Jorgenson, M. Torre et al. (2010). “Resilience and vulnerability of permafrost to climate change”. In: *Canadian Journal of Forest Research* 40.7, pp. 1219–1236. DOI: `10.1139/X10-060`.

Jump, Alistair S. and Josep Peñuelas (2005). “Running to stand still: adaptation and the response of plants to rapid climate change”. In: *Ecology letters* 8.9, pp. 1010–1020. DOI: `10.1111/j.1461-0248.2005.00796.x`.

Jung, Vincent et al. (2014). “Intraspecific trait variability mediates the response of subalpine grassland communities to extreme drought events”. In: *Journal of ecology* 102.1, pp. 45–53. DOI: `10.1111/1365-2745.12177`.

Kahmen, S. and P. Poschlod (2004). “Plant functional trait responses to grassland succession over 25 years”. In: *Journal of Vegetation Science* 15.1, pp. 21–32. DOI: `10.1111/j.1654-1103.2004.tb02233.x`.

Kattge, Jens et al. (2011). “TRY–a global database of plant traits”. In: *Global change biology* 17.9, pp. 2905–2935. DOI: `10.1111/j.1365-2486.2011.02451.x`.

Keeley, Jon E. (Feb. 2009). “Fire intensity, fire severity and burn severity: a brief review and suggested usage”. In: *International Journal of Wildland Fire* 18.1, pp. 116–126. ISSN: 1448-5516. DOI: `10.1071/WF07049`.

Keeley, Jon E. and C.J. Fotheringham (2003). “Impact of past, present, and future fire regimes on North American Mediterranean shrublands”. In: *Fire and climatic change in temperate ecosystems of the Western Americas*. Springer, pp. 218–262.

Keeley, Jon E. et al. (2005). “Fire suppression impacts on postfire recovery of Sierra Nevada chaparral shrublands”. In: *International Journal of Wildland Fire* 14.3, pp. 255–265. DOI: 10.1071/WF05049.

Keeley, Jon E. et al. (2008). “Fire severity and ecosytem responses following crown fires in California shrublands”. In: *Ecological Applications* 18.6, pp. 1530–1546. DOI: 10.1890/07-0836.1.

Keeley, Jon E et al. (2011). “Fire as an evolutionary pressure shaping plant traits”. In: *Trends in plant science* 16.8, pp. 406–411. DOI: 10.1016/j.tplants.2011.04.002.

Keith, David A. et al. (2007). “Plant functional types can predict decade-scale changes in fire-prone vegetation”. In: *Journal of Ecology* 95.6, pp. 1324–1337. DOI: 10.1111/j.1365-2745.2007.01302.x.

Keuper, Frida et al. (2012). “A frozen feast: Thawing permafrost increases plant-available nitrogen in subarctic peatlands”. In: *Global Change Biology* 18.6, pp. 1998–2007. DOI: 10.1111/j.1365-2486.2012.02663.x.

Khaled, Raouda Al Haj et al. (2006). “Using leaf traits to rank native grasses according to their nutritive value”. In: *Rangeland Ecology & Management* 59.6, pp. 648–654. DOI: 10.2111/05-031R2.1.

Kolden, Crystal and John Rogan (Feb. 2013). “Mapping Wildfire Burn Severity in the Arctic Tundra from Downsampled MODIS Data”. In: *Arctic, Antarctic, and Alpine Research* 45.1, pp. 64–74. DOI: 10.1657/1938-4246-45.1.64.

Kumordzi, Bright B. et al. (2019). “Geographic scale and disturbance influence intraspecific trait variability in leaves and roots of North American understorey plants”. In: *Functional Ecology* 33.9, pp. 1771–1784. DOI: 10.1111/1365-2435.13402.

Lady Bird Johnson Wildflower Center (2024). URL: https://www.wildflower.org/.

Lafleur, Peter M. and Elyn R. Humphreys (2018). “Tundra shrub effects on growing season energy and carbon dioxide exchange”. In: *Environmental Research Letters* 13.5, p. 055001. DOI: 10.1088/1748-9326/aab863.

Lantz, Trevor C. et al. (2010). “Response of green alder (Alnus viridis subsp. fruticosa) patch dynamics and plant community composition to fire and regional temperature in north-western Canada”. In: *Journal of Biogeography* 37.8, pp. 1597–1610. DOI: 10.1111/j.1365-2699.2010.02317.x.

Lavorel, Sandra and Eric Garnier (2002). “Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail”. In: *Functional ecology* 16.5, pp. 545–556. DOI: 10.1046/j.1365-2435.2002.00664.x.

Lepš, Jan et al. (2011). “Community trait response to environment: disentangling species turnover vs intraspecific trait variability effects”. In: *Ecography* 34.5, pp. 856–863. DOI: 10.1111/j.1600-0587.2010.06904.x.

Li, Daijiang and Donald M. Waller (May 2017). “Fire exclusion and climate change interact to affect long-term changes in the functional composition of plant communities”. In: *Diversity and Distributions* 23.5, pp. 496–506. ISSN: 1472-4642. DOI: 10.1111/DDI.12542.

Liang, Shuang and Matthew D. Hurteau (Aug. 2023). “Novel climate–fire–vegetation interactions and their influence on forest ecosystems in the western USA”. In: *Functional Ecology* 37.8, pp. 2126–2142. DOI: 10.1111/1365-2435.14263.

Liljedahl, Anna et al. (June 2007). “Physical short-term changes after a tussock tundra fire, Seward Peninsula, Alaska”. In: *Journal of Geophysical Research: Earth Surface* 112.F2, pp. 2–07. DOI: 10.1029/2006JF000554.

Linear Regression Model (2024). URL: https://www.ibm.com/topics/linear-regression.

Loranty, Michael M. et al. (2018). “Reviews and syntheses: Changing ecosystem influences on soil thermal regimes in northern high-latitude permafrost regions”. In: *Biogeosciences* 15.17, pp. 5287–5313. DOI: 10.5194/bg-15-5287-2018.

Louault, Frédérique et al. (Apr. 2005). “Plant traits and functional types in response to reduced disturbance in a semi-natural grassland”. In: *Journal of Vegetation Science* 16.2, pp. 151–160. DOI: 10.1111/J.1654-1103.2005.TB02350.X.

Lutes, Duncan C. et al. (2006). “FIREMON: Fire effects monitoring and inventory system”. In: *Gen. Tech. Rep. RMRS-GTR-164. Fort Collins, CO: US Department of Agriculture, Forest Service, Rocky Mountain Research Station. 1 CD.* 164. DOI: 10.2737/RMRS-GTR-164.

Mack, Michelle C. et al. (2004). “Ecosystem carbon storage in arctic tundra reduced by long-term nutrient fertilization”. In: *Nature* 431.7007, pp. 440–443. DOI: 10.1038/nature02887.

Mack, Michelle C. et al. (2011). “Carbon loss from an unprecedented Arctic tundra wildfire”. In: *Nature* 475.7357, pp. 489–492. DOI: 10.1038/nature10283.

Mallen-Cooper, Max et al. (2021). “Lichens buffer tundra microclimate more than the expanding shrub Betula nana”. In: *Annals of Botany* 128.4, pp. 407–418. DOI: 10.1093/aob/mcab041.

Marcos, Bruno et al. (2021). “A framework for multi-dimensional assessment of wildfire disturbance severity from remotely sensed ecosystem functioning attributes”. In: *Remote Sensing* 13.4, p. 780. DOI: 10.3390/rs13040780.

Meigs, Garrett W. et al. (2009). “Forest fire impacts on carbon uptake, storage, and emission: the role of burn severity in the Eastern Cascades, Oregon”. In: *Ecosystems* 12, pp. 1246–1267. DOI: 10.1007/s10021-009-9285-x.

Michaelides, Roger J. et al. (2019). “Inference of the impact of wildfire on permafrost and active layer thickness in a discontinuous permafrost region using the remotely sensed active layer thickness (ReSALT) algorithm”. In: *Environmental Research Letters* 14.3, p. 035007. DOI: 10.1088/1748-9326/aaf932.

Miller, E.A. et al. (2022). *ABoVE: Post-Fire and Unburned Field Site Data, Anaktuvuk River Fire Area, 2008-2017. ORNL DAAC, Oak Ridge, Tennessee, USA.*

Minnich, Richard A. (1995). “Fuel-driven fire regimes of the California chaparral”. In: *Brushfires in California wildlands: ecology and resource management. International Association of Wildland Fire, Fairfield, Washington*, pp. 21–27.

Mitchell, Rachel M. et al. (2021). “Intraspecific trait variability shapes leaf trait response to altered fire regimes”. In: *Annals of Botany* 127.4, pp. 543–552. DOI: 10.1093/aob/mcaa179.

Myers-Smith, Isla H. et al. (2011). “Shrub expansion in tundra ecosystems: dynamics, impacts and research priorities”. In: *Environmental Research Letters* 6.4, p. 045509. DOI: 10.1088/1748-9326/6/4/045509.

Myers-Smith, Isla H. et al. (2015). “Climate sensitivity of shrub growth across the tundra biome”. In: *Nature climate change* 5.9, pp. 887–891. DOI: 10.1038/nclimate2697.

Myers-Smith, Isla H. et al. (2019). “Eighteen years of ecological monitoring reveals multiple lines of evidence for tundra vegetation change”. In: *Ecological Monographs* 89.2, e01351. DOI: 10.1002/ecm.1351.

Narita, Kenji et al. (2015). “Vegetation and permafrost thaw depth 10 years after a tundra fire in 2002, Seward Peninsula, Alaska”. In: *Arctic, Antarctic, and Alpine Research* 47.3, pp. 547–559. DOI: 10.1657/AAAR0013-031.

Niu, Kechang et al. (2016). “Grazing-induced shifts in community functional composition and soil nutrient availability in Tibetan alpine meadows”. In: *Journal of Applied Ecology* 53.5, pp. 1554–1564. DOI: 10.1111/1365-2664.12727.

Noguer, Maria et al. (2001). *Climate change 2001: the scientific basis.* Ed. by John Theodore Houghton et al. Vol. 881. 9. Cambridge: Cambridge University Press.

Oechel, Walter C. et al. (2000). “Acclimation of ecosystem CO2 exchange in the Alaskan Arctic in response to decadal climate warming”. In: *Nature* 406.6799, pp. 978–981. DOI: 10.1038/35023137.

Oulehle, F. et al. (2016). “Plant functional type affects nitrogen use efficiency in high-Arctic tundra”. In: *Soil Biology and Biochemistry* 94, pp. 19–28. DOI: `10.1016/j.soilbio.2015.11.008`.

Pescador, David S. et al. (2015). “Plant trait variation along an altitudinal gradient in mediterranean high mountain grasslands: controlling the species turnover effect”. In: *PLoS One* 10.3, e0118876. DOI: `10.1371/journal.pone.0118876`.

Poorter, Hendrik and John R. Evans (1998). “Photosynthetic nitrogen-use efficiency of species that differ inherently in specific leaf area”. In: *Oecologia* 116, pp. 26–37. DOI: `10.1007/s004420050560`.

Poulos, Helen M. et al. (Feb. 2020). “Differences in leaf physiology among juvenile pines and oaks following high-severity wildfire in an Arizona Sky Island Mountain range”. In: *Forest Ecology and Management* 457, p. 117704. ISSN: 0378-1127. DOI: `10.1016/J.FORECO.2019.117704`.

Qu, Yuquan et al. (Oct. 2023). “Wildfire precursors show complementary predictability in different timescales”. In: *Nature Communications 2023 14:1* 14.1, pp. 1–9. DOI: `10.1038/s41467-023-42597-5`.

Querejeta, José Ignacio et al. (2022). “Higher leaf nitrogen content is linked to tighter stomatal regulation of transpiration and more efficient water use across dryland trees”. In: *New Phytologist* 235.4, pp. 1351–1364. DOI: `10.1111/nph.18254`.

Quétier, F. et al. (2007). “Linking vegetation and ecosystem response to complex past and present land use changes using plant traits and a multiple stable state framework”. In: *Ecological Monographs* 77, pp. 33–52.

Racine, Charles H. et al. (1987). “Patterns of vegetation recovery after tundra fires in northwestern Alaska, USA”. In: *Arctic and Alpine Research* 19.4, pp. 461–469. DOI: `abs/10.1080/00040851.1987.12002628`.

Rahmanian, Soroor et al. (2019). “Effects of livestock grazing on soil, plant functional diversity, and ecological traits vary between regions with different climates in northeastern Iran”. In: *Ecology and Evolution* 9.14, pp. 8225–8237. DOI: `10.1002/ece3.5396`.

Reich, Peter B. (2014). “The world-wide ‘fast–slow’plant economics spectrum: a traits manifesto”. In: *Journal of ecology* 102.2, pp. 275–301. DOI: `10.1111/1365-2745.12211`.

Rhodes, Edward C. et al. (2010). “Fire effects on cover and dietary resources of sage-grouse habitat”. In: *The Journal of Wildlife Management* 74.4, pp. 755–764. DOI: `10.2193/2009-143`.

Rocha, Adrian V. and Gaius R. Shaver (2011a). "Burn severity influences postfire CO2 exchange in arctic tundra". In: *Ecological applications* 21.2, pp. 477–489. DOI: 10.1890/10-0255.1.

— (Sept. 2011b). "Postfire energy exchange in arctic tundra: the importance and climatic implications of burn severity". In: *Global Change Biology* 17.9, pp. 2831–2841. DOI: 10.1111/J.1365-2486.2011.02441.X.

Rocha, Adrian V. et al. (2012). "The footprint of Alaskan tundra fires during the past half-century: implications for surface properties and radiative forcing". In: *Environmental Research Letters* 7.4, p. 044039. DOI: 10.1088/1748-9326/7/4/044039.

Romps, David M. et al. (Nov. 2014). "Projected increase in lightning strikes in the united states due to global warming". In: *Science* 346.6211, pp. 851–854. DOI: 10.1126/SCIENCE.1259100.

Rupp, T. Scott et al. (2000). "A frame-based spatially explicit model of subarctic vegetation response to climatic change: comparison with a point model". In: *Landscape Ecology* 15, pp. 383–400. DOI: 10.1023/A:1008168418778.

Safford, Hugh D. and Susan Harrison (2004). "Fire effects on plant diversity in serpentine vs. sandstone chaparral". In: *Ecology* 85.2, pp. 539–548. DOI: 10.1890/03-0039.

Sakschewski, Boris et al. (2015). "Leaf and stem economics spectra drive diversity of functional plant traits in a dynamic global vegetation model". In: *Global Change Biology* 21.7, pp. 2711–2725. DOI: 10.1111/gcb.12870.

Salmon, Verity G. et al. (2016). "Nitrogen availability increases in a tundra ecosystem during five years of experimental permafrost thaw". In: *Global Change Biology* 22.5, pp. 1927–1941. DOI: 10.1111/gcb.13204.

Santana, Victor M. et al. (2010). "Effects of soil temperature regimes after fire on seed dormancy and germination in six Australian Fabaceae species". In: *Australian Journal of Botany* 58.7, pp. 539–545. DOI: 10.1071/BT10144.

Schwilk, Dylan W. (2003). "Flammability is a niche construction trait: canopy architecture affects fire intensity". In: *The American Naturalist* 162.6, pp. 725–733. DOI: 10.1086/379351.

Sekretareva, Nadezhda A. (1999). *The vascular plants of the Russian Arctic and adjacent territories*. Pensoft.

Shaver, Gaius R. et al. (2006). "Carbon turnover in Alaskan tundra soils: effects of organic matter quality, temperature, moisture and fertilizer". In: *Journal of Ecology* 94.4, pp. 740–753. DOI: 10.1111/j.1365-2745.2006.01139.x.

Shevtsova, Iuliia et al. (2020). "Strong shrub expansion in tundra-taiga, tree infilling in taiga and stable tundra in central Chukotka (north-eastern Siberia) between 2000 and 2017". In: *Environmental Research Letters* 15.8, p. 085006. DOI: 10.1088/1748-9326/ab9059.

Shipley, Bill et al. (2006). "Fundamental trade-offs generating the worldwide leaf economics spectrum". In: *Ecology* 87.3, pp. 535–541. DOI: 10.1890/05-1051.

Siefert, Andrew and Mark E. Ritchie (2016). "Intraspecific trait variation drives functional responses of old-field plant communities to nutrient enrichment". In: *Oecologia* 181, pp. 245–255. DOI: 10.1007/s00442-016-3563-z.

Soliveres, Santiago et al. (2014). "Functional traits determine plant co-occurrence more than environment or evolutionary relatedness in global drylands". In: *Perspectives in plant ecology, evolution and systematics* 16.4, pp. 164–173. DOI: 10.1016/j.ppees.2014.05.001.

Sonnier, Grégory et al. (2010). "Quantifying relationships between traits and explicitly measured gradients of stress and disturbance in early successional plant communities". In: *Journal of Vegetation Science* 21.6, pp. 1014–1024. DOI: 10.1111/j.1654-1103.2010.01210.x.

Sørensen, Mia Vedel et al. (2019). "Drivers of C cycling in three arctic-alpine plant communities". In: *Arctic, Antarctic, and Alpine Research* 51.1, pp. 128–147. DOI: 10.1080/15230430.2019.1592649.

Soudzilovskaia, Nadejda A et al. (2013). "Functional traits predict relationship between plant abundance dynamic and long-term climate warming". In: *Proceedings of the National Academy of Sciences* 110.45, pp. 18180–18184. DOI: 10.1073/pnas.1310700110.

Structural Equation Modeling (2021). URL: https://bookdown.org/bean_jerry/using_r_for_social_work_research/structural-equation-modeling.html.

Sturm, Matthew et al. (2001). "Increasing shrub abundance in the Arctic". In: *Nature* 411.6837, pp. 546–547. DOI: 10.1038/35079180.

Subcommittee, Permafrost (1988). *Glossary of permafrost and related ground-ice terms.* Associate Committee on Geotechnical Research, National Research Council of Canada, Ottawa.

Swann, Abigail L. et al. (2010). "Changes in Arctic vegetation amplify high-latitude warming through the greenhouse effect". In: *Proceedings of the National Academy of Sciences* 107.4, pp. 1295–1300. DOI: 10.1073/pnas.0913846107.

Taber, Ethan M. and Rachel M. Mitchell (Aug. 2023). "Rapid changes in functional trait expression and decomposition following high severity fire and experimental warming". In: *Forest Ecology and Management* 541, p. 121019. DOI: 10.1016/J.FORECO.2023.121019.

Tape, Kenneth E.N. et al. (2006). “The evidence for shrub expansion in Northern Alaska and the Pan-Arctic”. In: *Global change biology* 12.4, pp. 686–702. DOI: 10.1111/j.1365-2486.2006.01128.x.

Theurillat, Jean-Paul and Antoine Guisan (2001). “Potential impact of climate change on vegetation in the European Alps: a review”. In: *Climatic change* 50.1, pp. 77–109. DOI: 10.1023/A:1010632015572.

Treharne, Rachael et al. (Oct. 2020). “Extreme event impacts on CO2 fluxes across a range of high latitude, shrub-dominated ecosystems”. In: *Environmental Research Letters* 15.10, p. 104084. ISSN: 1748-9326. DOI: 10.1088/1748-9326/ABB0B1.

Tsuyuzaki, Shiro et al. (2018). “Tundra fire alters vegetation patterns more than the resultant thermokarst”. In: *Polar biology* 41, pp. 753–761. DOI: 10.1007/s00300-017-2236-7.

Valladares, Fernando et al. (2007). “Ecological limits to plant phenotypic plasticity”. In: *New phytologist* 176.4, pp. 749–763. DOI: 10.1111/j.1469-8137.2007.02275.x.

Van Everdingen, Robert O. (2005). *Multi-language glossary of permafrost and related ground-ice terms*. International Permafrost Association.

Vavrek, Milan C. et al. (1999). “Recovery of productivity and species diversity in tussock tundra following disturbance”. In: *Arctic, Antarctic, and Alpine Research* 31.3, pp. 254–258. DOI: 10.1080/15230430.1999.12003306.

Velbert, Frederike et al. (2017). “Time lags in functional response to management regimes–evidence from a 26-year field experiment in wet meadows”. In: *Journal of Vegetation Science* 28.2, pp. 313–324. DOI: 10.1111/jvs.12497.

Venn, S.E. et al. (2016). “Using a model based fourth-corner analysis to explain vegetation change following an extraordinary fire disturbance”. In: *Oecologia* 182, pp. 855–863. DOI: 10.1007/s00442-016-3700-8.

Veraverbeke, Sander et al. (2021). “Direct and longer-term carbon emissions from arctic-boreal fires: A short review of recent advances”. In: *Current Opinion in Environmental Science & Health* 23, p. 100277. DOI: 10.1016/j.coesh.2021.100277.

Viereck, Leslie A. (1992). *The Alaska vegetation classification*. Vol. 286. US Department of Agriculture, Forest Service, Pacific Northwest Research Station.

Walker, Marilyn D. et al. (2006). “Plant community responses to experimental warming across the tundra biome”. In: *Proceedings of the National Academy of Sciences* 103.5, pp. 1342–1346. DOI: 10.1073/pnas.0503198103.

Walsh, John E. et al. (2020). “Extreme weather and climate events in northern areas: A review”. In: *Earth-Science Reviews* 209, p. 103324. DOI: 10.1016/j.earscirev.2020.103324.

Wein, Ross W. and Lawrence C. Bliss (1973). “Changes in arctic Eriophorum tussock communities following fire”. In: *Ecology* 54.4, pp. 845–852. DOI: `10.2307/1935679`.

Wein, Ross Wallace and David A MacLean (1983). *The role of fire in northern circumpolar ecosystems.*

Westoby, Mark et al. (2002). “Plant ecological strategies: some leading dimensions of variation between species”. In: *Annual review of ecology and systematics* 33.1, pp. 125–159. DOI: `10.1146/annurev.ecolsys.33.010802.150452`.

Wright, Ian J. et al. (2004). “The worldwide leaf economics spectrum”. In: *Nature* 428.6985, pp. 821–827. DOI: `10.1038/nature02403`.

Yoshikawa, Kenji et al. (2003). “Impacts of wildfire on the permafrost in the boreal forests of Interior Alaska”. In: *Journal of geophysical research* 108.D1, FFR4–1. DOI: `10.1029/2001JD000438`.

Zeigerwerte der Pflanzen Mitteleuropas nach Ellenberg (2024). URL: `https://www.forst-rast.de/ZeigerwerteEllenberg.html`.

A Appendices

Table 3: Representation of the estimated values and the associated p-value determining significance of the Structural Equation Model among the variables: Year; fire severity (dNBR); Ellenberg Indicator Value F of soil moisture (EIV F); CWM of plant height; CWM of SLA; and Active Layer Depth (ALD).

	Estimate	P value
CWM_PlantHeight ~		
ALD_mean	-0.343	0.002
Year	-0.514	0.112
dNBR	0.072	0.818
CWM_SLA ~		
ALD_mean	-0.248	0.020
Year	-0.292	0.368
dNBR	-0.108	0.748
ALD ~		
Year	-0.613	0.442
dNBR	0.322	0.588
EIV_F_mean ~		
CWM_PlantHeight	-0.560	0
CWM_SLA	-0.495	0
Year	-0.370	0.345
ALD_mean	-0.108	0.594
dNBR	-0.057	0.874

Table 4: Results of the ANODEV for the comparison of the independent variables among the active layer depth. The table displays the F-value and associated p-value indicating the significance of the differences observed.

	Active layer depth	
	F Value	P Value
dNBR	4.88	0.031

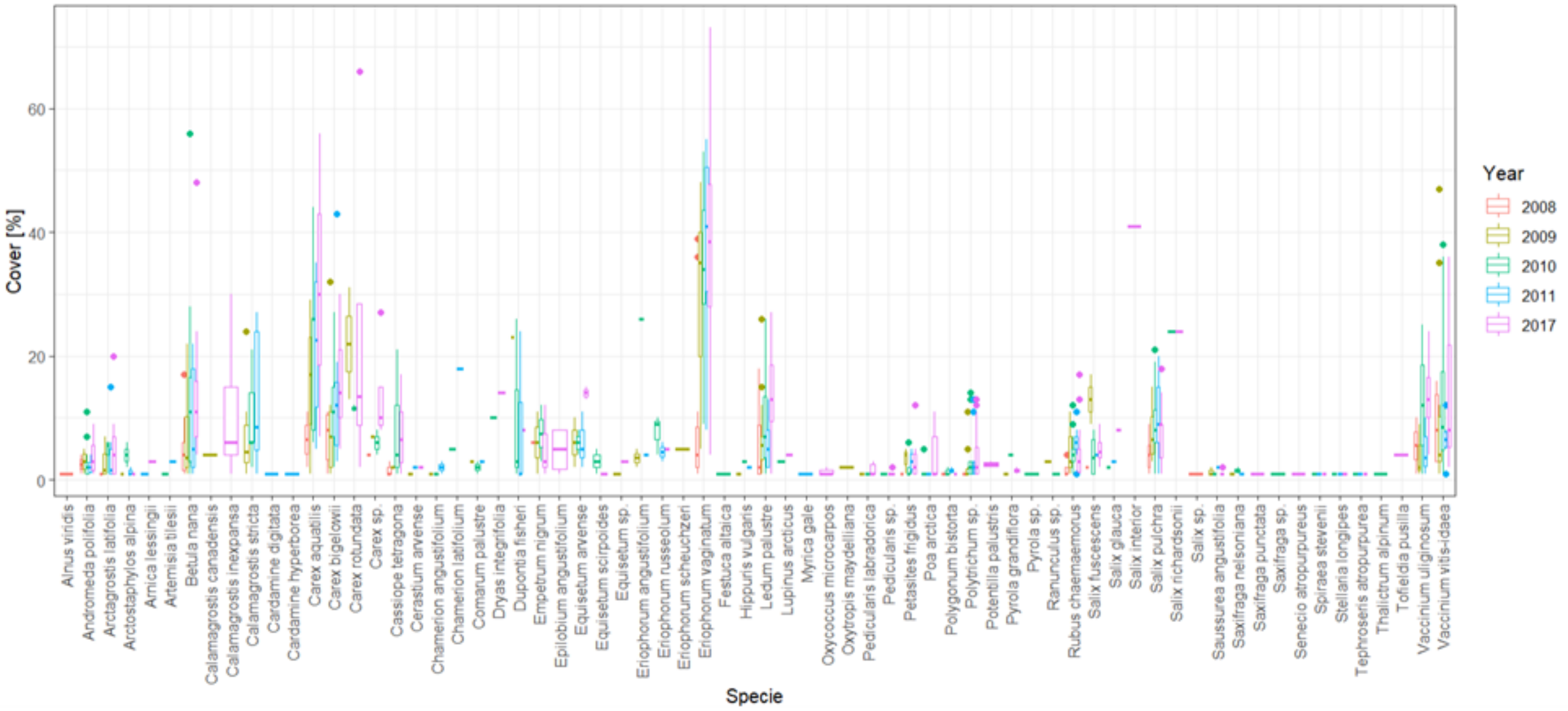

Figure 9: Percent of individuals of each species of vascular plant (cover) for the five different years (colors).

Personal declaration

I hereby declare that the submitted thesis is the result of my own, independent work. All external sources are explicitly acknowledged in the thesis.

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