



Investigating vegetational survey efficiency **using a long-term phenological survey along a** **subarctic elevation gradient**

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Abstract

Scientific abstract

The warming of the global climate system, particularly pronounced in Arctic regions, poses significant challenges to plant species, communities and ecosystems. Understanding the dynamics of Arctic flora in response to this changing climate is crucial for predicting and mitigating its impacts. Long-term vegetational surveys are crucial monitoring tools to capture these dynamics in species diversity, distribution and phenology. Nevertheless, their observations and projections are frequently based on data lacking sufficient temporal and spatial resolution and often neglect the error caused by imperfect observations. Here, we show that species detection is influenced not only by the inherent dynamics of vegetation, including seasonal and year-to-year fluctuations and the broader context of long-term climate change, but also by other temporal, spatial and species-specific variation within the plant community. Interdependent effects of factors such as growing season temperature, seasonal timing of observation, elevation, total plot species richness, and species-specific traits were found to have a crucial impact on species observation accuracy, often manifesting through changes in phenology and morphology across different dimensions. As such, the changing climate directly and indirectly influences these factors through space and time, making it challenging to make a distinction between inherent species dynamics and inaccurate observations. Our findings highlight the need for multiple surveys per year, effective timing of monitoring within the growing season, year-to-year comparisons and adopting adequate spatial scales to account for imperfect observations, especially when studying species' temporal dynamics. These insights contribute to broader discussions on the complexities of ecological monitoring and underscore the importance of adapting adequate survey methods to effectively capture species dynamics in a changing climate. This to avoid making misleading conclusions, resulting in over- or underestimations of species dynamics.

Public abstract

In a changing world, the warming of our planet, particularly in the Arctic, presents significant challenges to plant life and ecosystems. Understanding how Arctic flora responds to these shifts is crucial for predicting and addressing their impacts. Long-term vegetational surveys are crucial tools for tracking changes in, among others, species diversity and distribution over time. However, these surveys often lack the necessary detail and precision, leading to oversights in our understanding of plant dynamics. Our research shows that species observations are influenced not only by seasonal patterns, year-to-year fluctuations and long-term climate change, but also by inaccurate species detections. Elements like growing season temperature, seasonal timing of observation, elevation, species richness and species-specific traits all play a role in shaping how accurately we perceive plant dynamics. These factors are further complicated by the changing climate, which impacts them in over both space and time, making it difficult to distinguish between natural changes in plant communities and errors in our observations. To address these challenges, we emphasize the importance of conducting multiple surveys per year, timing observations effectively, comparing data across different years and adopting adequate spatial scales to capture the full breadth of plant diversity. These insights are vital not only for ecological research but also for informing policies aimed at mitigating the impacts of climate change on our planet's flora and ecosystems. By adapting our survey methods and improving our understanding of plant dynamics, we can better protect and manage our natural environment. This is essential for ensuring the resilience and sustainability of ecosystems in the face of ongoing climate change.

Introduction

As global average air temperatures are increasing and snow and ice masses undergo widespread melting, the warming of the global climate system is undisputable (IPCC, 2013). Moreover, the Arctic climate, distinguished as one of the most expeditiously changing climates on the planet, has witnessed a temperature surge of 2-3 °C over the last century, with projections suggesting further increases reaching 4-5 °C (Nogués-Bravo et al., 2007; Overland et al., 2014; Post et al., 2019). This exceptionally rapid warming of the Arctic has the potential to significantly impact Arctic plant species, communities and ecosystems leading to, among others, species loss, introduction and distributional shifts (Bjorkman et al., 2020; Lenoir et al., 2008; Prev  y et al., 2019; Steinbauer et al., 2018). This all can in turn have important implications for ecosystem functioning leading to climate feedback, with potential global impacts as a result (Bjorkman et al., 2020; IPCC, 2013). Subsequently, documenting and predicting the impacts on Arctic flora worldwide is of great importance in global change ecology. Long-term repeated plant surveys form an essential resource in this biodiversity monitoring research (Magurran et al., 2010). They are a crucial monitoring tool to capture the dynamics of fundamental ecosystem components, such as species diversity, distribution and phenology, in a changing environment. Nevertheless, their observations and projections are frequently based on data lacking sufficient temporal and spatial scales and resolutions (MacDougall et al., 2021; Steinbauer et al., 2018). Subsequently, they often get overlooked and underserved in the detail and effort they demand. As climate change is ongoing and at an increasingly fast pace (Jansen et al. 2020), there is an increasing need for efficient long-term survey conduction to accurately capture species dynamics.

Investigating Arctic flora dynamics

Current and future climatic changes are capable of causing clear warming on high-latitude mountains, creating finite high-elevation refugia normally temporarily offering relatively stable conditions. Additionally, these changes can also alter growing seasons, thaw depths, and snow regimes. Following this, the diversity and distribution of high-altitude Arctic mountain flora are expected to transform (e.g. MacDougall et al., 2021; Niskanen et al., 2019; Rosbakh et al., 2021). Their persistence will depend on how fast or even if they are able to adjust or adapt to climate change and maintain reproduction and growth. The ability of mountain plants to sustain reproduction and growth under these warming conditions will shape their biological impact (MacDougall et al., 2021). At least two pathways facilitate this capability. The first one being spatial shifts across generations, occurring through progressively moving northward and uphill.

The second one being life-cycle timing (phenological) adjustments, to better align growth and reproduction to seasonal variabilities. However, the long-term resilience emerging from these mechanisms remains uncertain, and recent models already highlight concerning projections for Arctic mountain flora, suggesting significant range contractions and potential species decline (Niskanen et al., 2019).

Nevertheless, given the frequently limited information on background rates and trends and restricted understanding of temporal shifts in ecological systems, there is a pressing need for high-quality long-term vegetation monitoring datasets (Magurran et al., 2010). The rapid detection of and response to significant biodiversity-related pressures, and trends, impacting the circumpolar world is essential (Bjorkman et al., 2020). Yet this can only be done when data on the ongoing spatiotemporal changes is available at a sufficiently high resolution and scale. Long-term surveys form an essential resource in this plant biodiversity monitoring research (Magurran et al., 2010). Since these multidimensional monitoring tools come with fundamental logistic obstacles and require extensive resources, it is of ecological and economic relevance to optimize these techniques.

Long-term survey efficiency

Time series data on diversity, distribution and phenological changes across large temporal and geographical extents are crucial in filling the knowledge gap on the impacts of climate change on Arctic plant species, communities and ecosystems. Several studies explored these impacts, capturing and predicting species loss, introduction, distributional shifts and other species dynamics, over the past 30 years (e.g. Alexander et al., 2015, 2018; Assmann et al., 2019; Bjorkman et al., 2020; Chapin et al., 2012; Lesica & McCune, 2004; MacDougall et al., 2021; Rosbakh et al., 2021; Wookey et al., 1993). These systematic monitoring studies were often conducted at plot-based sites across the Arctic, covering various spatial scales, spanning durations ranging from 5 to 43 years and revisiting with frequencies ranging from every 5 days to only once a year. These factors often varied depending on variables like research objective, ecological questions and logistical constraints. Time, accessibility, funding and other resources often limit possibilities. Nevertheless, it remains essential for these survey-based studies to accurately capture those species dynamics, while avoiding over- or underestimation of these observations.

These surveys require a substantial timeframe to effectively capture the influence of seasonal and year-to-year fluctuations of environmental conditions and long-term climate change on species diversity dynamics, as these lead to variability within and among years, as well as

changes in the longer term. Not adopting an adequate temporal scale and resolution could lead to making misleading conclusions, such as over- or underestimating the loss or introduction of species (MacDougall et al., 2021; Steinbauer et al., 2018). The temporal scale of these long-term monitoring studies depends on the accessibility and accuracy of historical data. Historical limitations may stem from factors such as inconsistent data collection methods, the availability of archival records, or the difficulties in precisely recording past ecological conditions (Magurran et al., 2010). Meanwhile, the temporal resolution depends on, among others, the presence of year-to-year comparisons and a sufficient visitation frequency. Additionally, these surveys also require an adequate spatial scale and resolution to effectively capture the species diversity dynamics, as variations in spatial characteristics within landscapes often mirror differences in species diversity (Rocchini et al., 2011).

Besides capturing these true dynamics, identifying factors affecting the detection of plants is essential (Chen et al., 2009, 2013; Kery et al., 2006, 2010; Moore et al., 2011; Roth et al., 2018). We expect multiple factors to affect species observation accuracy and in turn survey efficiency (Box 1.1 & 1.2). First, year-to-year fluctuations and trends of environmental conditions, such as snowmelt or temperature, do not only influence fundamental species dynamics. More into detail, they can influence species' phenology, growth and development (e.g. Assmann et al., 2019; Bjorkman et al., 2015; Hatfield & Prueger, 2015; Høye et al., 2013; MacDougall et al., 2021; Niittynen et al., 2020; Prevéy et al., 2019; Van Der Wal & Stien, 2014; Walker et al., 2006; Wilson & Nilsson, 2009), which could affect species observations. Second, the timing of observation within the growing season could affect observations, as species dynamics vary during the onset and conclusion of the season (Chen et al., 2013; Körner et al., 2023; Wilson & Nilsson, 2009). Some species may still be emerging or are already completing their life cycles during these periods. Third, site-specific variability, such as total species richness, could impact observations. For example by providing more opportunities to overlook certain species in species-rich plots. Finally, species-specific traits, such as growth form, life cycle, flower color, plant height and temperature optima, may impact the likelihood of detection, by causing certain species to stand out more prominently than others across survey periods (Chen et al., 2009, 2013; Hatfield & Prueger, 2015; Kery et al., 2006; Roth et al., 2018). Furthermore, these characteristics might also be dependent on elevation, as plant height and individual cover often tend to be lower at high elevations (Halbritter et al., 2018; Körner et al., 1989).

Additionally, variability introduced by observer bias, methodological limitations, misidentifications and other noise calls for the need for multiple monitoring events through time and space to capture this variation while investigating the full spectrum of species within

an area (Chen et al., 2009; Kery et al., 2006; Moore et al., 2011). Observer bias might cause the systematic tendency of observers to over- or under-estimate certain species, potentially skewing survey results, whilst methodological limitations might affect the accuracy or reliability of observations and misidentifications might lead to errors in species richness records.

Together, all factors mentioned above could potentially impede the precise capture of species dynamics. While many of them are known, imperfect detection often gets neglected and even more rarely quantified during plant ecological studies (Kellner & Swihart, 2014). To conclude, employing robust survey methods that capture true species diversity dynamics is crucial (Magurran et al., 2010).

Research objective

This thesis is part of a project encompassing species-level long-term phenology surveys that took place on a transect along a subarctic elevation gradient in the Scandes Mountains, Sweden. The transect was established in 1916 by the Swedish botanist Thore C. E. Fries (1886-1930). Surveys were carried out repeatedly throughout the growing season both in the 20th century (1917 to 1919) and in the 21st century (2017 to 2023). The significance of conducting these long-term plant phenological studies is emphasized by their pivotal role in examining community dynamics and processes, including species coexistence, interactions and biodiversity (Grubb, 1977; Moulin et al., 2021). Additionally, adopting species resolution here is crucial for understanding the effect of climate change on this biodiversity (Forrest & Miller-Rushing, 2010). Eventually, a long-term dataset spanning a period of more than 100 years, in which sampling took place over 10 years, was created. The unique set-up of this intensive long-term monitoring campaign, resulting in a total of 248 field site visits throughout the growing seasons, allows us to better understand seasonal and long-term phenological and distributional dynamics, particularly in relation to climate change impacts.

Using this intensive long-term survey, MacDougall et al. (2021) reported that all species observed in the first era were observed again in the second era, on or near the transect. Furthermore, they observed 15 additional species, during the contemporary survey (2017-2018), to species already observed during the historical survey (1917-1919). This meant that no species loss was observed yet, despite pronounced warming in recent decades. As Arctic mountain species are being progressively squeezed from all sides, due to phenological limitations, non-arctic invaders along the whole gradient and downward contraction of some species towards areas with more persistent snow beds (MacDougall et al., 2021), less intensive

survey methods might prematurely indicate the disappearance of species. However, this intensive repeated survey method proved the possible misperception of these dynamics.

In this context, we aim to critically evaluate the efficacy of the monitoring methods used in capturing the dynamics of plant diversity, through space and time, in a changing environment. Our goal is to improve the accuracy and reliability of this type of ecological research and get optimal levels of survey effort required for robust assessment of plant dynamics. This will help minimize the risk of drawing misleading conclusions, which could lead to over- or underestimations of species dynamics. To achieve this, we investigate how survey efficiency, represented by species observation proportions across time and space, is influenced by factors such as growing season temperature, seasonal timing of observation, elevation, total plot species richness and species-specific traits. The hypotheses guiding our investigation are detailed in Box 1.1 and Box 1.2. Box 1.1 explores the impact of temporal and spatial variation within the plant community on survey efficiency, while Box 1.2 focuses on the effects of species-specific traits on survey efficiency.

Box 1.1 Hypotheses

Growing season temperature:

A higher survey efficiency is expected during years characterized by a higher growing season temperature, as this could cause advanced phenology and enhanced growth, resulting in earlier and easier identification.

Total plot species richness:

A lower survey efficiency is expected at plots characterized by a higher total species richness, as a greater number of species provides more opportunities to overlook certain species during the sampling process.

Elevation:

A lower survey efficiency is expected at higher elevations, as species at higher elevations are often smaller, have a lower cover and start their growing period later, possibly resulting in compromised observations.

Seasonal timing:

A lower survey efficiency is expected at the beginning and the end of the growing season, as species dynamics vary during the onset and conclusion of the season. Some species may still be emerging or have already completed their life cycle during these periods, restricting the window during which species are detectable.

Box 1.1 Hypotheses (Continued)

Growing season temperature - Total plot species richness:

Years with a warmer growing season temperature are expected to result in a more distinct increase in survey efficiency at plots characterized by a high total species richness, as lengthening of the growing season in warmer years might enhance the chances of species to be present at the same time, especially in plots with a high species richness, leading to more optimal observations.

Growing season temperature - Elevation:

Years with a warmer growing season temperature are expected to result in a more distinct increase in survey efficiency at higher elevations, as the effect of temperature on the advancement of the growing season and on plant growth might be more critical and noticeable here.

Growing season temperature - Seasonal timing:

Years with a warmer growing season temperature are expected to result in a less distinct reduction in survey efficiency near the beginning of the season, as plants might sprout earlier, advancing the window during which species are detectable. Additionally, enhanced snowmelt – especially in plots with snow beds normally persisting till late in the season – might drastically increase survey efficiency.

Total plot species richness - Elevation:

Plots characterized by a low total species richness are expected to result in a reduction in survey efficiency at higher elevations, as plants are smaller here and might be harder to detect. The opposite is expected at lower elevations.

Total plot species richness - Seasonal timing:

Plots characterized by a high total species richness are expected to result in a more distinct reduction in survey efficiency near the beginning and end of the season, as species richness might be lowest during these periods.

Elevation - Seasonal timing:

Plots located at a higher elevation are expected to result in a more distinct reduction in survey efficiency in the beginning and end of the growing season, as the growing season tends to be more compressed here.

Box 1.2 Hypotheses

Growing season temperature:

Species are expected to have a higher proportion of identification during years characterized by a warmer growing season temperature, as this could cause advanced phenology and enhanced growth, resulting in earlier and easier identification.

Growth form:

Trees, shrubs and subshrubs are expected to have a higher proportion of identification than graminoids, forbs and herbs, as growth form is expected to influence how visible plants are.

Box 1.2 Hypotheses (Continued)

Life cycle:

Perennial plants are expected to have a higher proportion of identification than annuals, as many of them maintain aboveground biomass throughout the whole year, can allocate energy towards reproduction in multiple growing seasons, and persist over multiple years, increasing the chance of detection over time.

Flower color:

Brightly colored flowers are expected to be observed more/faster.

Average plant height:

Taller plants are expected to be observed more/faster.

Temperature optimum:

Plants with a lower temperature optimum are expected to have a higher proportion of identification than plants with a higher temperature optimum, as they have a higher growth and development due to being better adapted to Arctic conditions, and therefore could be observed more/faster.

Survey period (century):

As we are looking at two different centuries, methodologies and identifications might have changed and plants might be identified more easily over time as we know which plants to expect.

Growing season temperature - Average plant height:

Smaller plants are expected to be observed more during warmer years, as warmer conditions may enhance their growth (size and cover) and visibility, leading to more opportunities for detection compared to taller plants. For taller plants, seasonal temperatures are not expected to affect their detection rate.

Growing season temperature - Life cycle:

Annual plants are expected to be observed more during warmer years, as they may be more sensitive to increasing temperatures affecting their germination and growth, influencing their observation. For perennial plants, the effect of seasonal temperatures on their detection rate is expected to be less.

Growing season temperature - Growth form:

Graminoid, herbs and forb growth forms are expected to be observed more during warmer years, as their germination and growth might be affected more by warmer temperatures, influencing their observation. For trees, shrubs and subshrubs, seasonal temperatures are not expected to affect their detection rate.

Growing season temperature - Temperature optimum:

Plants with a lower temperature optimum are expected to have a more distinct increase in observation frequency during warmer years than plants with a higher temperature optimum, as their growth and development might be more susceptible to these temperature changes, which in turn is expected to affect their observation.

Methods and Materials

Study site: Mount Nuolja

The site of investigation was a 900 m transect on Mount Nuolja (1168 m ASL) in Abisko National Park, Sweden, situated 95 km north of the Arctic Circle (68.3495 °N, 18.8312 °E). The Abisko region extends vegetatively across the boreal and Arctic biomes of northern Scandinavia. In these zones, boreal areas are dominated by subalpine mountain birch forest (*Betula pubescens*) and some pine (*Pinus sylvestris*). Unforested Arctic-alpine areas show a high diversity of dwarf shrubs and herbaceous Arctic plants. On Mount Nuolja the transition zone between birch forest and alpine tundra is dominated by a highly diverse willow shrubland. The area of study is located within the rain shadow of the Scandes Mountains to the west. Due to this location, this area is considered as relatively dry, as the leeward side of these mountains experiences reduced precipitation due to the rain shadow effect, where descending air tends to be drier after crossing the mountain range. Depending on the elevation and annual snowfall, snow beds can persist well into summer. The summit and lower forested areas of Mount Nuolja consistently become snow-free earlier in the season than locations in the middle of the transect. This difference is likely attributable to increased wind and solar exposure at the summit and warmer temperatures in the lower forested areas, accelerating melting (MacDougall et al., 2021).

Climate data were collected from a meteorological station at the Abisko Scientific Research station near the base of the transect (388 m ASL). From 1913 to 2004 data were measured every 3 hours and every hour from then on (Callaghan et al., 2010; Kohler et al., 2006). The mean annual temperatures are -0.5 °C and the average long-term precipitation (1913-2018) is 307 mm per year. Since 1917, warming trends have shown an overall (2.31 °C) and seasonal increase, with the most consistent period of increase since the 1980s. Before, inter-decadal changes in temperature were more variable, with extended cold winters between 1950 and 1970. Snowfall forms about 50% of the annual precipitation, and falls typically between October and April. Nevertheless, over 40% of the annual precipitation takes place only in summer and merely 15% occurs in spring (McDougall et al., 2021).

The establishment of the year-round Abisko Scientific Research Station, at which this project was conducted, took place in 1912 (Kohle et al., 2006). Phenological surveys took place along the study transect, established in 1916 by the Swedish botanist Thore C. E. Fries (1886-1930), during the growing seasons of 1917, 1918 and 1919 (Fries, 1925). The transect is located on the east-facing slopes of Mount Nuolja, spanning from the base to the summit. It consists of 78

subplots located in 20 contiguous permanent monitoring plots (each plot evenly subdivided into 4 subplots, except at the summit), separated by 18.6 m of elevation on average, depending on the steepness of the mountain face (range 8.9-63.06 m). This arrangement results in uniform lengths among the plots, rather than uniform elevational distances. Marking of these plots was done by 2-meter-high wooden poles. Additionally, 5 more phenological surveys took place during the growing seasons of 2017 to 2023 (MacDougall et al., 2021). Until the 1960s the transect plot markers were periodically maintained, yet the sturdy wooden markers remained relatively undisturbed after that as well. This made it possible to relocate 59 of the 78 subplots in 2016. Nevertheless, areas without a pole were identified effortlessly due to the piles of rocks used to support the poles, and a detailed description of the distance between the poles (Fries, 1925). This made it possible to perform contemporary surveys that exactly match the locations of the historical survey. However, a chairlift was installed in 1964 that bisected the gradient within the birch woodland at ~650m ASL, which consequently asked for the shift of 3 poles by ~10 m in the summer of 1964. This was done perpendicular to the axis of the gradient.

Data collection

All species were identified to the species level using repeated visitations of the whole transect with a 5-day interval. This interval was chosen to efficiently capture the timing of the phenophase transitions, as the transect's main usage is to study seasonal and long-term trajectories of plant phenology, regarding onset and senescence of leafing and flowering (MacDougall et al., 2021). The start and ending of the sampling period always fell within the growing season, however, the exact dates varied (Table 1).

Species presence (and phenology, yet the latter was not used any further in this study) was captured at the subplot level, yet no abundance or cover estimates were made. Each five days within these sampling periods, data was gathered in all 78 subplots by walking the mountain transect and noting down which species were present and the phenophase they were in. However, from the original surveys by Fries in the early 20th century, subplot data was lost, with available data aggregated across the 20 plots (Fries, 1925).

To create a unified dataset (*Species.data*), several adjustments were made. Observations of primitive plants (ferns, horsetails and clubmosses) were excluded from the final dataset, as over the years of data collection optimization measures were implemented, focusing exclusively on capturing information related to vascular flowering plants. Species identified up to their genus level only (1% of total observations or 5% of all species) were excluded. To align 20th-century historical data with 21st-century contemporary data, synonymous species names were equated.

Eventually, a total of 200 distinct species were identified throughout the extensive long-term survey. The lowest count of unique species, 122, was recorded in 1917, while the highest count, 166, was observed in 2023 (Table 1).

The mean annual growing season temperatures (Table 2) were calculated. The growing season was defined as the period from the earliest survey start date (May 5th) to the latest survey end date (October 13th). The calculation was based on manual measurements for the years 1917 to 2018 and weather station data for the years 2017 to 2023. In the case of 2017 and 2018, a combined mean was derived from both manual measurements and weather station data, as their differences were negligible. These measurements were employed to capture the interannual variability in terms of temperature, as we expected an effect of temperature on the species observation efficiency.

Table 1: Start and end of the survey period each growing season, as well as number of surveys and total observed species richness per survey year.

Year of survey	Start of survey	End of survey	Number of surveys	Species richness
1917	25th of May	7th of October	28	122
1918	25th of May	31st of September	22	145
1919	25th of May	24th of June	6	124
2017	21st of May	13th of October	28	123
2018	10th of May	22nd of September	28	160
2019	5th of May	27th of September	31	163
2020	5th of May	17th of September	27	154
2021	15th of May	27th of September	28	156
2022	5th of May	18th of September	27	162
2023	14th of May	4th of September	23	166

Table 2: Annual mean growing season temperature. Growing season = the 5th of May (minimum start of survey) to the 13th of October (maximum end of survey).

Year of survey	Mean growing season temperature (°C)
1917	6.002
1918	7.263
1919	7.385
2017	7.337
2018	8.686
2019	8.191
2020	8.172
2021	8.085
2022	8.694
2023	9.135

Data analysis

Our primary objective was to assess survey efficiency, particularly in terms of detecting species over both time and space. To achieve this, we conducted two key analyses: Analysis 1 and Analysis 2. Both analyses were designed to investigate the hypotheses regarding the influence of mean growing season temperature, elevation of the plot, seasonal timing of observation, total plot species richness, and their interactions on survey efficiency (Box 1.1). With these factors in mind, we aimed to evaluate the efficiency of species detection over multiple survey occasions and identify adequate scales and resolutions to capture true species dynamics. Analysis 1 focused on determining the cumulative proportion of species observed per year per plot after a specific number of surveys relative to the total species count per year per plot. With this, the analysis aimed to identify an adequate number of surveys needed to observe all species. Analysis 2 complemented these findings by examining the proportion of species observed per year per plot, throughout the season. The calculations considered both the total species count per year per plot and the total species count for the entire dataset per plot, on distinct levels of data analysis (Table 3). With this, the analysis aimed to evaluate the effectiveness of species detection across different dimensions and identify the benefits of conducting yearly surveys. A supplementary analysis, Analysis 3, centered on testing our hypotheses on the effect of species traits (flower color, average plant height, life cycle, temperature optimum and growth form) on their probability of detection (Box 1.2). This was done by calculating species-specific observation proportions per year. With this, we aimed to identify traits enhancing or diminishing species-specific observation efficiencies, providing insights into detectability variations among species. For all data analyses, we used R statistics, version 4.3.3 (2023-12-01).

Analysis 1: Species observation per survey count

We initiated the analysis by constructing species accumulation curves (SAC). Three distinct types of SAC were employed. The first approach focused on species accumulation per year, represented by the mean annual growing season temperature, the second approach focused on species accumulation per plot and the third approach focused on species accumulation over the entire long-term survey, transcending yearly and plot-specific variations. In this final approach, species accumulation was depicted in relation to both year and yearly growing season temperature. The temperature data was used, as species diversity is recognized to be influenced by climatic conditions. These SAC enabled us to visualize the trends in observed species richness over those respective units.

Next, we calculated survey efficiency as the cumulative proportion of species observed per year per plot, after each survey, relative to the total species count per year per plot. Next, a detection-effort curve was made. Survey efficiency after 5, 10 and 15 surveys was investigated further, as these time points cover the progression from the beginning of the growing season to its peak. However, since only 6 surveys were conducted in 1919, data on survey efficiency after 10 and 15 surveys for that year were unavailable. A generalized linear mixed model was fitted using `glmmTMB()` (Brooks et al., 2017). The response variable, survey efficiency, was modeled as a function of growing season temperature, elevation and total plot species richness. The full model (Table 4) was based on our hypotheses (Box 1.1). It contained only two-way interactions to prioritize the examination of our pairwise relationships and maintain a manageable model complexity. Plot ID was taken as a random effect, as observations were repeated over time within each plot. The model was specified with the beta distribution family and the logit link function, as our predictor variable was a proportion bounded between 0 and 1. Before modeling, we transformed our response variable, survey efficiency, to adjust extreme values, as beta regression modeling needs continuous data within the $]0,1[$ interval. The transfer function adjusted the response variable (y) by scaling it with the number of observations (n_{obs}) minus one, adding 0.5, and then dividing by the total number of observations: $Transf(y) = \frac{y * (n_{obs} - 1) + 0.5}{n_{obs}}$. The Variance Inflation Factor (VIF) was used to detect multicollinearity. Highly correlated predictor variables with a $VIF > 5$ were removed. Model selection started from the full model and used the Akaike Information Criterion (AIC) to select the final model. The model with the lowest AIC value was considered the most favorable compromise between fit and complexity. All key assumptions of the beta regression model, including linearity, homoscedasticity, normality of residuals, independence of observations, and overall goodness of fit, were assessed and deemed acceptable. The significance level for model testing was set at $p \leq 0.05$.

Analysis 2: Species observation throughout the season

Survey efficiency was calculated as the proportion of species observed per year, per week, per (sub)plot, across three distinct levels of analysis (Table 3). Firstly, we segregated the historic dataset (1917-1919) from the contemporary dataset (2017-2023). Then, the contemporary dataset included data at both plot and subplot levels. Finally, we calculated survey efficiency in relation to the total species count per year per (sub)plot and across all years per (sub)plot. While the primary focus of the investigation was on contemporary survey efficiency at the subplot

level, as this was the most elaborate data available, supplementary details on the other data arrangements are available in the appendix.

A generalized linear mixed model was fitted using `glmmTMB()` (Brooks et al., 2017). The response variable, survey efficiency, was modeled as a function of growing season temperature, elevation, seasonal timing (represented by week of the year) and total (sub)plot species richness. The full model (Table 4) was based on our hypotheses (Box 1.1). Anticipating an increase of survey efficiency at the beginning and a subsequent decrease towards the end of the growing season, we integrated the quadratic effect of seasonal timing into the model. Our model again only contained two-way interactions to prioritize the examination of our pairwise relationships and maintain a manageable model complexity. As for Analysis 1, plot ID was taken as a random effect, as observations were repeated over time within each plot. Variable transformation and model specification, selection and interpretation were done on the same terms as described for Analyses 1. Heat maps depicting the observation proportions over time and space were made. They visualized the proportion of species observed per week per (sub)plot and per week per total (sub)plot species richness.

Table 3: Three distinct levels of survey efficiency, used to investigate species observation throughout the season. Survey efficiency was calculated as the proportion of species observed per year, per week, per (sub)plot, relative to the total species count per year per (sub)plot and relative to the total species count over the entire long-term dataset per (sub)plot.

1.	2.	3.
Historic data	Plot level	Total species count per year
		Total species count over the entire period
Contemporary data	Plot level	Total species count per year
		Total species count over the entire period
	Subplot level	Total species count per year
		Total species count over the entire period

Analysis 3: Species-specific observation efficiency

We identified newly observed and no longer observed species over consecutive years and centuries (Appendix 1) and noted that some species disappeared and reappeared from our dataset over the years. As the goal is to confirm true dynamics along the elevation gradient, we investigated the effect of species-specific traits on species-specific observation proportions. These proportions were calculated as the average proportion that the species was detected over the plots per year. The species-specific traits chosen for this analysis were growth form (forb, graminoid, herb, subshrub, shrub or tree), life cycle (perennial or annual), flower color (black, blue, brown, green, pink, purple, red, white or yellow), average plant height (m) and temperature optimum (a scale from 1; high-alpine/arctic species to 18; subtropic species). All species-specific traits, except the temperature optima, were obtained through a combination of

data from the Botanical Information and Ecology Network (BIEN) and the Gridded Species Distribution and Trait (GIFT) packages (Denelle & Wiegelt, 2024; Maitner, 2023). Additionally, some supplementary data on these characteristics not available through these packages were acquired from iNaturalist. The species-specific temperature optima were adopted from Tyler et al. (2021). These values were based on the temperature regime at the center of the species' geographic range and were derived from their values for heat and cold requirements. As the variable is used as a general climate indicator here, it can be used independently of those two. An 18-degree scale was used, with 1 representing subtropical species and 18 high-alpine/Arctic species. For the sake of a more intuitive interpretation, we switched this scale around; with 1 representing high-alpine/Arctic (cold-adapted) species and 18 representing subtropical (warm-adapted) species.

A generalized linear mixed model was fitted using `glmmTMB()` (Brooks et al., 2017). The response variable, species-specific observation proportion, was modeled as a function of growing season temperature, century, growth form, life cycle, flower color, average plant height and temperature optimum. The full model (Table 4) was based on our hypotheses (Box 1.2). It again only contained two-way interactions to prioritize the examination of our pairwise relationships and maintain a manageable model complexity. Species was taken as a random effect, as observations were repeated among the species. Again, variable transformation and model specification, selection and interpretation were done on the same terms as described for Analyses 1. Additionally, we conducted pairwise comparisons of estimated marginal means for the categorical variables present, using the `tukey` method for comparing.

The following packages were used for data handling and visualization in R: '`betareg`' (Grün et al., 2012), '`BIEN`' (Maitner, 2023), '`emmeans`' (Lenth, 2024), '`ggeffects`' (Lüdecke, 2018), '`GIFT`' (Denelle & Wiegelt, 2024), '`glmmTMB`' (Brooks et al., 2017), '`lubridate`' (Grolemund & Wickham, 2011), '`performance`' (Lüdecke et al., 2021), '`tidyverse`' (Wickham et al., 2019), '`TMB`' (Thygesen et al., 2017) and '`viridis`' (Garnier, 2024).

Table 4: Full models used to investigate survey efficiency in terms of our 3 main analyses. A generalized linear mixed model was fitted using *glmmTMB()* and the model was further specified with a beta-regression and the logit link function.

Analysis	Full Model
1	<i>glmmTMB</i> (Survey_Efficiency ~ Growing_Season_Temperature + Elevation + Total_Plot_Species_Richness + Total_Plot_Species_Richness:Elevation + Total_Plot_Species_Richness: Growing_Season_Temperature + Growing_Season_Temperature:Elevation + (1 Plot_ID), data = Species_Identification_per_Survey_Count, family = beta_family(link = "logit"))
2	<i>glmmTMB</i> (Survey_Efficiency ~ Week + I(Week^2) + Elevation + Growing_Season_Temperature + Total_Plot_Species_Richness + Total_Plot_Species_Richness:Elevation + Total_Plot_Species_Richness: Growing_Season_Temperature + Total_Plot_Species_Richness:Week + Week:Elevation + Week: Growing_Season_Temperature + Elevation: Growing_Season_Temperature + (1 Plot_ID), data = Species_Identification_Throughout_the_Season, family = beta_family(link = "logit"))
3	<i>glmmTMB</i> (Species_Specific_Observation_Proportion ~ Growing_Season_Temperature + Century + Growth_form + Life_cycle + Flower_color + Average_Plant_Height + Temperature_Optimum + Growing_Season_Temperature:Growth_form + Growing_Season_Temperature:Life_cycle + Growing_Season_Temperature:Average_Plant_Height + Growing_Season_Temperature:Temperature_Optimum + (1 Species), data = Observations_and_Traits_per_Species, family = beta_family(link = "logit"))

Results

Analysis 1: Species observation per survey count

The SAC (Figure 1) enabled us to visualize the trends in observed species over the sampling years, highlighted plot-specific trends and unveiled the overarching narrative of the cumulative observed species richness. Across all representations of SAC per year (Figure 1a), per plot (Figure 1b), and for the entire dataset (Figure 1c), a consistent trend emerges: species accumulation is nearly continuous throughout the season and over survey years. It's important to note that species addition doesn't necessarily denote novelty or introduction but rather recent observations along the elevation gradient. Contemporary surveys tended to accumulate more species throughout the season than historical surveys (Figure 1a). The latter also started later and thus commenced with a higher number of species. Additionally, a greater number of species was observed in warmer years. It is important to keep in mind that in 1919 only 6 surveys were performed. Next, on average, the plots at the outer ends of the trail showed a lower number of total accumulated species than the plots located on the middle of the transect (Figure 1b). Furthermore, it becomes clear that each year additional species were observed on the transect (Figure 1c). However, a decreasing trend in number of additional species can be observed over the years. Lastly, it is also true that additional species were observed with increasing growing season temperature (Figure 1c).

The detection-effort curve (Figure 2) depicts that during the survey conduction, a plateau was reached near the end of the survey period. It was reached faster during warmer survey seasons, looking at the contemporary data. However, the historical surveys also reached the plateau quite early.

Lastly, survey efficiency (proportion of species observed after 5, 10 or 15 surveys) was negatively affected by an increasing total plot species richness (all cases), elevation (after 10 and 15 surveys) and mean annual growing season temperature (after 15 surveys only) (Figure 3, Appendix 2 and 3). Noteworthy, an increase in growing season temperature showed to have a positive effect on the survey efficiency after 5 and 10 surveys, however, this was found to be non-significant.

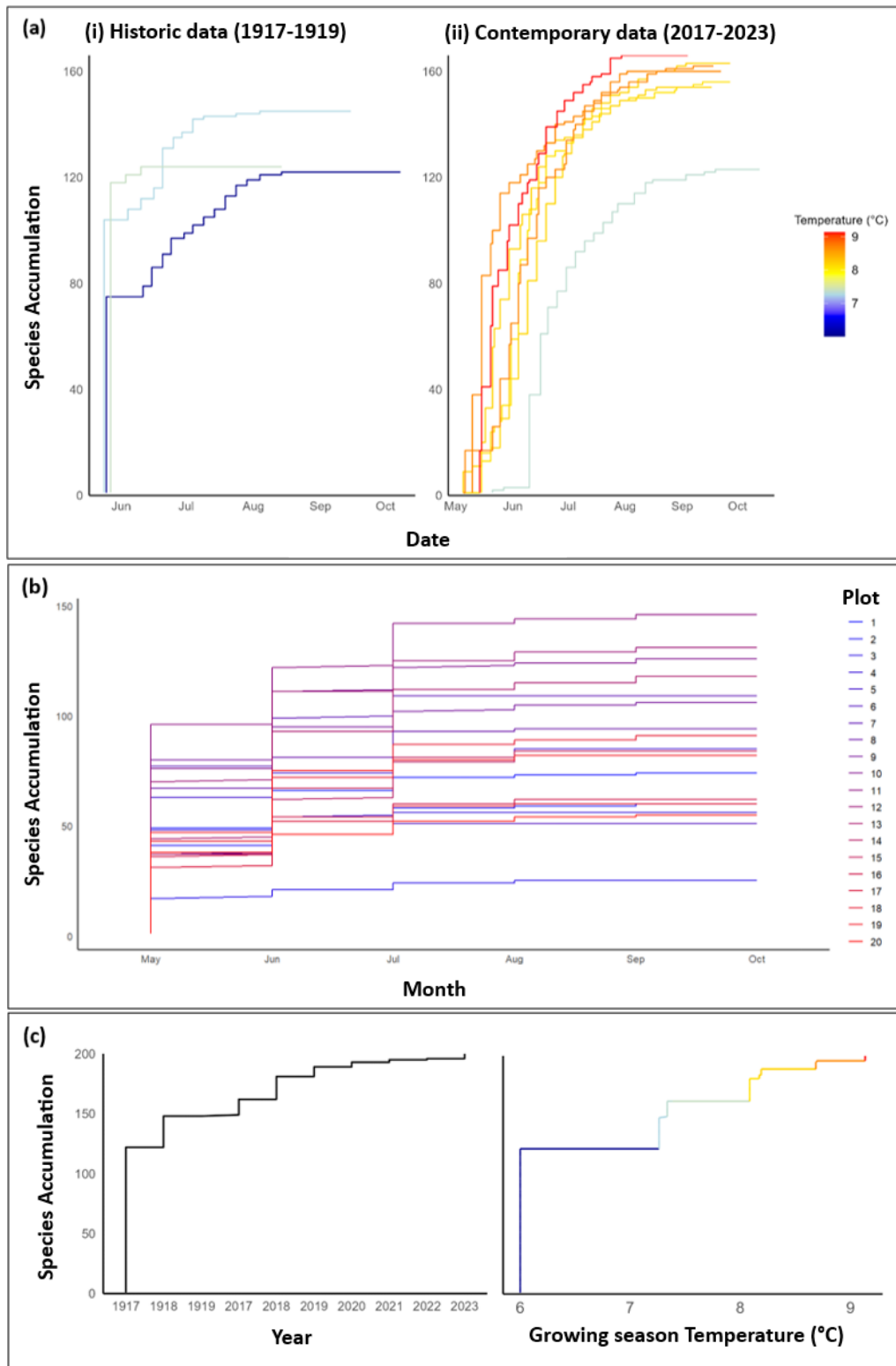


Figure 1: Species accumulation curves (SAC). (a) SAC per year (separated into (i) Historic data and (ii) Contemporary data), with the years represented by their mean annual growing season temperature (°C). (b) SAC per plot. (c) SAC for the entire long-term dataset over the years and along a mean growing season temperature gradient (°C).

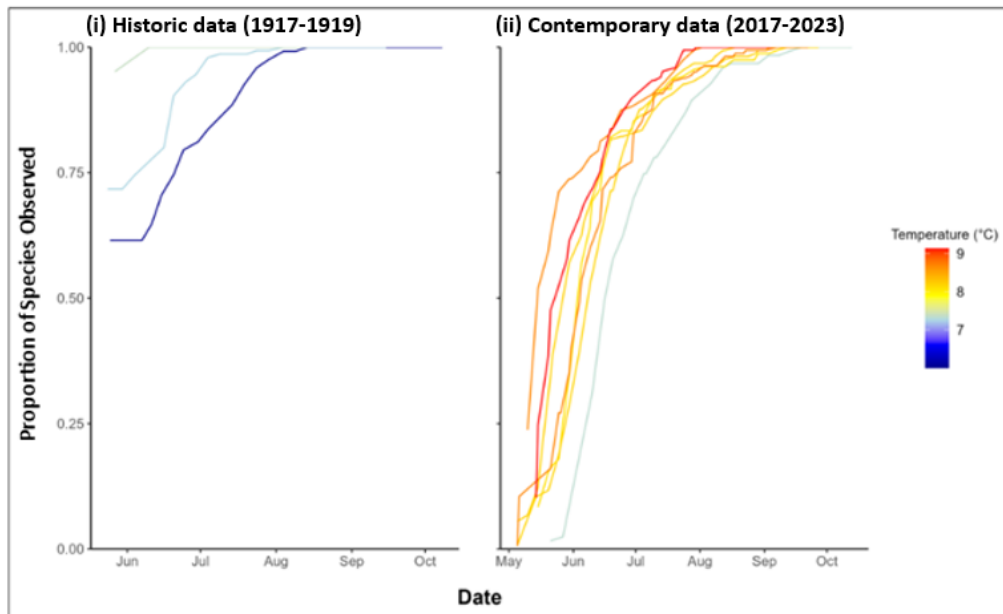


Figure 2: Detection-effort curve across the different survey years represented by their mean annual growing season temperature (°C). The detection is represented by the cumulative proportion of species observed per year, relative to the total species count per year. The effort is represented by the dates of survey conduction during the growing season, depicting the cumulative number of surveys.

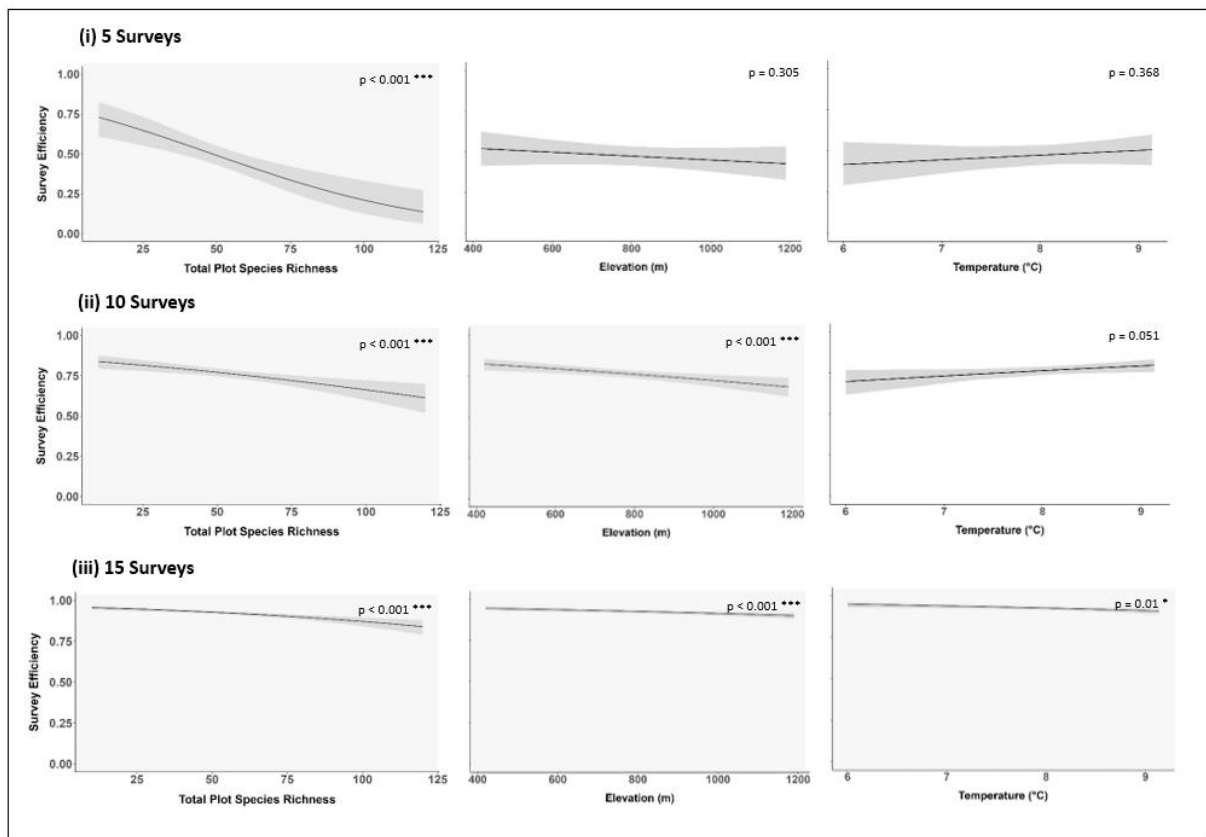


Figure 3: Predicted survey efficiency as a function of total plot species richness (left), elevation (m ASL; middle) and mean growing season temperature (°C; right) after (i) 5, (ii) 10 and (iii) 15 surveys. The final models used and their summary can be found in appendix 2 & 3. Thin lines highlight predictions, grey zones the confidence intervals. P-values and significance levels are marked in the top right of each panel.

Analysis 2: Species observation throughout the season

Regardless of the way we analyzed it, seasonal timing of observation, elevation of the plot, mean growing season temperature and total (sub)plot species richness significantly affected survey efficiency (Figures 4 and 5, Appendix 4 and 5). Overall, we observed pronounced interdependent effects of these factors on the observation of species through space and time.

The following findings all consider survey efficiency as the proportion of species observed per year, per week, per (sub)plot, relative to the total species count per year and relative to the total species count over the entire period. Survey efficiency increased towards the peak of the growing season and decreased towards the end of the growing season. However, the optimum reached near the middle of the growing season occurred later in time the higher the total (sub)plot species richness was and the lower the growing season temperature was and was most pronounced in low-elevation subplots. Furthermore, it appeared that a higher total (sub)plot species richness had a negative effect on the survey efficiency at the beginning of the season and at lower growing season temperatures and elevations. Next, higher growing season temperatures positively influenced survey efficiency, especially at the season's onset, higher elevations, and in (sub)plots with high total species richness. Lastly, increasing elevations were found to decrease survey efficiency, predominantly during the middle of the growing season and colder growing seasons, and in plots with limited species richness.

The contemporary dataset ((sub)plot level), as well as the historic dataset (plot level), showed these patterns for both calculations of the proportion of observed species (Figures 6 and 7, Appendix 6 and 7). Nevertheless, they differed in the fact that in general, the survey efficiency relative to the total species count over the entire period was 36.6% lower, for the contemporary data, and 18.5% lower, for the historic data, than the survey efficiency relative to the total species count per year. Lastly, the historic data indicated an average survey efficiency that was 57.6% higher than that of the contemporary data.

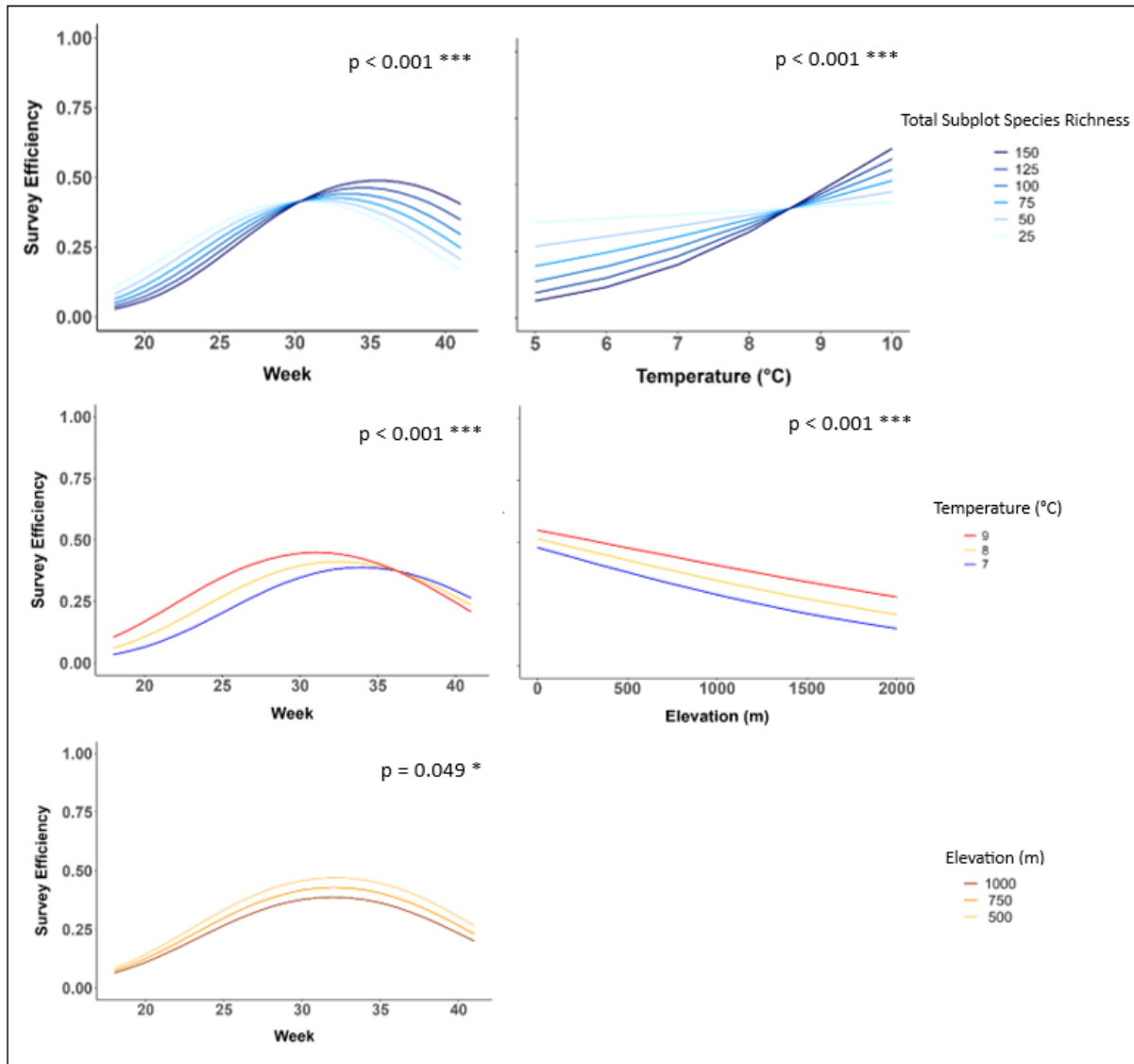


Figure 4: Predicted survey efficiency in function of seasonal timing (week of the year), total subplot species richness, elevation (m ASL) and mean growing season temperature (°C) for our contemporary data (2017-2023) on the subplot level (relative to the total species count over the entire period). Survey efficiency is represented by the proportion of species observed per year, per week, per subplot, relative to the total species count over the entire period per subplot. The final model used and its summary can be found in appendix 4 & 5. P-values and significance levels are marked in the top right of each panel.

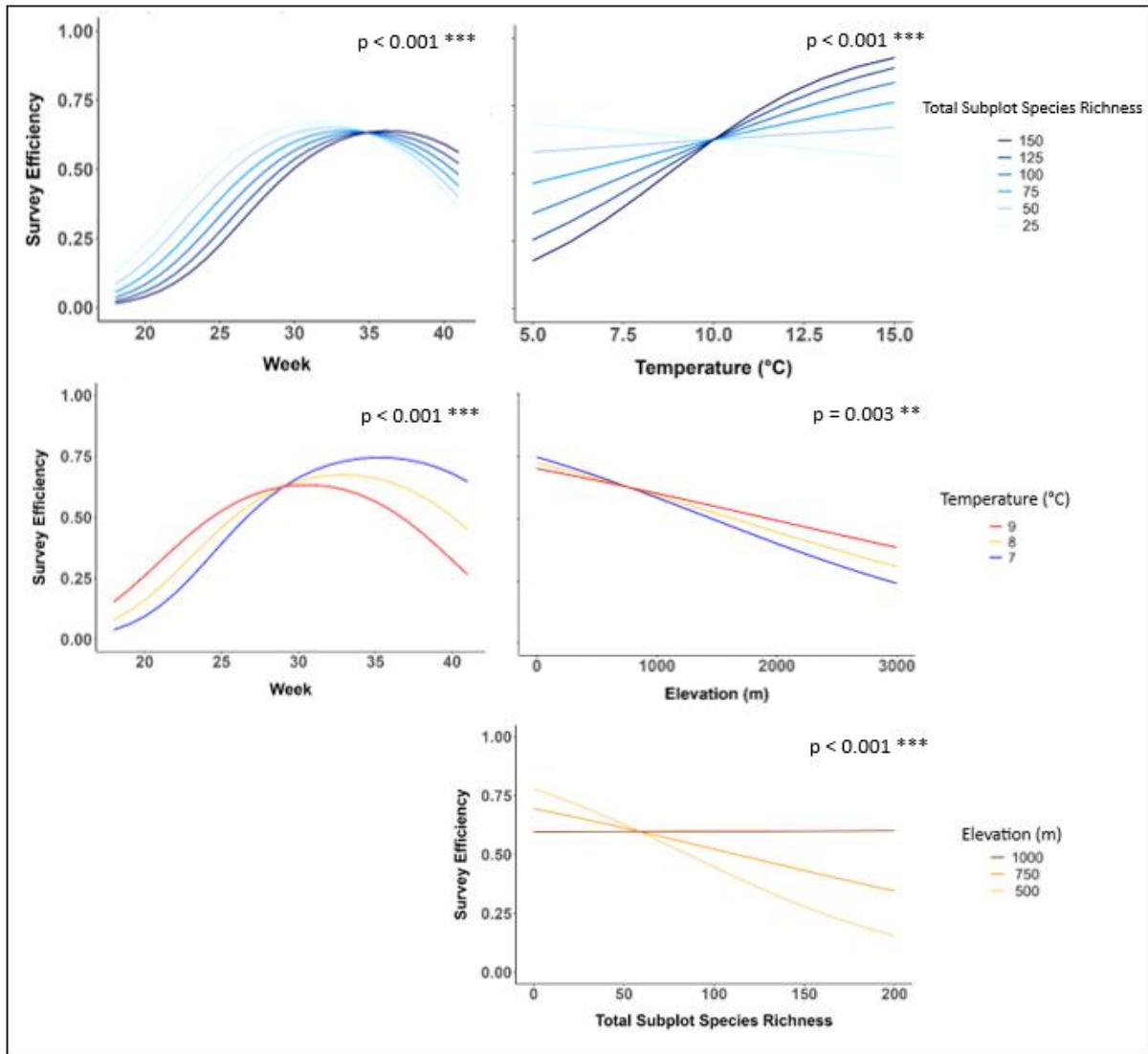


Figure 5: Predicted survey efficiency in function of seasonal timing (week of the year), total subplot species richness, elevation (m ASL) and mean growing season temperature ($^{\circ}\text{C}$) for our contemporary data (2017-2023) on the subplot level (relative to the total species count per year). Survey efficiency is represented by the proportion of species observed per year, per week, per subplot, relative to the total species count per year per subplot. The final model used and its summary can be found in appendix 4 & 5. P-values and significance levels are marked in the top right of each panel.

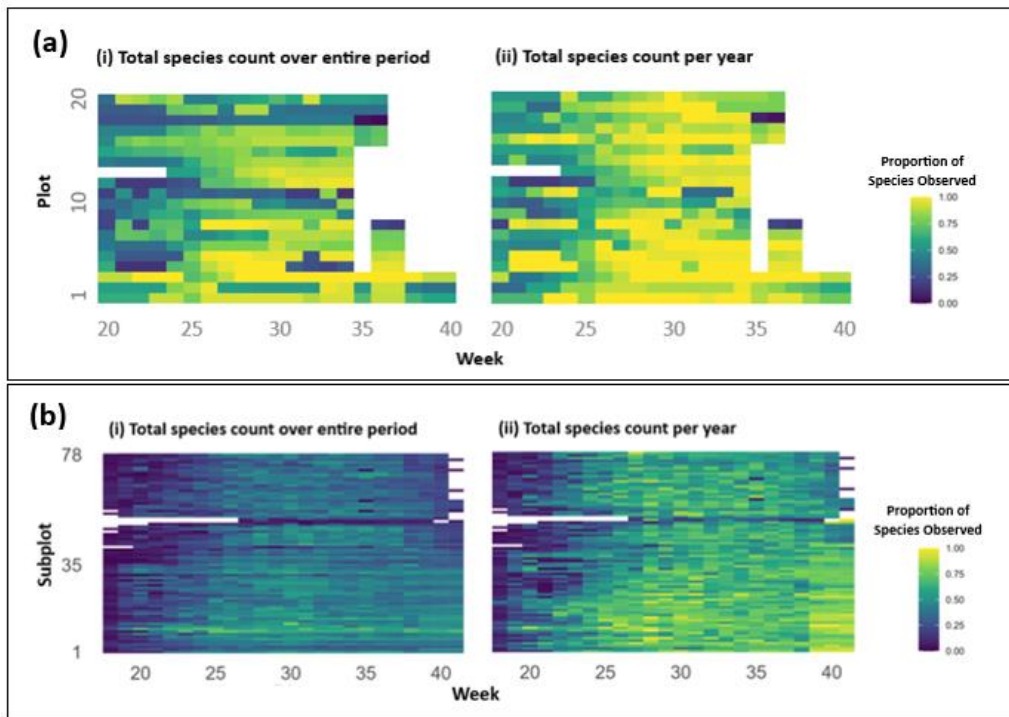


Figure 6: Heat maps of the mean survey efficiency represented as the proportions of species observed per week, per (a) plot, for the historic data, and (b) subplot, for the contemporary data, relative to the total species count over the entire period (i) and the species count per year (ii). Plots are numbered from 1 (427.253 m ASL) to 20 (1189.597 m ASL.), subplots from 1 (419.398 m ASL) to 78 (1193.990 m ASL). If no species were observed (either due to snow cover or lack of visits) a plot is colored white.

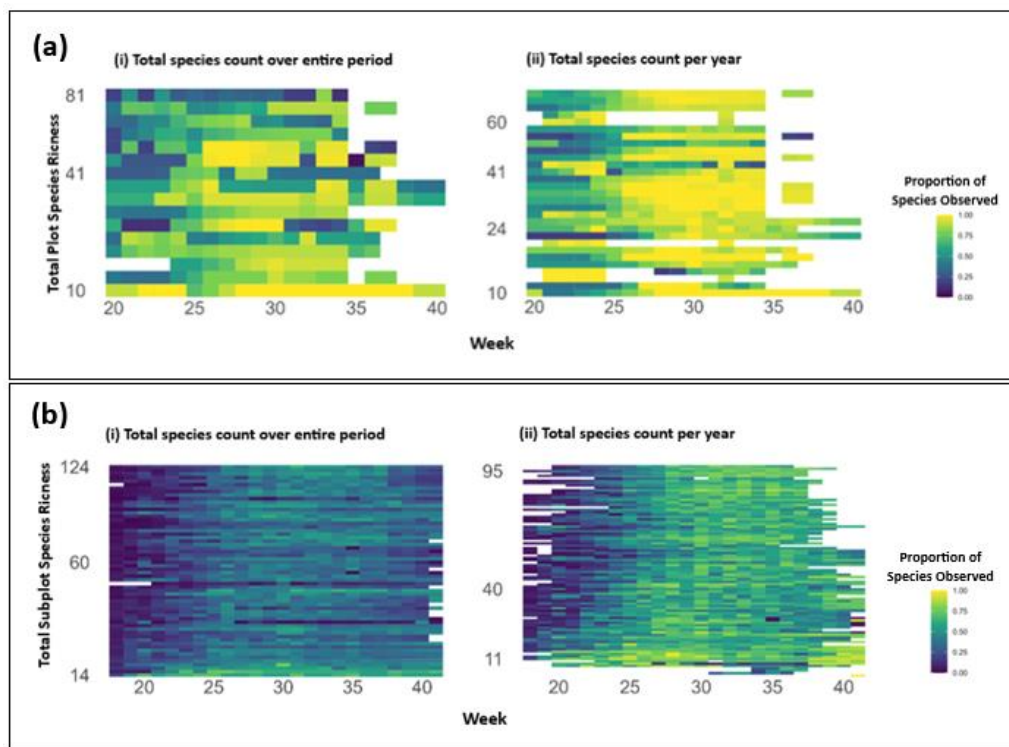


Figure 7: Heat maps of the mean survey efficiency represented as the proportions of species observed per week, per (a) total plot species richness, for the historic data, and (b) total subplot species richness, for the contemporary data, relative to the total species count over the entire period (i) and the species count per year (ii). If no species were observed (either due to snow cover or lack of visits) a plot is colored white.

Analysis 3: Species-specific observation efficiency

An increasing growing season temperature caused an increase in species-specific observation efficiencies for the more cold-adapted plants (Figure 8, Appendix 8 and 9). The more warm-adapted the species, the weaker this effect of temperature. Species-specific identification efficiencies were also higher during the 20th century compared to the 21st century (Figure 8, Appendix 8 and 9). Lastly, forbs were observed proportionally less than shrubs and graminoids were observed proportionally less than subshrubs and shrubs (Figure 8, Appendix 8, 9 and 10). As average plant height correlated with this growth form we decided to leave this first variable out of the investigation, after following the correct model selection steps. Life form, flower color and average plant height eventually did not seem to affect the species-specific observation proportions.

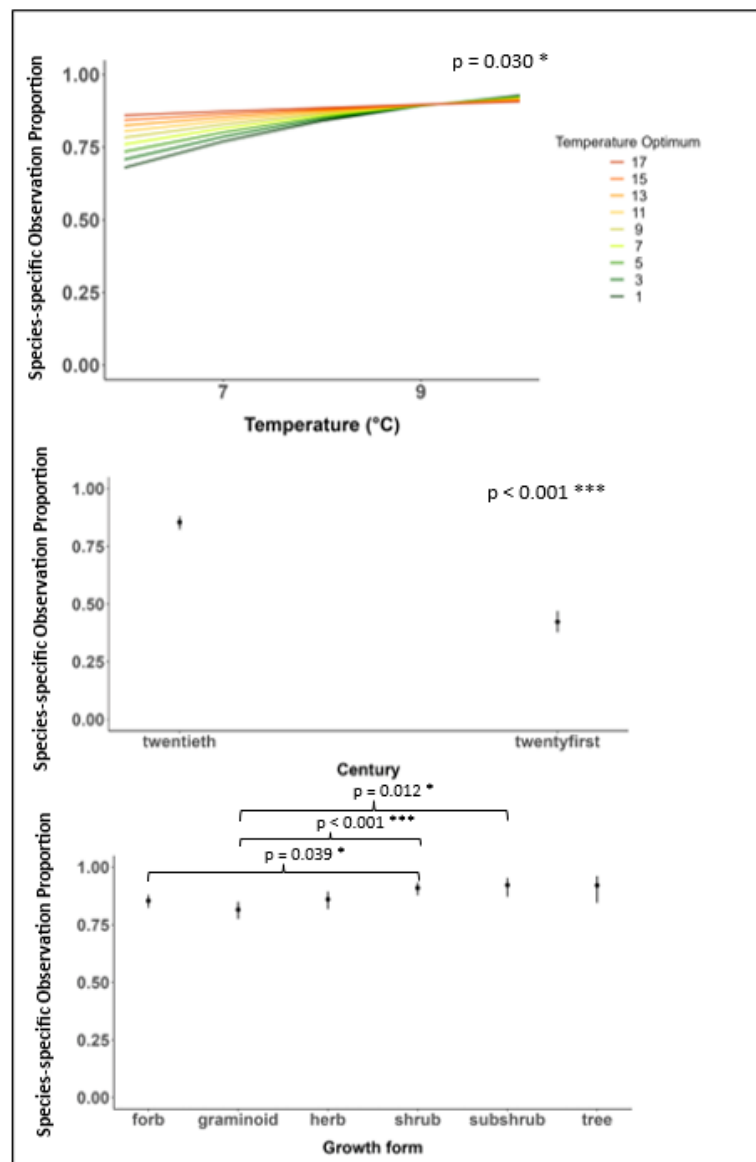


Figure 8: Predicted species-specific observation efficiency in function of growing season temperature and species-specific temperature optimum (green = cold adapted and red = warm adapted; top), survey period (century; middle) and growth form (bottom). The final model used and its summary can be found in appendix 8, 9 & 10. P-values and significance levels are marked in the top right of each panel or between the significant pairwise comparisons.

Discussion

Survey efficiency was found to be dependent on spatial, temporal and species-specific variation within the plant community. Overall, we did observe pronounced interdependent effects of elevation, seasonal timing of observation, growing season temperature, total plot species richness, species-specific temperature optima, growth form and survey period on the proportion of species observed through space and time. Indeed, single-site visits identified between 1 and 100% (on average 54.5% per subplot) of all species eventually observed in a year, often leaving a substantial part of the vegetation unnoticed upon single observation. These conclusions are far from trivial, as they show that insufficient site visitations, incorrect timing of the surveys, absence of year-to-year comparisons and inadequate spatial scales can lead to misleading conclusions, potentially leading to an over- or underestimation of species dynamics, including, among others, species loss, introduction and distributional shifts.

To start, additional species kept on being observed with each survey performed during the growing season. The accumulation of additional species often persisted until late into the season. It wasn't until the middle to the end of the growing season that most plots had fully documented their total species richness. It became evident that, if we start surveying in the beginning of the growing season, at least 15 surveys were necessary to capture a reasonable portion of the species richness within a plot. This necessity arises from the gradual increase in species richness at the onset of the season, a phenomenon dependent on species phenology (Körner et al., 2023). Furthermore, in May and June the last stages of snow-melt could still be occurring, regulating the phenological emergence of the vegetation (Bjorkman et al., 2015; Karlsen et al., 2006). However, the need for additional surveys was particularly apparent in conditions of higher growing season temperatures, at higher plot elevations, and plots with a higher species richness. This could be attributed to the increased height and cover of Arctic species as a consequence of climatic warming, causing crowdedness and hindering observations in the middle of the season (Van Der Wal & Stien, 2014; Walker et al., 2006). Furthermore, smaller vegetational dimensions and a later start of the growing season at higher elevations could also negatively impact observations, due to species being less visible and exhibiting sparsity across time (Halbritter et al., 2018; Körner et al., 1989; MacDougall et al., 2021; Wilson & Nilsson, 2009). Lastly, a higher species richness could provide more opportunities for species to be overlooked. Additionally, the variability and abundance of phenological patterns may also increase with increasing species richness, resulting in more dispersed phenological phases over the growing season, making species observation more gradual.

Next, the amount of species observed during each survey also varied across the growing season. We noted that observation efficiency peaked by the middle of the growing season. This variability in observations can be attributed to the various growth and developmental phases of plants, which vary across different periods of the season (Chen et al., 2013). Plant phenology, especially for annual plants and perennials spending winter belowground, restricts the window during which these species are detectable. New species continuously emerge in early season, while plant growth peaks in the middle, and various species complete their life cycles towards the season's end. Subsequently, species can also be overlooked more easily during the beginning and end of the season.

The aforementioned seasonal variations varied from year to year. This variability can be linked to the advancement of the growing season and earlier snowmelt in warmer years, resulting in advanced phenology (Assmann et al., 2019; Høye et al., 2013; Prev  y et al., 2019). However, incorporating additional climate data when accounting for imperfect observations could enhance our ability to accurately record and interpret species dynamics. This, especially, as tundra vegetation responses are known to be more intricate than direct responses to warming, with snowmelt acting as a significant local driver of phenological changes (Assmann et al., 2019; Bjorkman et al., 2020). Particularly, snowmelt is closely associated with winter precipitation levels, topography, radiative exposure, and prevailing wind conditions across the landscape, rather than solely with seasonal temperatures (Bjorkman et al., 2015).

Comparing survey efficiency calculated relative to the total species count over the entire period with efficiency relative to the total species per year revealed the benefits of long-term surveys spanning multiple years. This is because relatively fewer species were observed within each year compared to those detected over the entire duration of the study. Additionally, with each survey conducted over the years, new species were consistently discovered, although certain species were noted to intermittently disappear and reappear during this period. To draw accurate conclusions and projections regarding the impacts of climate change on species loss and introductions, it is essential to precisely document these dynamics over time and not over- or underestimate them (Rew et al., 2020). While these changes may reflect genuine shifts in vegetation composition, typically reported as such in temporal analyses, it's important to acknowledge that other factors could contribute to interannual variation in species composition. These factors may include species intermittently not being present each year, seasonality influencing the timing and abundance of species occurrences, as well as potential observer bias arising from variations in observer teams each year, which could result, among other issues, in

systematic misidentifications or identification misses. Additionally, the intensity of search efforts can vary based on resource availability, observer experience, and specific study conditions, further affecting detection. All above mentioned factors already emphasize the need for multiple surveys a year, efficient timing of these surveys within the growing season and year-to-year comparisons. This to capture all species dynamics through time and avoid misleading conclusions resulting from adapting insufficient scales and resolutions.

In addition to considering these inherent dynamics, it is crucial to account for other factors influencing plant detection. Elevation, total plot species richness, seasonal timing of observation, and mean growing season temperature all interdependently influenced survey efficiency (Box 2). Nevertheless, these effects can largely be explained by patterns associated with plant phenology and morphology, often across different contexts, as also seen for the cumulative survey efficiency. First, vegetational dimensions, such as individual cover and size, are generally smaller at higher elevations (Halbritter et al., 2018; Körner et al., 1989). This could cause plants to be less visible, hindering observations. Second, phenological performance also differs with elevation, resulting in a shorter growing season at higher elevations, restricting the window during which species are detectable (MacDougall et al., 2021; Wilson & Nilsson, 2009). Third, species exhibit a diverse range of phenological responses (Assmann et al., 2019; Körner et al., 2023), suggesting that as species richness increases, so does the variability and abundance of phenological patterns across different species. This could result in more dispersed phenological phases over the growing season, making species observation more gradual. Moreover, increased species richness may also provide more opportunities for species to go unnoticed, impeding observations.

Overall, rising temperatures, attributed to climate change (Post et al., 2019), emerged as a primary driver directly and indirectly shaping these patterns, as proven by analysis 2. Especially in temperature-limited tundra ecosystems, advancing phenology, and thus subsequent lengthening of the growing season has been suggested as one of the most visible effects of climate change on plant communities (Arft et al., 1999; Høye et al., 2007; Oberbauer et al., 2013; Prev  y et al., 2019; Wilson & Nilsson, 2009). Furthermore, at higher elevations growing season length is found to be more susceptible to increasing temperatures, compared to growing season length at lower elevations (Wilson & Nilsson, 2009). Warming temperatures are also known to increase the height and cover of Arctic species (Van Der Wal & Stien, 2014; Walker et al., 2006). Arctic plants are known to be more positively affected by increasing temperatures than more warm-adapted plants because their growth is more limited by lower temperatures

(Lin et al., 2010; Parmesan, 2007; Root et al., 2003). The observed temperatures will likely be too low to affect the growth of more warm-adapted species. Collectively, these factors can impact the presence and overall appearance of different species throughout the survey, affecting the likelihood of their observation.

Finally, some species-specific traits were found to affect species detectability. Our results revealed that graminoids were observed proportionally less than subshrubs and shrubs and that forbs were observed proportionally less than shrubs. According to Chen et al. (2013), grasses are more likely to be overlooked due to their morphology and lack of distinctive flowers, fruit or vegetation parts. We propose that similar morphological characteristics, such as size, may also contribute to overlooking forbs. Additionally, as mentioned above, being cold-adapted could also increase observation probabilities during climate warming in the Arctic. This as the growth of these plants might be positively affected by these temperatures (Lin et al., 2010; Parmesan, 2007; Root et al., 2003), enhancing detectability. Despite these significant findings, our analysis indicated that life form, average plant height, and flower color did not seem to affect species-specific observation proportions. However, the limited representation of annual species, constituting only 4% of our dataset, may have contributed to the observed lack of effects regarding life form. While plant height was found to not directly impact species observations, its correlation with growth form, which did affect observations, led us to exclude it as a crucial factor in our assessment. Nevertheless, studies by Chen et al. (2013) and Roth et al. (2018) suggest a direct effect of plant height on species observations, with larger plant species often being more detectable than smaller ones. Finally, considering the influence of physical aspects of color, such as flower color, on subjective experience (Hatfield, 2003), we anticipated that it would affect how we perceive species. However, we found no significant evidence to suggest that flower color played a substantial role in species observation in our study.

Lastly, it is also worth considering potential shortcomings in our dataset. The notable difference in survey efficiency between our two main periods (1917-1919 & 2017-2023) may signal limitations within our data. Acknowledging methodological disparities over extensive temporal scales is crucial when inferring results. Eventually, all these factors together emphasize the need for multiple surveys a year, efficient timing of these surveys within the growing season, year-to-year comparisons and adapting adequate spatial scales. This to capture all species dynamics through space and time and avoid misleading conclusions resulting from misidentifications and identification misses or adapting insufficient scales and resolutions.

Box 2. Pattern elucidations

Seasonal timing – Elevation:

The higher the elevation of the plot, the lower and more condensed the increase of survey efficiency throughout the growing season. This can be attributed to smaller vegetational dimensions and shorter growing seasons at higher elevations.

Seasonal timing - Total plot species richness:

The higher the total plot species richness the more delayed the effect of seasonal timing is. However, the higher the total plot species richness, the more pronounced this increase and decrease of survey efficiency throughout the growing season is. This could be attributed to the diverse phenological responses among species, suggesting that as species richness increases, so does the variability and abundance of phenological patterns across different species. Consequently, this provides fewer opportunities to observe all species at the beginning of the season and more opportunities to observe all species at the end of the season, as species richness might increase and decrease more gradually. However, we anticipate the most species to be observed during the middle of the season when most species are present.

Seasonal timing - Growing season temperature:

An increasing growing season temperature advances the response of survey efficiency to seasonal timing. This can be caused by an advance of the growing season and earlier snowmelt during warmer years, affecting plant phenology. However, in the middle of the season, warmer temperatures reach a lower survey efficiency relative to the total species count per year. This could be attributed to increasing biomass with temperature, causing crowdedness, impairing observations. However, the higher survey efficiency relative to the total species count over the entire period, in the middle of warmer growing season, can be explained by the fact that during warmer years, simply more species were present.

Total plot species richness – Elevation:

An increasing total plot species richness decreases the survey efficiency the lower the elevation of the plot is. This can be because of the additive impact of the higher cover and size of species at lower elevations couples with the higher species richness in these areas, providing more opportunities for species to go unnoticed due to crowdedness. On the contrary, proportionally fewer species are observed at higher elevation plots with low total species richness, compared to low elevation plots. This can be because of the additive impact of a lower cover and size of species at these elevations, coupled with the lower species richness in these areas, proving more opportunities for species to go unnoticed due to sparsity. However, the higher the elevation of the plot, the less and less the effect of an increasing total plot species richness on survey efficiency is.

Box 2. Pattern elucidations (Continued)

Total plot species richness - Growing season temperature:

An increasing total plot species richness decreases the survey efficiency the lower the growing season temperature is. The higher the growing season temperature, the less and less the effect of an increasing total plot species richness on survey efficiency is. Furthermore, as temperatures keep on rising an increasing total plot species richness might even have a positive effect on survey efficiency. This shift from a negative to a positive influence of species richness with increasing temperature can be attributed to a lengthening of the growing season with increasing temperatures, causing species to be observed more throughout the whole survey conduction, especially in plots with a high species richness as there is more chance of species to be present at the same time.

Elevation - Growing season temperature:

At higher elevations the survey efficiency gets the least decreased during warmer growing seasons. This can be attributed to an increasing growing season length during warmer years, which is found to be higher at high elevations. Additionally, the enhanced growth caused by warmer temperatures might also be of more prominence at these elevations. The effect of high elevation on survey efficiency might thus be compensated by higher temperatures, increasing the chances of being observed.

Conclusion

Based on our findings, it is evident that species observations are influenced not only by the inherent dynamics of the vegetation, including seasonal and year-to-year fluctuations and the broader context of long-term climate change, but also by other temporal, spatial and species-specific variations within the plant community. This as these variations have a crucial impact on species observation accuracy, often manifesting through changes in phenology and morphology across spatial and temporal dimensions. It is worth noting that while actual trends and changes resulting from climate change will likely be present in many long-term studies, they are challenging to detect accurately due to the complex interplay of these various factors (such as the seasonal timing of observation, elevation, total plot species richness, growing season temperature, growth form and temperature optimum tested here). These factors interdependently influence species detection efficiency, potentially leading to inaccurate observations and subsequent implications for the assessment of species and community distribution changes over time, including an overestimation of the rate of extinction.

As such, the changing climate directly and indirectly influences these factors through space and time, making it increasingly pressing to consider these complexities in future research and survey designs. We would therefore suggest that imperfect observations should be accounted for whenever possible in diversity studies of plants to gain control over such errors that may compromise results on species dynamics in this changing climate. However, we recognize that limitations such as time constraints, data accessibility, funding, and resource availability often impose constraints on such efforts.

Nevertheless, all these factors underscore the importance of at least conducting multiple surveys per year, timing them effectively within the growing season, making year-to-year comparisons, and ensuring a sufficient spatial scale for survey implementation. In conclusion, our study points out that in survey-based investigations, imperfect species observations through space and time are important to account for, to the extent possible.

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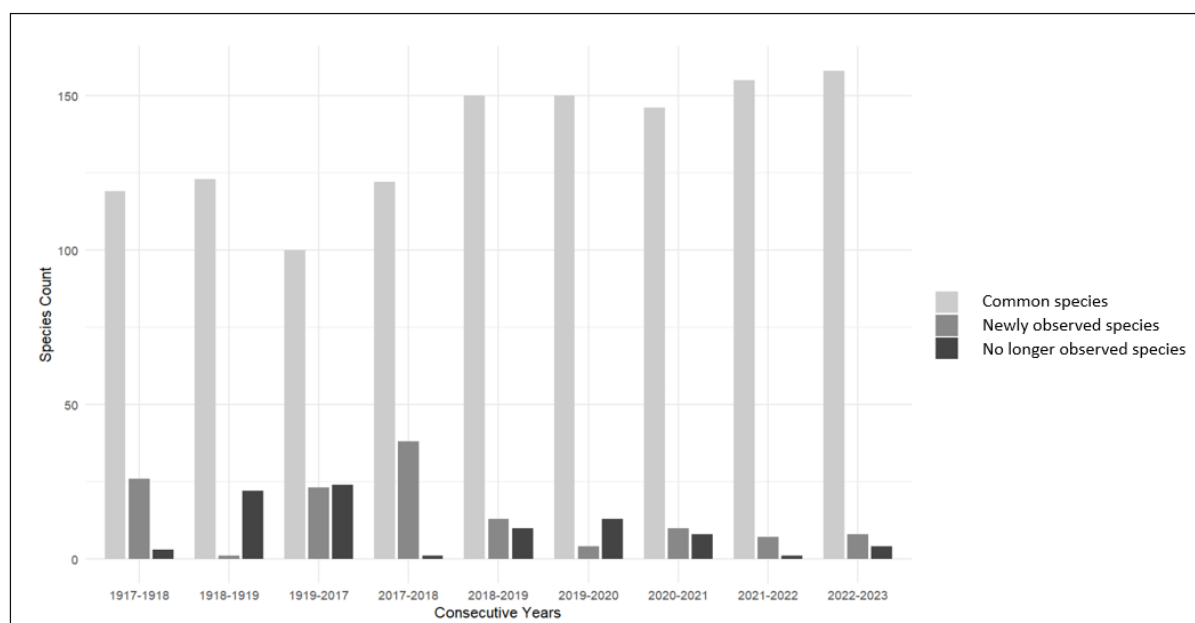
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Appendix

Appendix 1: Newly observed and no longer observed species



Appendix 1: Count of common, newly and now longer observed species between consecutive survey years. List of species available upon request.

Appendix 2: Final models Analysis 1

Appendix 2: Final models used to investigate survey efficiency after 5, 10 & 15 surveys (Analysis 1). A generalized linear mixed model was fitted using `glmmTMB()` and the model was further specified with a beta-regression and the logit link function. VIF was used to detect multicollinearity ($VIF > 5$) and AIC was used to select these final models.

Survey efficiency	Final model
5 Surveys	<code>glmmTMB(Survey_Efficiency_5Suveys ~ Growing_Season_Temperature + Elevation + Total_Plot_Species_Richness + (1 Plot_ID), data = Species_Identification_per_Survey_Count, family = beta_family(link = "logit"))</code>
10 Surveys	<code>glmmTMB(Survey_Efficiency_10Suveys ~ Growing_Season_Temperature + Elevation + Total_Plot_Species_Richness + (1 Plot_ID), data = Species_Identification_per_Survey_Count, family = beta_family(link = "logit"))</code>
15 Surveys	<code>glmmTMB(Survey_Efficiency_15Suveys ~ Growing_Season_Temperature + Elevation + Total_Plot_Species_Richness + (1 Plot_ID), data = Species_Identification_per_Survey_Count, family = beta_family(link = "logit"))</code>

Appendix 3: Summary results of final models Analysis 1

Appendix 3: Summary() results of the final models (Appendix 2) used to investigate survey efficiency after 5, 10 & 15 surveys (Analysis 1).

	Estimate	Std. Error	z value	p-value
5 Surveys				
(Intercept)	0.7227011	0.9471553	0.763	0.445
Growing Season Temperature	0.1150388	0.1279107	0.899	0.368
Total Plot Species Richness	-0.0257432	0.0061050	-4.217	2.48 ^e -05 ***
Elevation	-0.0004811	0.0004692	-1.026	0.305
10 Surveys				
(Intercept)	1.2098694	0.6744377	1.794	0.072830 .
Growing Season Temperature	0.1684000	0.0863244	1.951	0.051083 .
Total Plot Species Richness	-0.0107649	0.0028755	-3.744	0.000181 ***
Elevation	-0.0009986	0.0002856	-3.497	0.000471 ***
15 Surveys				
(Intercept)	5.4669343	0.6190738	8.831	< 2 ^e -16 ***
Growing Season Temperature	-0.1992112	0.0773973	-2.574	0.010057 *
Total Plot Species Richness	-0.0129710	0.0024699	-5.252	1.51 ^e -07 ***
Elevation	-0.0008173	0.0002161	-3.781	0.000156 ***

Appendix 4: Final models Analysis 2

Appendix 4: Final models used to investigate survey efficiency relative to the total species count over the entire period and to the total species count per year, for contemporary data ((sub)plot level) and historic data (plot level). A generalized linear mixed model was fitted using glmmTMB() and the model was further specified with a beta-regression and the logit link function. VIF was used to detect multicollinearity (VIF > 5) and AIC was used to select these final models.

Survey efficiency	Final Model
Contemporary data	
Total species count over entire period -Subplot level	<i>glmmTMB(Survey_Efficiency ~ Week + I(Week^2) + Elevation + Growing_Season_Temperature + Total_Subplot_Species_Richness + Total_Subplot_Species_Richness: Growing_Season_Temperature + Total_Subplot_Species_Richness: Week + Week: Elevation + Week: Growing_Season_Temperature + Elevation: Growing_Season_Temperature + (1 Subplot_ID), data = Species_Identification_Throughout_the_Season, family = beta_family(link = "logit"))</i>
Total species count per year -Subplot level	<i>glmmTMB(Survey_Efficiency ~ Week + I(Week^2) + Elevation + Growing_Season_Temperature + Total_Subplot_Species_Richness + Total_Subplot_Species_Richness: Elevation + Total_Subplot_Species_Richness: Growing_Season_Temperature + Total_Subplot_Species_Richness: Week + Week: Growing_Season_Temperature + Elevation: Growing_Season_Temperature + (1 Subplot_ID), data = Species_Identification_Throughout_the_Season, family = beta_family(link = "logit"))</i>
Total species count over entire period -Plot level	<i>glmmTMB(Survey_Efficiency ~ Week + I(Week^2) + Elevation + Growing_Season_Temperature + Total_Plot_Species_Richness + Total_Plot_Species_Richness: Growing_Season_Temperature +</i>

	<i>Total_Plot_Species_Richness:Week + Week: Growing_Season_Temperature + Elevation: Growing_Season_Temperature + (1 Plot_ID), data = Species_Identification_Throughout_the_Season, family = beta_family(link = "logit"))</i>
Total species count per year -Plot level	<i>glmmTMB(Survey_Efficiency ~ Week + I(Week^2) + Elevation + Growing_Season_Temperature + Total_Plot_Species_Richness + Total_Plot_Species_Richness:Elevation + Total_Plot_ Species_Richness:Week + Week:Elevation + Week: Growing_Season_Temperature + (1 Plot_ID), data = Species_Identification_Throughout_the_Season, family = beta_family(link = "logit"))</i>
Historic data	
Total species count over entire period -Plot level	<i>glmmTMB(Survey_Efficiency ~ Week + I(Week^2) + Elevation + Growing_Season_Temperature + Total_Plot_Species_Richness + Total_Plot_Species_Richness:Week + Week:Elevation + Week: Growing_Season_Temperature + Elevation: Growing_Season_Temperature + (1 Plot_ID), data = Species_Identification_Throughout_the_Season, family = beta_family(link = "logit"))</i>
Total species count per year -Plot level	<i>glmmTMB(Survey_Efficiency ~ Week + I(Week^2) + Elevation + Growing_Season_Temperature + Total_Plot_Species_Richness + Total_Plot_Species_Richness:Week + Week:Elevation + Elevation: Growing_Season_Temperature + (1 Plot_ID), data = Species_Identification_Throughout_the_Season, family = beta_family(link = "logit"))</i>

Appendix 5: Summary results of final models Analysis 2

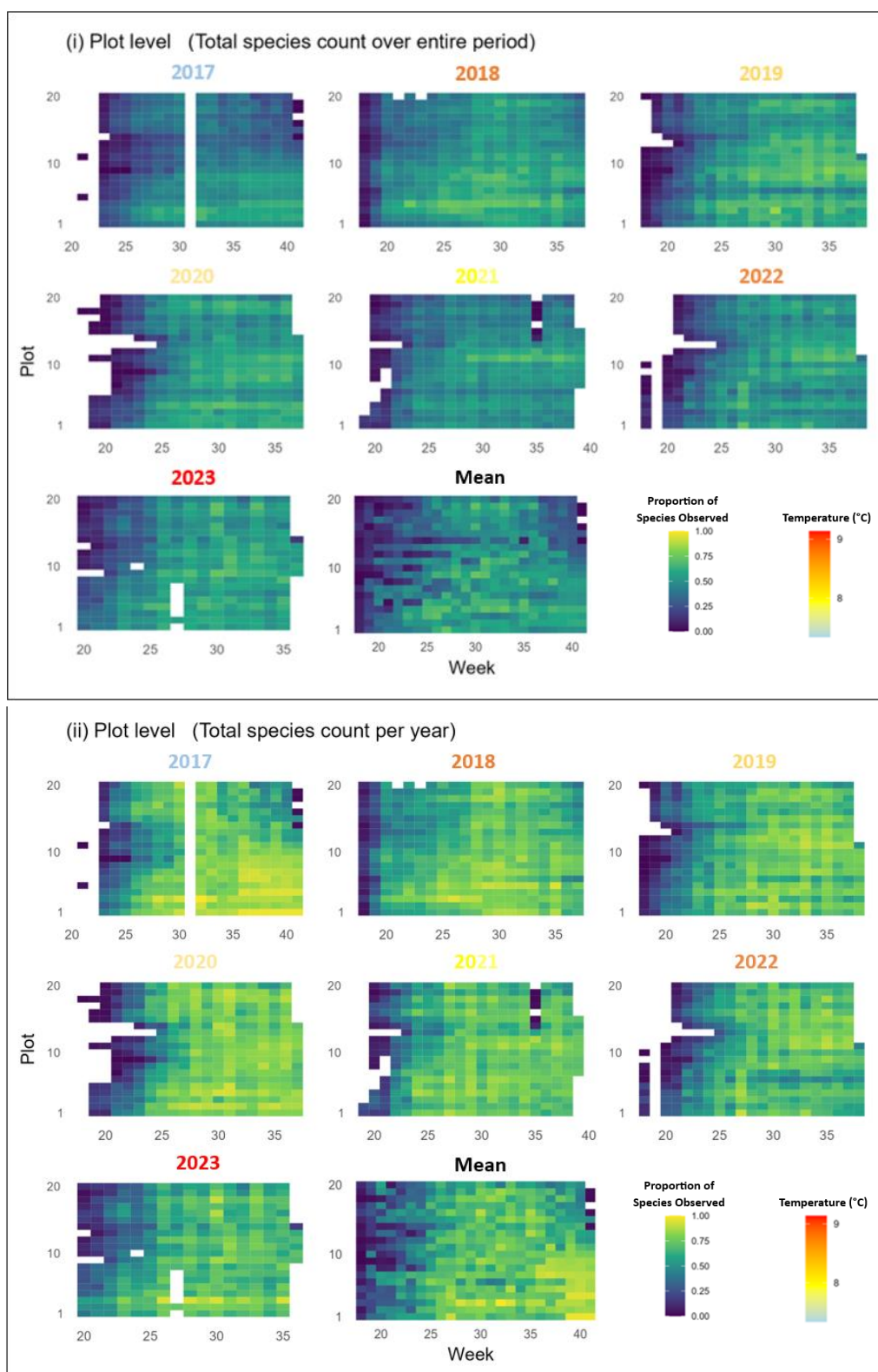
Appendix 5: Summary() results of the final models (Appendix 4) used to investigate survey efficiency relative to the total species count over the entire period and to the total species count per year, for contemporary data ((sub)plot level) and historic data (plot level) (Analysis 2).

	Estimate	Std. Error	z value	p-value
Contemporary data				
Total species count over entire period (Subplot level)				
(Intercept)	-1.657 ^{e+01}	5.563 ^{e-01}	-29.79	< 2 ^{e-16} ***
Week	9.518 ^{e-01}	1.946 ^{e-02}	48.91	< 2 ^{e-16} ***
I(Week^2)	-1.140 ^{e-02}	1.614 ^{e-04}	-70.68	< 2 ^{e-16} ***
Elevation	-1.493 ^{e-03}	3.513 ^{e-04}	-4.25	2.15 ^{e-05} ***
Growing Season Temperature	8.000 ^{e-01}	5.598 ^{e-02}	14.29	< 2 ^{e-16} ***
Total Subplot Species Richness	-6.660 ^{e-02}	3.460 ^{e-03}	-19.25	< 2 ^{e-16} ***
Growing Season Temperature : Total Subplot Species Richness	4.684 ^{e-03}	3.200 ^{e-04}	14.64	< 2 ^{e-16} ***
Week : Total Subplot Species Richness	9.094 ^{e-04}	3.308 ^{e-05}	27.49	< 2 ^{e-16} ***
Week : Growing Season Temperature	-3.282 ^{e-02}	1.636 ^{e-03}	-20.06	< 2 ^{e-16} ***
Elevation : Growing Season Temperature	1.231 ^{e-04}	3.269 ^{e-05}	3.76	0.000167 ***
Week : Elevation	-6.508 ^{e-06}	3.307 ^{e-06}	-1.97	0.049098 *

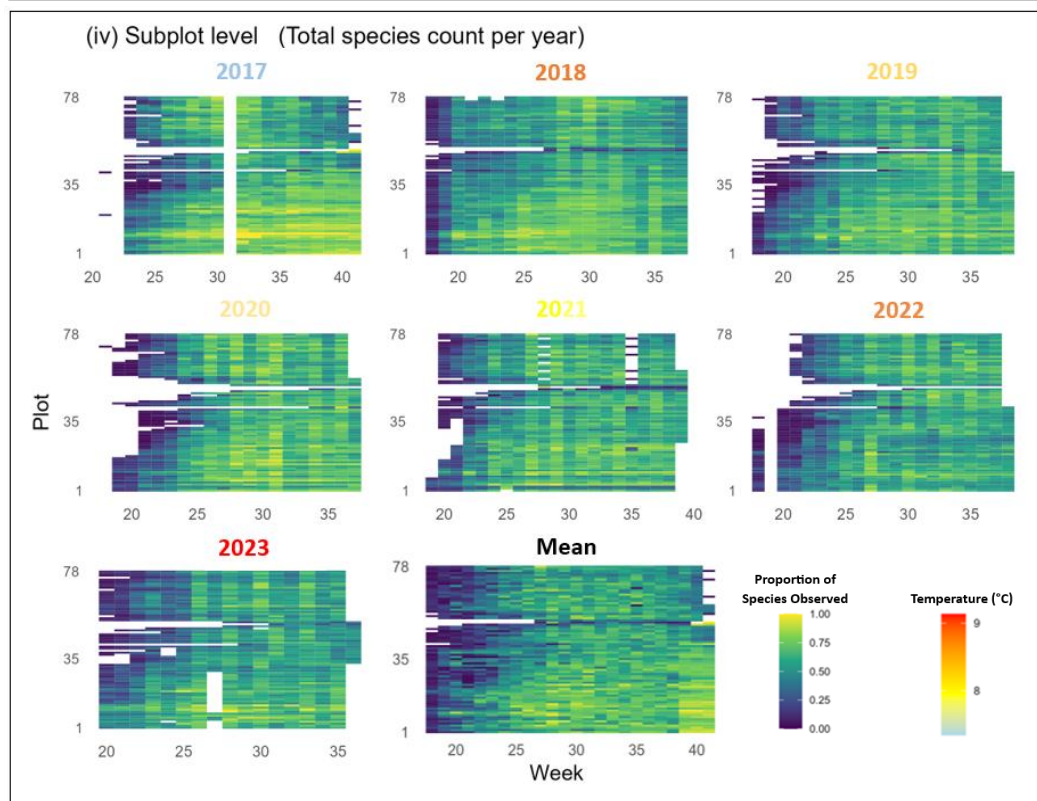
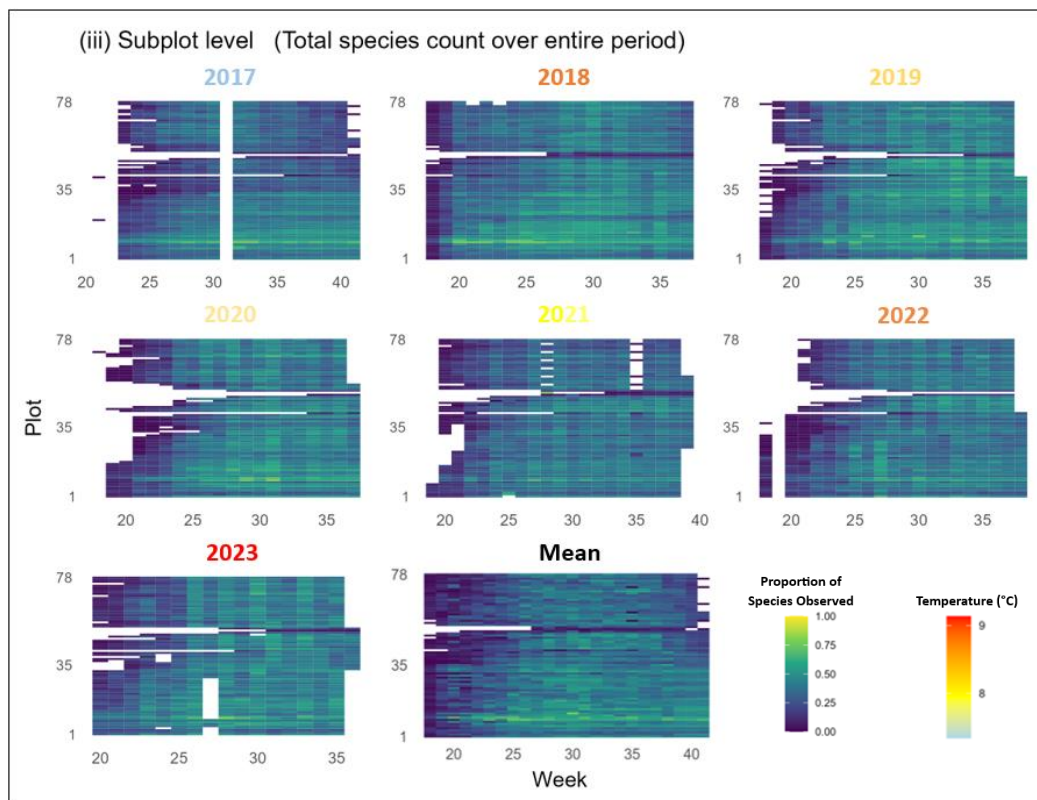
Total species count per year (Subplot level)				
(Intercept)	-2.542 ^{e+01}	7.442 ^{e-01}	-34.16	< 2 ^{e-16} ***
Week	1.442 ^{e+00}	2.666 ^{e-02}	54.07	< 2 ^{e-16} ***
I(Week^2)	-1.431 ^{e-02}	2.184 ^{e-04}	-65.54	< 2 ^{e-16} ***
Elevation	-3.007 ^{e-03}	3.937 ^{e-04}	-7.64	2.19 ^{e-14} ***
Growing Season Temperature	1.699 ^{e+00}	8.065 ^{e-02}	21.07	< 2 ^{e-16} ***
Total Subplot Species Richness	-9.139 ^{e-02}	7.575 ^{e-03}	-12.06	< 2 ^{e-16} ***
Elevation : Total Subplot Species Richness	2.963 ^{e-05}	4.810 ^{e-06}	6.16	7.27 ^{e-10} ***
Growing Season Temperature : Total Subplot Species Richness	3.715 ^{e-03}	6.530 ^{e-04}	5.69	1.28 ^{e-08} ***
Week : Total Subplot Species Richness	1.067 ^{e-03}	5.825 ^{e-05}	18.31	< 2 ^{e-16} ***
Week : Growing Season Temperature	-6.778 ^{e-02}	2.285 ^{e-03}	-29.67	< 2 ^{e-16} ***
Elevation : Growing Season Temperature	1.522 ^{e-04}	5.112 ^{e-05}	2.98	0.00291 **
Total species count over entire period (Plot level)				
(Intercept)	-1.804 ^{e+01}	1.138 ^{e+00}	-15.85	< 2 ^{e-16} ***
Week	1.109 ^{e+00}	4.025 ^{e-02}	27.56	< 2 ^{e-16} ***
I(Week^2)	-1.390 ^{e-02}	3.329 ^{e-04}	-41.77	< 2 ^{e-16} ***
Elevation	-2.678 ^{e-03}	5.677 ^{e-04}	-4.72	2.39 ^{e-06} ***
Growing Season Temperature	7.952 ^{e-01}	1.200 ^{e-01}	6.63	3.41 ^{e-11} ***
Total Plot Species Richness	-6.175 ^{e-02}	6.030 ^{e-03}	-10.24	< 2 ^{e-16} ***
Growing Season Temperature : Total Plot Species Richness	4.552 ^{e-03}	6.377 ^{e-04}	7.14	9.39 ^{e-13} ***
Week: Total Plot Species Richness	8.443 ^{e-04}	6.091 ^{e-05}	13.86	< 2 ^{e-16} ***
Week : Growing Season Temperature	-3.456 ^{e-02}	3.384 ^{e-03}	-10.22	< 2 ^{e-16} ***
Elevation : Growing Season Temperature	2.302 ^{e-04}	6.704 ^{e-05}	3.43	0.000597 ***
Total species count per year (Plot level)				
(Intercept)	-3.314 ^{e+01}	1.261 ^{e+00}	-26.29	< 2 ^{e-16} ***
Week	1.761 ^{e+00}	5.031 ^{e-02}	35.01	< 2 ^{e-16} ***
I(Week^2)	-1.760 ^{e-02}	4.129 ^{e-04}	-42.63	< 2 ^{e-16} ***
Elevation	-1.956 ^{e-03}	4.607 ^{e-04}	-4.25	2.17 ^{e-05} ***
Growing Season Temperature	2.359 ^{e+00}	1.275 ^{e-01}	18.51	< 2 ^{e-16} ***
Total Plot Species Richness	-5.885 ^{e-02}	6.007 ^{e-03}	-9.80	< 2 ^{e-16} ***
Elevation : Total Plot Species Richness	3.318 ^{e-05}	6.677 ^{e-06}	4.97	6.71 ^{e-07} ***
Week: Total Plot Species Richness	1.222 ^{e-03}	9.300 ^{e-05}	13.14	< 2 ^{e-16} ***
Week : Growing Season Temperature	-8.313 ^{e-02}	4.309 ^{e-03}	-19.29	< 2 ^{e-16} ***
Week : Elevation	-1.663 ^{e-05}	7.962 ^{e-06}	-2.09	0.0368 *
Historic data				
Total species count over entire period (Plot level)				
(Intercept)	-1.812 ^{e+01}	2.906 ^{e+00}	-6.234	4.53 ^{e-10} ***
Week	7.208 ^{e-01}	1.256 ^{e-01}	5.737	9.62 ^{e-09} ***
I(Week^2)	-1.442 ^{e-02}	1.410 ^{e-03}	-10.222	< 2 ^{e-16} ***
Elevation	7.258 ^{e-03}	1.583 ^{e-03}	4.585	4.54 ^{e-06} ***

Growing Season Temperature	3.111 ^e -01	3.336 ^e -01	0.933	0.3510
Total Plot Species Richness	2.572 ^e -02	1.019 ^e -02	2.524	0.0116 *
Week: Total Plot Species Richness	-1.641 ^e -03	3.252 ^e -04	-5.046	4.52 ^e -07 ***
Week : Elevation	-1.152 ^e -04	2.328 ^e -05	-4.948	7.51 ^e -07 ***
Week : Growing Season Temperature	5.274 ^e -02	1.085 ^e -02	4.861	1.17 ^e -06 ***
Elevation : Growing Season Temperature	-7.658 ^e -04	1.845 ^e -04	-4.151	3.31 ^e -05 ***
Total species count per year (Plot level)				
(Intercept)	-2.924 ^e +01	2.216 ^e +00	-13.199	< 2 ^e -16 ***
Week	1.303 ^e +00	1.038 ^e -01	12.559	< 2 ^e -16 ***
I(Week^2)	-1.906 ^e -02	1.648 ^e -03	-11.567	< 2 ^e -16 ***
Elevation	6.017 ^e -03	1.810 ^e -03	3.324	0.000888 ***
Growing Season Temperature	1.643 ^e +00	1.868 ^e -01	8.795	< 2 ^e -16 ***
Total Plot Species Richness	3.129 ^e -02	1.128 ^e -02	2.774	0.005542 **
Week: Total Plot Species Richness	-1.742 ^e -03	3.742 ^e -04	-4.656	3.22 ^e -06 ***
Week : Elevation	-5.975 ^e -05	2.802 ^e -05	-2.132	0.033007 *
Elevation : Growing Season Temperature	-7.819 ^e -04	2.175 ^e -04	-3.595	0.000324 ***

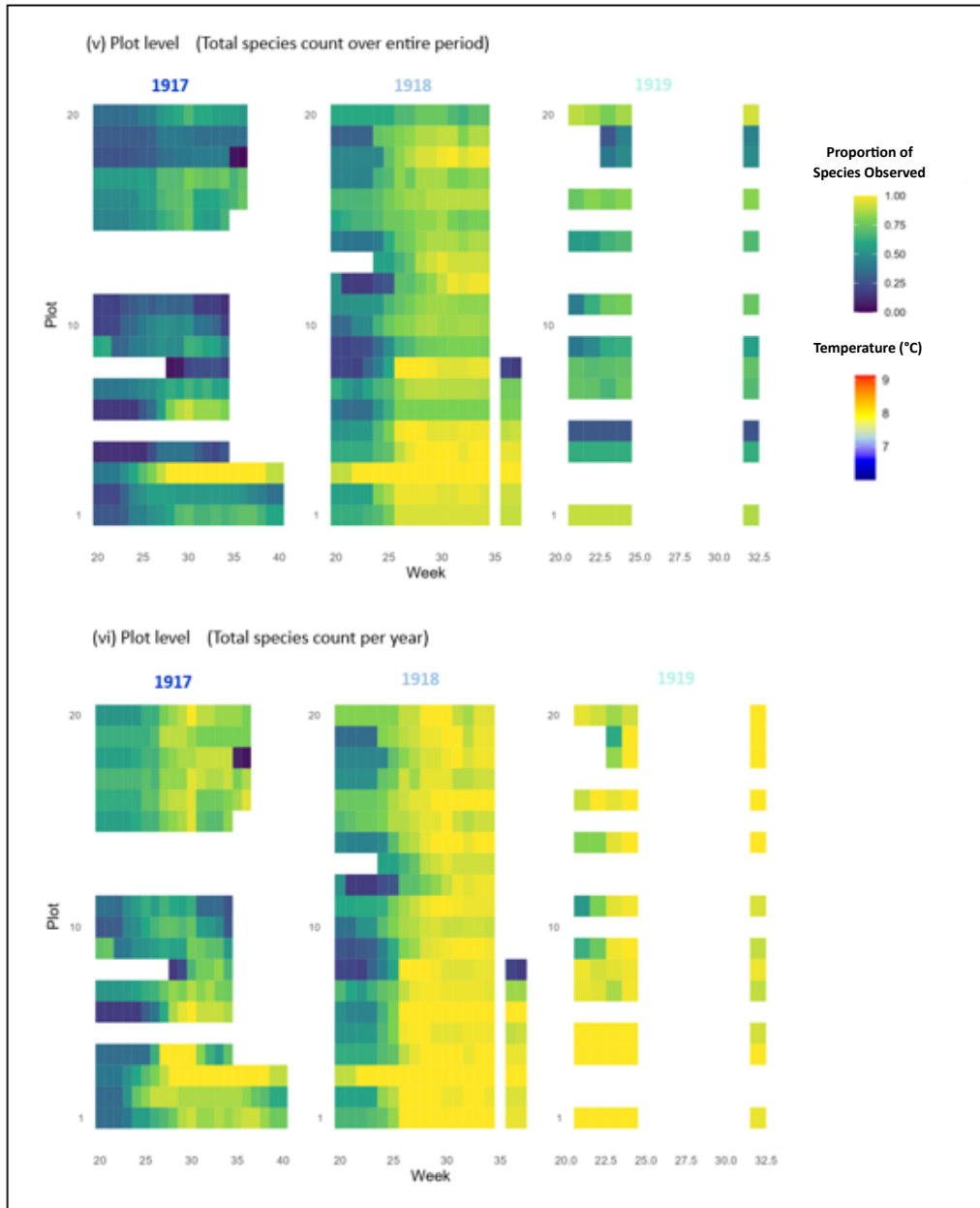
Appendix 6: Heat maps survey efficiency per week per (sub)plot



Appendix 6 (i-ii): Heat Maps of the survey efficiency of the contemporary data (2017-2023), representing the survey efficiency as the proportion of species found per year, per week, per plot. Year gets represented by the mean annual growing season temperature. (i) Plot level (Total species count over entire period); depicts the survey efficiency as the proportion of species observed per year, per week, per plot, relative to the total species count per plot over the entire period of data collection. (ii) Plot level (Total species count per year); depicts the survey efficiency as the proportion of species observed per year, per week, per plot, relative to the total species count per plot per year of data collection.

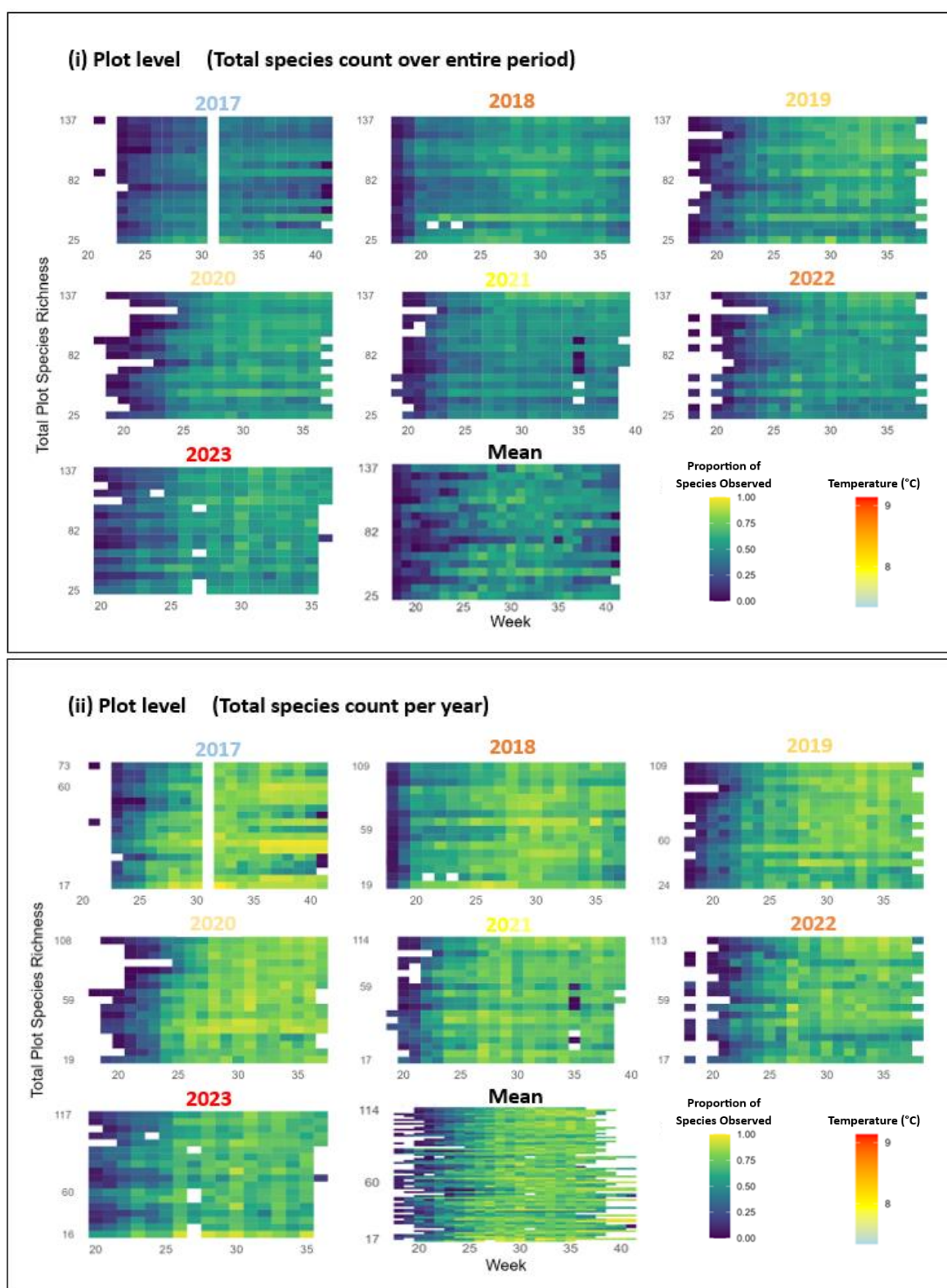


Appendix 6 (iii-iv): Heat Maps of the survey efficiency of the contemporary data (2017-2023), representing the survey efficiency as the proportion of species found per year, per week, per subplot. Year gets represented by the mean annual growing season temperature. (iii) Subplot level (Total species count over entire period); depicts the survey efficiency as the proportion of species observed per year, per week, per subplot, relative to the total species count per subplot over the entire period of data collection. (iv) Subplot level (Total species count per year); depicts the survey efficiency as the proportion of species observed per year, per week, per subplot, relative to the total species count per subplot per year of data collection.

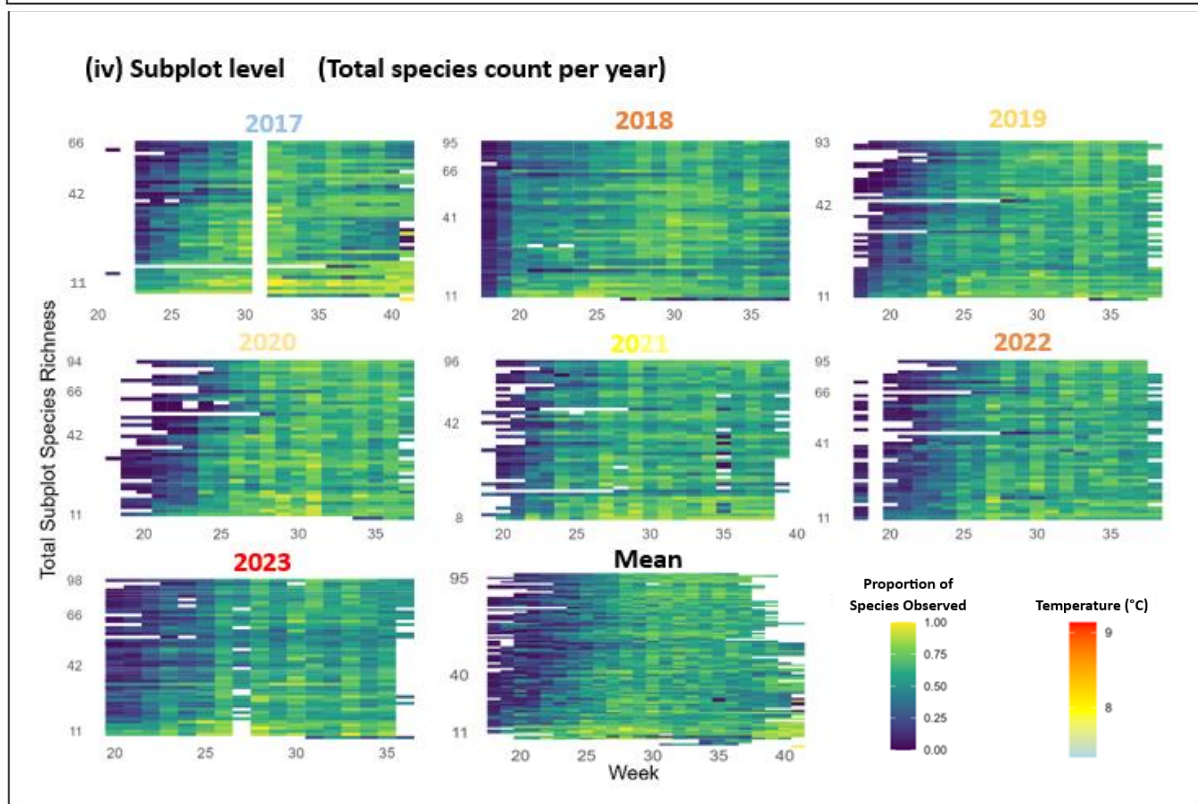
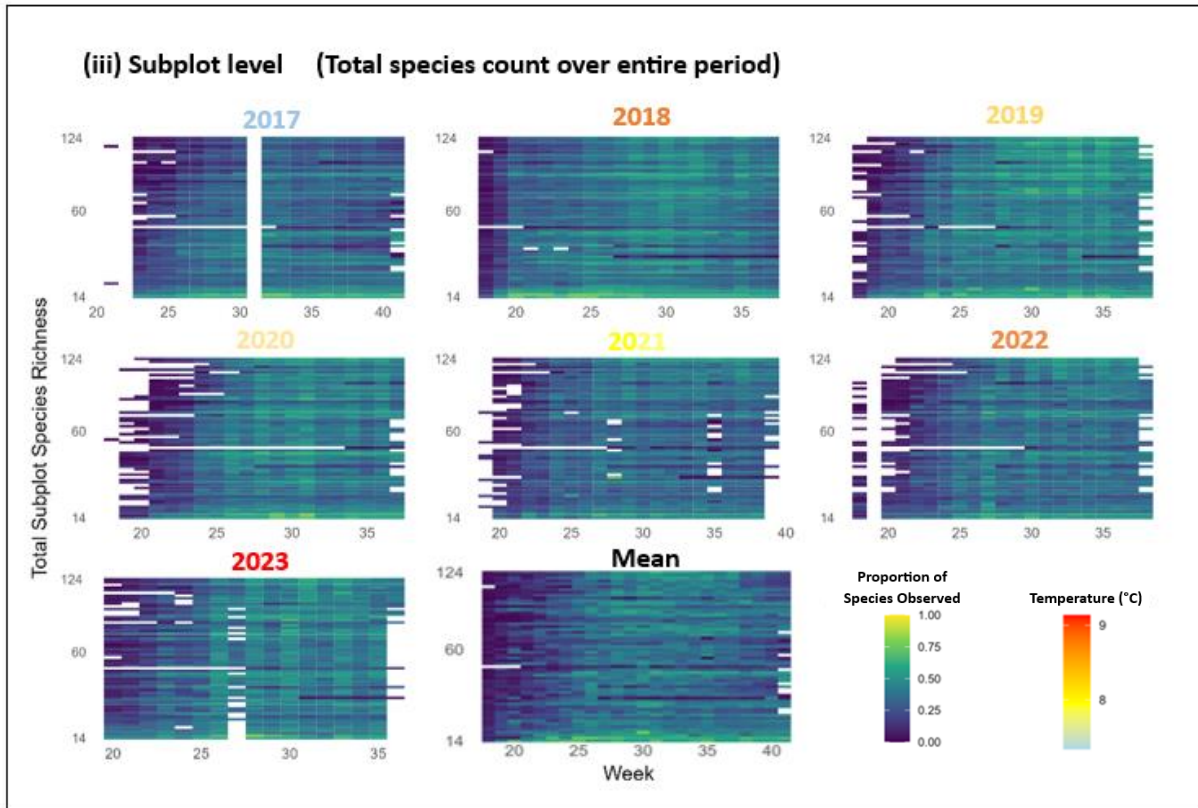


Appendix 6 (v-vi): Heat maps of the historic data (1917-1919), representing the survey efficiency as the proportion of species found per week, per plot. Year gets represented by the mean annual growing season temperature. (v) Plot level (Total species count over entire period); depicts the survey efficiency as the proportion of species observed per year, per week, per plot, relative to the total species count per plot over the entire period of data collection. (vi) Plot level (Total species count per year); depicts the survey efficiency as the proportion of species observed per year, per week, per plot, relative to the total species count per plot per year of data collection.

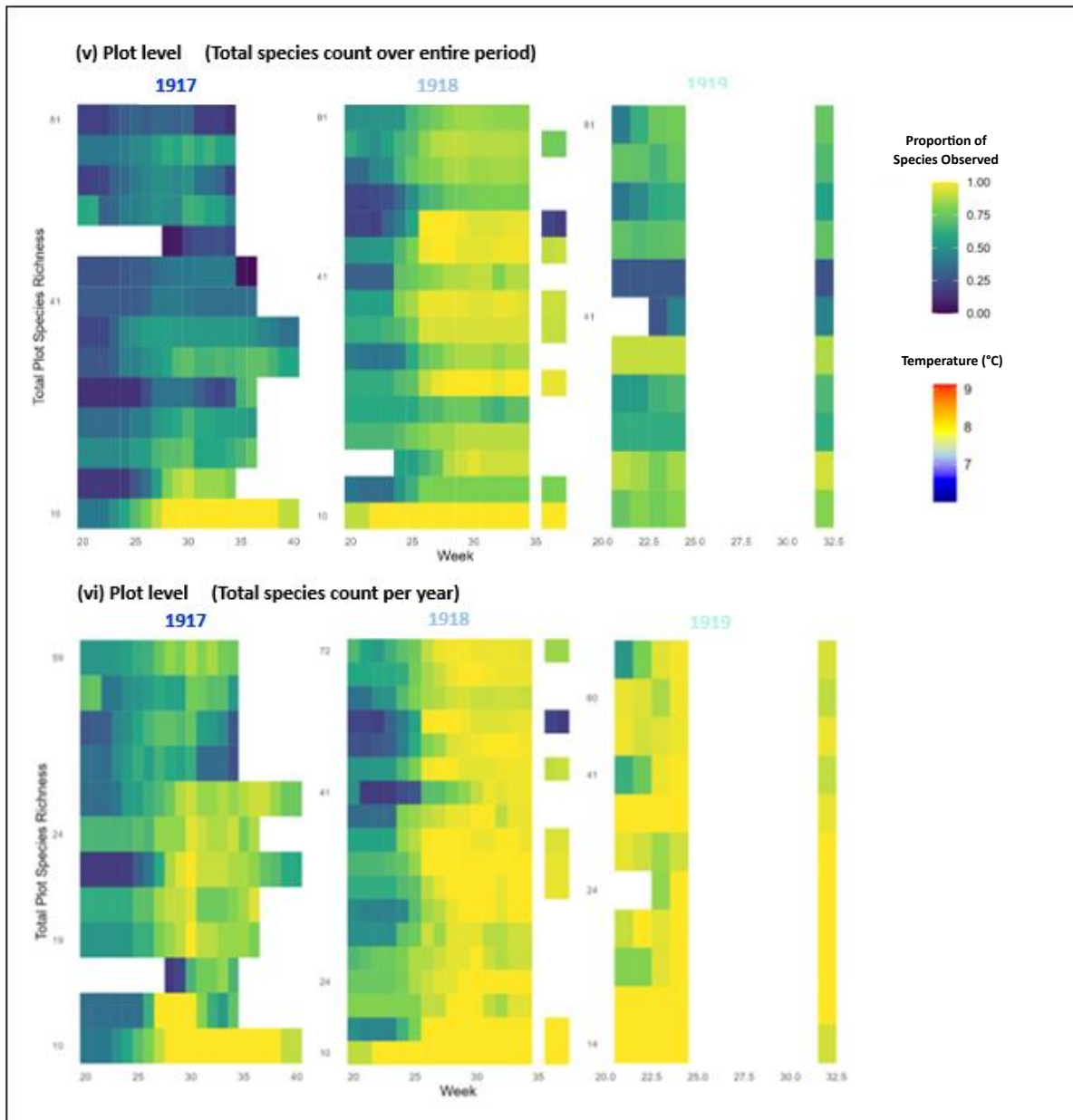
Appendix 7: Heat maps survey efficiency per week per total (sub)plot species richness



Appendix 7 (i-ii): Heat Maps of the survey efficiency of the contemporary data (2017-2023), representing the survey efficiency as the proportion of species found per year, per week, per total plot species richness. Year gets represented by the mean annual growing season temperature. (i) Plot level (Total species count over entire period); depicts the survey efficiency as the proportion of species observed per year, per week, per plot, relative to the total species count per plot over the entire period of data collection. Plot is being represented by its total plot species richness. (ii) Plot level (Total species count per year); depicts the survey efficiency as the proportion of species observed per year, per week, per plot, relative to the total species count per plot per year of data collection. Plot is being represented by its total plot species richness.



Appendix 7 (iii-iv): Heat Maps of the survey efficiency of the contemporary data (2017-2023), representing the survey efficiency as the proportion of species found per year, per week, per total subplot species richness. Year gets represented by the mean annual growing season temperature. (iii) Subplot level (Total species count over entire period); depicts the survey efficiency as the proportion of species observed per year, per week, per subplot, relative to the total species count per subplot over the entire period of data collection. Subplot is being represented by its total subplot species richness. (iv) Subplot level (Total species count per year); depicts the survey efficiency as the proportion of species observed per year, per week, per subplot, relative to the total species count per subplot per year of data collection. Subplot is being represented by its total subplot species richness.



Appendix 7 (v-vi): Heat maps of the historic data (1917-1919), representing the survey efficiency as the proportion of species found per week, per total plot species richness. Year gets represented by the mean annual growing season temperature. (v) Plot level (Total species count over entire period); depicts the survey efficiency as the proportion of species observed per year, per week, per plot, relative to the total species count per plot over the entire period of data collection. Plot is being represented by its total plot species richness. (vi) Plot level (Total species count per year); depicts the survey efficiency as the proportion of species observed per year, per week, per plot, relative to the total species count per plot per year of data collection. Plot is being represented by its total plot species richness.

Appendix 8: Final model Analysis 3

Appendix 8: Final model used to investigate survey efficiency in terms of species-specific observation proportions. A generalized linear mixed model was fitted using `glmmTMB()` and the model was further specified with a beta-regression and the logit link function. VIF was used to detect multicollinearity ($VIF > 5$) and AIC was used to select these final models.

Survey Efficiency	Final model
Species-specific Observation Proportions	<code>glmmTMB(Species_Specific_Observation_Proportion ~ Growing_Season_Temperature + Century + Growth_form + Temperature_Optimum + Growing_Season_Temperature:Temperature_Optimum + (1 Species), data = Observations_and_Traits_per_Species, family = beta_family(link = "logit"))</code>

Appendix 9: Summary results of final model Analysis 3

Appendix 9: Summary() results of the final model (Appendix 8) used to investigate survey efficiency in terms of species-specific observation proportions (Analysis 3).

	Estimate	Std. Error	z value	p-value
(Intercept)	-2.15839	0.56116	-3.846	0.00012 ***
Growing Season Temperature	0.47430	0.07172	6.613	3.77e-11 ***
Century 21st	-2.08103	0.08646	-24.070	< 2e-16 ***
Growthform graminoid	-0.28135	0.14560	-1.932	0.05332 .
Growthform herb	0.04924	0.17662	0.279	0.78041
Growthform shrub	0.53912	0.18383	2.933	0.00336 **
Growthform subshrub	0.70014	0.29136	2.403	0.01626 *
Growthformtree	0.68299	0.39176	1.743	0.08127 .
Temperature optimum	0.19263	0.08051	2.393	0.01673 *
Growing Season Temperature : Temperature optimum	-0.02104	0.00967	-2.176	0.02955 *

Appendix 10: Results of the pairwise comparison of the categorical variables in our final model of Analysis 3

Appendix 10: Results of the pairwise comparison of the estimated marginal means of the variable growth form in our final model (Appendix 8) of analysis 3.

Contrast	Estimate	SE	df	z value	p-value
forb - graminoid	0.2813	0.146	Inf	1.932	0.3822
forb - herb	-0.0492	0.177	Inf	-0.279	0.9998
forb - shrub	-0.5391	0.184	Inf	-2.933	0.0394 *
forb - subshrub	-0.7001	0.291	Inf	-2.403	0.1550
forb - tree	-0.6830	0.392	Inf	-1.743	0.5029
graminoid - herb	-0.3306	0.185	Inf	-1.788	0.4732
graminoid - shrub	-0.8205	0.193	Inf	-4.257	0.0003 ***
graminoid - subshrub	-0.9815	0.297	Inf	-3.304	0.0123 *
graminoid - tree	-0.9643	0.394	Inf	-2.445	0.1409
herb - shrub	-0.4899	0.215	Inf	-2.284	0.2007
herb - subshrub	-0.6509	0.312	Inf	-2.087	0.2941
herb - tree	-0.6337	0.402	Inf	-1.576	0.6142
shrub - subshrub	-0.1610	0.316	Inf	-0.509	0.9959
shrub - tree	-0.1439	0.407	Inf	-0.353	0.9993
subshrub - tree	0.0172	0.466	Inf	0.037	1.0000