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Phenological shifts of herbaceous species
A comparative analysis of different data sets

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Abstract

Climate change affects ecosystems worldwide. Specifically, plants are stationary organisms and are therefore particularly vulnerable to environmental changes. In temperate climate zones, plant phenology is closely linked to annual temperature changes. Plants in these zones, especially, respond to spring warming by advancing their life history development.
Various methods are used in research to explore the impact of climate change on shifts in plant phenology events such as flowering time. For example, herbarium specimens, historical data records, and satellite images are used in different studies and data from these different sources are analyzed together.

However, studies observing the same phenomena of shifts in plant events with different methods and subsequently comparing the results are rare. One aim of the following study is comparing the patterns of various data sets. For this purpose, ground-based phenological data on flowering onset (FO) from the PhenObs project, a collaboration of botanical gardens worldwide and ground-based data on FO from DI Wolfgang Matzke at the gardening school in Vienna are utilized. Additionally, herbarium data from the jointly administered herbarium management system and specimen database (JACQ) are used.

In Chapter I, phenological shifts in the flowering events of 7 species in Vienna over the past 30 years were compared, using ground-based data from gardens and data from herbaria. The observed patterns are then illustrated by data from the corresponding annual average temperatures in Vienna. In Chapter II, the patterns of ground-based garden data of various species concerning FO are compared between a temporally developed temperature gradient and an existing spatial temperature gradient in recent years. Here, the FO of both temperature gradients of 35 different species is modeled in relation to temperature using various statistical models, and afterward, similarities and differences are discussed.

In the present study, no differences between the compared data sets or methodologies were found in either chapter. These findings of both chapters provide that data from different sources can potentially be analyzed together and that „Space-for-time" (SFT) approaches can also be helpful. Additionally, they offer a basis for the idea that herbaria can provide extensive validation of the SFT substitution method and offer further insights for field conditions.

Zusammenfassung

Der Klimawandel wirkt sich weltweit auf Ökosysteme aus. Speziell Pflanzen sind sesshafte Organismen und als solche besonders anfällig für Veränderungen der Umwelt. In der gemäßigten Klimazone ist die Phänologie der Pflanzen eng gekoppelt an die jährliche Temperaturentwicklung. Besonders hier reagieren Pflanzen im Frühjahr mit einer Vorverlegung ihrer lebensgeschichtlichen Entwicklung.

Um zu erforschen, wie der Klimawandel zu Verschiebungen von Pflanzenmerkmalen wie dem Blühzeitpunkt führt, werden in der Forschung unterschiedliche Methoden angewendet. Beispielsweise werden Daten aus Herbarien, historische Datenaufzeichnungen und Satellitenbilder in verschiedenen Studien verwendet und gegebenenfalls auch miteinander verknüpft. Studien, welche dieselben Phänomene von Verschiebungen von Pflanzenmerkmalen mit verschiedenen Methoden beobachten und die Ergebnisse anschließend miteinander vergleichen sind jedoch selten, obwohl diese Erkenntnisse weitreichende Möglichkeiten bieten können. Ein Ziel der folgenden Arbeit besteht darin verschiedene Datensätze miteinander zu vergleichen.

In Kapitel I werden phänologische Verschiebungen der Blühereignisse von 7 Pflanzenarten in Wien über die letzten 30 Jahre untersucht, indem bodenbasierte Beobachtungen aus Gärten mit Daten aus Herbarien verglichen werden. Die auftretenden Muster werden dabei mit den Daten der entsprechenden Jahresdurchschnittstemperaturen in Wien in Beziehung gesetzt. In Kapitel II werden die Muster bodenbasierter Beobachtungen zwischen einem räumlichen und einem zeitlichen Temperaturgradienten in Bezug auf den Blühbeginn miteinander verglichen. Hier wird der Zeitpunkt des Blühbeginns von 35 unterschiedlichen Spezies in Abhängigkeit zur Temperatur zwischen beiden Temperaturgradienten mit verschiedenen statistischen Verfahren modelliert und anschließend in Betracht auf Gemeinsamkeiten und Unterschiede diskutiert.

In der vorliegenden Arbeit konnten in keinem der beiden Kapitel deutliche Unterschiede zwischen den verglichenen Datensätzen bzw. Methodiken festgestellt werden. Diese Erkenntnisse bieten insgesamt eine Grundlage dafür, dass Daten aus unterschiedlichen Quellen gemeinsam analysiert werden können, und "Space-for-time" Ansätze ebenfalls hilfreich sein können. Zudem bieten sie eine Grundlage für die Annahme, dass Herbarien eine umfassende Validierung der SFT-Substitutionsmethode ermöglichen und weitere Erkenntnisse für Feldbedingungen liefern können.

1. General introduction

Lieth (1974) defined phenology as the study of recurring growth and developmental patterns in animals and plants throughout the year. The origins of phenological research can be traced back thousands of years when early societies recognized the value of documenting seasonal phenomena for agricultural purposes. From its beginnings, phenology has evolved into a diverse field, including expanded observations, experiments, and modeling. During the last 30 years, increasing concerns about global climate change have led to clear advancements in phenology monitoring techniques and in modeling approaches (Piao et al., 2019). As noted by Chmielewski et al. (2013) and Templ et al. (2018), the creation of international phenology networks has significantly facilitated standardized data collection and sharing. Additionally, advancements in the development of remote sensing technologies has expanded the geographic scope of phenological studies (White et al., 1997; Zhang et al., 2003). This growth in research has given critical insights into how ecosystems respond to climate change, with observed shifts in phenological events such as advances in spring and postponements in autumn (Gill et al., 2015; König et al., 2018; Menzel et al., 2006; Piao et al., 2006) leading to discrepancies throughout trophic levels (Piao et al., 2019; Renner & Zohner, 2018; Tylianakis et al., 2008). These changes can significantly impact on community structures and ecosystem functions (Suttle et al., 2007; L. H. Yang & Rudolf, 2010). Additionally, warming-induced shifts in phenology contribute to increased vegetation activity and carbon uptake (Piao et al., 2017). Moreover, alterations in plant phenology can influence the climate system by adapting water and energy exchanges in the interplay of terrestrial ecosystems and the atmosphere (Peñuelas et al., 2009; Richardson et al., 2013). Therefore, for modeling ecosystem-climate interactions it is crucial to achieve a better understanding of plant phenological drivers and the ecosystem impacts of phenological changes (Piao et al., 2019).

Herbaceous plants, which remain in a primary state throughout their lifespan due to the absence of secondary thickening (Kadereit et al., 2021), are more efficient at carbon sequestration than woody plants (Deng et al., 2022). However, herbaceous plants have been comparatively less studied (Hassan et al., 2024; Rauschkolb et al., 2024).

1.1 Different methods in data collection and analysis of phenological data sets

Research on phenology has grown rapidly in recent decades, and achieving the highest possible understanding of various drivers and their interplay under field conditions is crucial.

To accomplish this, it is essential to develop diverse methods at various scales which can be interconnected with each other (Piao et al., 2019). The subsequent paragraphs will provide specific descriptions of certain methods and the manner in which they are interconnected.

1.1.1 Ground based observations of plant phenology

Classical studies utilize historical field observations made by botanists from the field and from gardens (Aono & Kazui, 2008; Orlandi et al., 2014). These ground-based observations offer the distinct advantage of precisely identifying specific phenological events and their exact dates for particular species at designated locations (Piao et al., 2019). In recent years, in the burgeoning digital era, new communication technology enables citizen science projects observation, resulting in the gathering of phenological data on a larger scale across many species in diverse areas (Dickinson et al., 2012; Hufkens et al., 2019). Although the observations coming from citizen science especially in fast climate change times are useful, they underlie some limitations (Piao et al., 2019). As the observations primarily focus on congested areas in temperate and subalpine forests, with limited occurrences in grasslands, there are rare observations in subtropical and tropical regions (Richardson et al., 2013). Moreover, as the number of observers increases, the risk of data falsification also rises (Piao et al., 2019), especially if the observers are nonscientific personal (Mayer, 2010). To minimize these limitations, employing a protocol is advisable. This protocol should be strictly adhered in order to reduce interpretation uncertainties (Piao et al., 2019). In addition to citizen science projects, new technologies enable the combination of different herbaria data with large databases to be used in ground-based observations in ecological examinations (Lang et al., 2019).

In the present work ground-based observations in botanical gardens and herbaria were focused. It has to be considered that in gardens, care factors such as soil type, irrigation frequency, weed control, availability of light and shade, and microclimatic conditions are planned, resulting in a more traceable environment compared to field conditions (Rauschkolb et al., 2024; Sporbert et al., 2022). Although this provides a very fruitful approach to additional factors, it may not lead to the final insights desired for the field, where especially the non-stationary environments of the Anthropocene and species communities play a role (Damgaard, 2019).

1.1.2 Remote-sensing-based phenology observations

With the advancement of technology, also remote sensing techniques have additionally emerged, opening new opportunities to examine phenological shifts from above (Piao et al., 2019; Shen et al., 2015). Particularly, satellites were used to find out when plant events occurred

by looking at the profile of greenness of the vegetation over time (Piao et al., 2019; Shen et al., 2015; Zhang et al., 2014). However, the availability of data is weather-dependent, and factors such as sensor shifts (Tucker et al., 2005), BRDF effects (Bidirectional Reflectance Distribution Function), and coarse spatial and temporal resolutions complicate data analysis (Piao et al., 2019). For this reason, another possibility has been increasingly explored in recent years. Sensed solar-induced chlorophyll fluorescence (SIF) were remotely used to study variation in seasonal gross primary production (Meroni et al., 2009; Sun et al., 2017). For instance Sun et al., (2017) describe, how SIF can be used to study the relationship between gross primary productivity (GPP) and SIF, as well as vegetation functional gradients at various spatial and temporal scales. It has to be considered that currently, temporal and spatial resolution of available satellite SIF data is still comparatively weak (Sun et al., 2017), and has to be upgraded for a higher quality of examinations (Piao et al., 2019).

As well as satellite-derived vegetation greenness indices and SIF, ground-based remote sensing has also seen a surge in popularity over the previous decade (Piao et al., 2019). This method involves using commercial network cameras to collect images at frequent intervals (ranging from half to one hour) (Nasahara & Nagai, 2015). Such data collection has successfully been used in phenology studies. Camera-based observation networks for phenology have been established in the United States, Japan, and Europe, with similar initiatives underway in China (Nasahara & Nagai, 2015; Peichl et al., 2015; Piao et al., 2019; Richardson et al., 2018). Like the other, already described methods, also this method is subject to limitations such as complex, error-prone calibration procedures and the need for careful interpretation of various phenological events (Piao et al., 2019; Wingate et al., 2015). Utilizing unmanned aerial vehicles equipped with spectroradiometers could potentially address the limitations of phenology cameras (Klosterman et al., 2018). This approach offers the advantage of providing multispectral or hyperspectral images, allowing a direct spatial connection between field and satellite observations (Klosterman et al., 2018). Furthermore, automating unmanned aerial vehicles (UAV) sensing could maximize temporal resolution, particularly during spring and autumn, enhancing the accuracy of plant phenology monitoring (Klosterman et al., 2018).

1.1.3 Multi-source data fusion

Remote sensing has greatly improved the ability to study plant phenological events and their relationship with climate and the environment (Piao et al., 2019). However, satellite datas' coarse resolution can lead to biases, in the detection of phenological events, especially in heterogeneous areas (Zhang et al., 2014). Combining different spatiotemporal data sets can help overcome these limitations (see Figure 1) (Piao et al., 2019). Up to 2018, 60 spatiotemporal

data fusion models have been developed (Feng Gao et al., 2006; Piao et al., 2019; Zhu et al., 2018), including the spatial and temporal adaptive reflectance fusion models (STARFM) (Feng Gao et al., 2006) and the enhanced STARFM (ESTARFM) (Zhu et al., 2010) which have become common for phenology monitoring due to their simplicity and effectiveness. Studies utilizing images of fused satellites have achieved satisfactory estimations of phenology, as the time series derived from fused images effectively characterize seasonal plant activity and exhibit strong correlation with field observations (J. J. Walker et al., 2014). The combination of spatiotemporal data fusion techniques, alongside multi-scale phenological observations (as illustrated in Figure 1), promises to offer unparalleled opportunities for validating satellite retrievals of plant phenology, particularly on diverse land surfaces (Piao et al., 2019).

1.1.4 Manipulative experiments of plant phenological development to climate change

Observations made on the ground and through remote sensing deliver direct evidence of how plant phenology varies across different spaces and changes over time (Piao et al., 2019). However, plant phenology is influenced by various environmental factors, which are often interconnected (Kadereit et al., 2021; Richardson et al., 2018). Therefore, relying solely on observations of phenology makes it challenging to untangle the effects of these different factors and understand the underlying mechanisms driving observed patterns and changes (Piao et al., 2019). Variegated manipulative experiments have proven to be invaluable in gaining a mechanistic understanding of plant phenology (Dorji et al., 2013; Piao et al., 2019; M. D. Walker et al., 2006). These experiments generally generate similar conclusions to observational studies, emphasizing for instance, the significant impact of warming on spring leaf emergence (Arft et al., 1999; De Frenne et al., 2010). While manipulative experiments improve the understanding of important drivers, they also have limitations, such as their short-term examinations, focus on specific species, and significant differences from natural conditions (Leuzinger et al., 2011; Piao et al., 2019; Wolkovich et al., 2014; Zavaleta et al., 2003). Nevertheless, these are controlled environments that are ideal for testing hypotheses and advancing our knowledge of how plant phenology reacts to climate change. This understanding is crucial for accurately predicting changes in phenology and ecosystem dynamics (Piao et al., 2019).

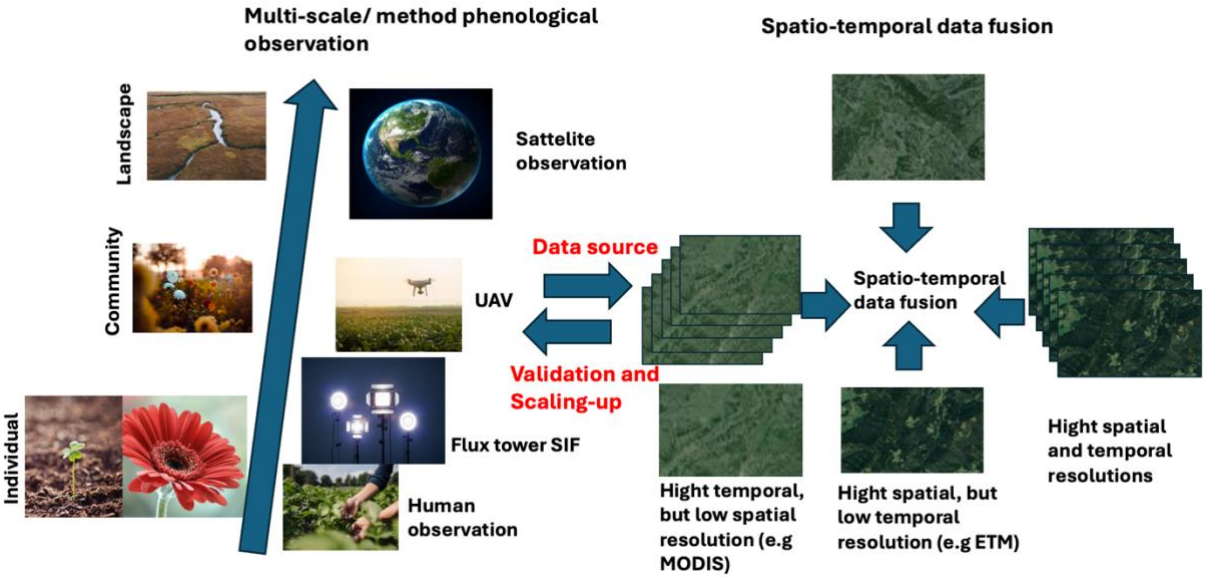

Figure 1 The map illustrates the process of observing, validating, and expanding plant phenological data. It showcases the validation of satellite-derived phenology information and the expansion of ground-based data and near-surface phenological observations through the integration of various scales and methods, along with spatial-temporal data fusion techniques. (Piao et al., 2019, S. 1926, modified by the author)

1.1.5 Phenology modeling approaches

Phenology models are vital tools in phenology research, aiming to understand how plant phenology responds to future climate changes (Cleland et al., 2007; Q. Liu et al., 2019). They allow the integration of phenology into advanced earth system models to study carbon and water cycles, as well as energy fluxes on regional to global scales (Krinner et al., 2005). Additionally they predict changes in species distributions in a shifting world (Chuine et al., 2010). However, previous modeling efforts have primarily focused on spring phenological events, with relatively less attention given to autumn phenology (Piao et al., 2019).

Early models, relying on statistical methods like "degree-days", assume that an event occurs when a specific accumulation of heat units is accomplished (Reaumur, 1735). These models are potentially biased when projecting future changes due to anticipated warming trends, as they probably exceed temperature ranges from the past (Piao et al., 2019). To address this, the Space-for-Time (SFT) substitution method assumes that changes in space can approximate changes in time (Damgaard, 2019), enabling predictions of plant reactions to higher temperatures in the future compared to those in the past. For more information on this method, please refer to the Introduction of Chapter II. Furthermore, additional models have been developed to address this issue, which can be categorized into two types: one-phase models, including the ForcTT, ForcSar, and UniForc models (Chuine, 2000; Chuine et al., 1999), and two-phase models that consider the developmental stages preceding the specific phenological event (Lang, 1987), such as the Sequential, Parallel, and Unified models (Chuine,

2000; Hänninen, 2016; Landsberg, 1974). While two-phase models propose that both chilling and warming phases are necessary for plant annual development, evidence conclusively supporting their superiority over one-phase models remains scarce (Q. Liu et al., 2018). Despite advancements, current models still exhibit shortcomings, particularly in large-scale studies, where factors beyond temperature, such as light and water availability, are insufficiently incorporated (Piao et al., 2019). Autumn phenology modeling presents additional challenges owing to the rare examination of underlying processes (Richardson et al., 2012). Models typically rely on specific temperature, photoperiodic thresholds or cooling degree-days (White et al., 1997), which are similar to the concept of “degree-days” (Delpierre et al., 2009). However, these models often suffer from limited spatial coverage and significant errors. Despite recent progress, several critical issues persist. These include the need for a better understanding of the mechanisms governing phenological events and the challenge of scaling up models from local to regional scales. Furthermore, models based solely on "degree-days" struggle to accurately predict phenology dates under extreme climate conditions due to temporal temperature variations (Piao et al., 2019).

1.2 Plant Phenology

It's crucial to understand the drivers and mechanisms behind recent shifts in plant phenology to anticipate future changes and their effects on ecosystems. The timing of these events hinges on a mix of biological and environmental factors. However, the degree to which these factors affect plant phenology varies greatly depending on the developmental stages of the events and the unique life history strategies of different plant species (Piao et al., 2019).

1.2.1 Drivers and influences

Phenological events such as initial growth, young leaves unfolding, first flowering, peak flowering and senescence (Nordt et al., 2021) result directly from a complex interplay of genetics and site factors which include climate, topography, soil, and biotic influences from other organisms (Kadereit et al., 2021). Additionally, external environmental factors which are immediately effective and highly variable in the short-term. These external environmental factors include temperature, moisture, light conditions, mechanical and biological disturbances as well as chemical factors such as CO_2 concentration, nutrient availability, trace elements and pH values (Forrest & Miller-Rushing, 2010; Kadereit et al., 2021). Temperature is commonly considered the primary regulator of plant phenology (Piao et al., 2019; Rauschkolb et al., 2024). It affects the development of organisms, and the speed of biochemical processes which accelerates development to a certain optimum (Forrest & Miller-Rushing, 2010; Gillooly et al.,

2002; Kadereit et al., 2021). Besides temperature, the photoperiod also plays a critical role on plant phenology, especially influencing leaf senescence during autumn (Cook et al., 2012). Moreover, water availability is often cited as the third most important factor (König et al., 2018; Piao et al., 2019). The impact of precipitation on plant phenology can be understood through its indirect effects on the thermal requirements ("degree-days", or "cooling degree-days" (White et al., 1997)) for spring as well as autumn phenological events (Fu et al., 2014; Hänninen, 2016). It could also be linked to the interaction between nutrient availability and soil moisture content (Estiarte & Peñuelas, 2015).

In addition to those site factors, biotic influences from other organisms within ecosystems, such as changes in fitness and species interactions, also play a role in regulating plant phenological processes (Doi et al., 2010; Piao et al., 2019). For instance, the earlier flowering day of plants in response to climate change might also be connected to plants' strategies for evading heightened insect feeding during summer, driven by boosted growth and reproduction in warmer years (Bale et al., 2002; Kawagoe & Kudoh, 2010). However, this ecological interactions and adaptations have not been sufficiently studied (Kehrberger & Holzschuh, 2019; Matesanz & Ramírez-Valiente, 2019; Piao et al., 2019; Senior et al., 2020).

Due to the fact that herbaceous plants make up the majority of vegetation in many ecosystems and they have an impact on climate change, research was increasingly focused on examining herbaceous plant phenology (Deng et al., 2022). In this context new evidence shows that the relatedness of species and the life history strategies which are indicated by functional traits such as height and specific leaf area, are closely related with the phenological development of herbaceous plants (König et al., 2018; Rauschkolb et al., 2024; Sporbert et al., 2022). For example, Sporbert et al. (2022) demonstrated that taller plants exhibited delays in initial growth, flowering, fruiting and leaf senescence. Furthermore, Bruelheide et al. (2018) showed that functional trait compositions are especially more connected to external factors such as fine-scale soil conditions, disturbance, niche partitioning and biotic interactions than to macro-environmental drivers. As a result, it could mean that these fine-scale factors, together with consideration of functional traits, have also high impact on phenological stages.

As can be seen from the cited articles, phenological research has made significant progress in recent years. To further deepen our understanding of the impacts of ongoing temperature rise on our ecosystems, it is necessary to identify further insights into the complex interactions among the drivers and increasingly integrate these into phenological models (Piao et al., 2019).

1.2.2 Herbaceous plant flowering

It is clear that the flowering process is complex and largely determined by the plant species and their life history strategy, which stimuli trigger flowering (Campbell et al., 2016). Plant phenology is primarily influenced by temperature variability, resulting for many species to earlier flowering times in warm years (Chuine et al., 2010; Cleland et al., 2007; Peñuelas et al., 2009; Rauschkolb et al., 2024). However, flowering effects can also depend on cool temperatures (see also "cooling degree-dates" under "1.1.5 Phenology modeling approaches"). Plants often rely on cool temperatures, therefore warm temperatures can delay phenological development (Forrest & Miller-Rushing, 2010; Suonan et al., 2018). This requirement, applied to flowering, is known as vernalization (Greenup et al., 2010; Kadereit et al., 2021; Senior et al., 2020). König et al. (2018) summarized, based on data from various studies, that among 562 examined species 80.4% exhibited an advancement in the first flowering day with a higher temperature, while the remaining 19.6% experienced delays. Additionally they found that the intensity of the advancement is significantly more pronounced in trees and shrubs than in herbs and grasses (König et al., 2018).

The optimal timing in flowering is crucial for plants fitness (Austen et al., 2017). It is influenced by environmental conditions experienced during pollen, ovule, seed development (Rathcke & Lacey, 1985) as well as interactions with mutualists (for e.g. pollinators, Kehrberger & Holzschuh, 2019; Rafferty & Ives, 2011) and antagonists (for e.g. seed predators, Augspurger, 1981; Parachnowitsch & Caruso, 2008). For instance, synchronized temporal shifts of early plant species and pollinators were observed under global rising temperatures (Kehrberger & Holzschuh, 2019). Thus, it appears that less interspecific competition for pollinators to be one of the main factors for early flowering (Kehrberger & Holzschuh, 2019; Mosquin, 1971). Nevertheless, it remains unclear how this trade-off evolves throughout the season and how timing affects reproductive success and the plant fitness (Kehrberger & Holzschuh, 2019).

1.3 Resource focus

Based on the importance of accurate phenological data for understanding plant responses to environmental change and the potential benefits of integrating different data sets, it is crucial to validate different methods. Our core hypothesis is that the combination of these data sets is advantageous for certain phenological questions. To test this, we focus data sets of ground-based worldwide botanical garden observation data and herbarium data from Vienna. We hypothesized that the phenological analysis of plant flowering show the same pattern and

no significant differences under similar conditions. The comparison of various data sets is conducted in two chapters:

1) Chapter I: Comparison of plant flowering between herbaria data and ground-based garden data in Vienna.
2) Chapter II: Ground-based garden data collected on a spatial temperature gradient from different botanical gardens with ground-based garden data on a temporal temperature gradient in Vienna.

2. Chapter I: A comparative analysis of herbarium data with ground-based observation data from gardens

2.1 Introduction

Since 1945, human influences have led to increased temperatures and consequently to a change in the functioning of the Earth system (Hamilton, 2016). As plants are sessile, they are exposed to these changes without simple possibilities to change the location (Mittler et al., 2012). Therefore, plant species in the temperate vegetation zone of the earth frequently react with phenological shifts (Pau et al., 2011).

Herbaria are seen by the scientific community as windows into the past (Meineke et al., 2018; Primack & Miller-Rushing, 2009; Vellend et al., 2013). Digitization of herbarium collections enhances accessibility, enabling the compilation of large cross-species data sets for phylogenetic analyses and understanding evolutionary processes (Rafferty & Nabity, 2017). Herbaria provide insights into climate-related plant responses as well as their impacts on herbivores, pollinators, and nutrient cycling, capturing geographic variations across the globe (Hart et al., 2014; Panchen & Gorelick, 2017). For example, Lee et al., (2022) used herbarium specimens to demonstrate that the phenological sensitivity to spring temperatures remains remarkably conserved for understory plants across North America, Europe, and Asia.

Although the use of herbaria is a recognized practice, it must be considered that data from herbaria underly some certain limitations. For instance, imbalanced sampling presents a challenge for tasks such as species distribution mapping or diversity assessment (Daru et al., 2018; Meyer et al., 2016) and temporal biases emerge from seasonal preferences and variable concentrated collection periods (Holmes et al., 2016). Furthermore, collections often prioritize easily accessible or frequently visited sites, as well as common or intriguing species, leading to geographic and taxonomic biases (Feeley, 2012; Sofaer & Jarnevich, 2017). Addressing those biases explicitly is crucial when working with herbarium data to avoid skewed trends (Jácome et al., 2007). To correct the data from biases, different methods are possible. For instance, assessing the spread of invasive species in relation to native species (Delisle et al., 2003), collection efforts across diverse reference sets (Case et al., 2007; Hedenäs et al., 2002), or validating trends with further data sets (Kouwenberg et al., 2003; Lienert et al., 2002; Ramirez-Parada et al., 2022), for instance even those of citizen science (Lang et al., 2019; Spellman & Mulder, 2016).

In Vienna, ground-based observations in herbaceous plant phenology are increasingly based on data from botanical gardens in recent years (e.g. iDiv (German Center for integrative Biodiversity Research) under the following Link https://www.idiv.de/de/web/phenobs.html) as well as other ground-based records from the past in Vienna (e.g. Büntgen et al., (2022); Fitter & Fitter, (2002); GeoSphere Austria under https://www.phenowatch.at/ueber-phaenologie/phaenologie-in-oesterreich; Horticultural School in Vienna). Some limitations of garden observation can be found under 1.1.1 Ground based observations of plant phenology.

Despite general recognition of both method limitations, validation of herbarium-based approximations of phenological sensitivity against approximations obtained using ground-based observations is still rare and limited in scope (Ramirez-Parada et al., 2022). For example, in a large-scale validation of herbarium data compared to field data regarding the "peak of flowering", Ramirez-Parada et al. (2022) demonstrated the reliability of sensitivity approximations for a variety of plant species. In order to test the compatibility of herbarium data with data from ground-based garden observations in Vienna, a comparison of two data sets was conducted. We hypothesized that both views in the past, with data sets from herbaria and ground-based observations, show the same pattern in regard of temperature sensitive shifts.

2.2 Materials and methods

Data set

Data from 1988 to 2010 and 2011 to 2023 from the herbarium and ground-based data from gardens were used for the calculation. The data source regarding the onset of flowering under garden conditions was collected from the botanical garden in Vienna, according to the protocol of Nordt et al., (2021), and at the horticultural school in Vienna by DI Wolfgang Matzke, according the description of Appendix 1. Species present in both of those garden data sets were then taken from the “jointly administered herbarium management system and specimen database” (JACQ). The JACQ includes 43 different herbaria worldwide and accessible via the link https://www.jacq.org/. In the database, filtering was done for Lower Austria and Vienna as locality, and then the collection year, the flowering day (see flowering day data), and the precise coordinates of the collection site were extracted. Herbarium specimens with non-exact collection dates and no precise location information were not included in the data set. If only one location was provided, without exact coordinates, these were subsequently approximated using Google Maps. Thereafter the data in the data set were limited to those collected within a 20 km radius of the botanical garden Vienna (Coordinates: 16.38402, 48.19233).

Only the species that had at least one data point in each data source for each time interval (see temperature data and distribution in time intervals) were retained. The remaining data sets

were filtered for each species and data source by applying a variance threshold of <900. This threshold is based on the proposed rule by Schaber & Badeck, (2002), which is based on a tolerance of +/- 30 days and provides a robust method for identifying outliers. The data from both sources (garden and herbarium) were adjusted so that both filtered data sets contain the same species. Overall, the data set contains 125 data points, of which 54 come from herbaria and 71 from gardens. Herbaria include 26 data points from the interval [1988-2010] and 28 from [2011-2023], while gardens provide 41 data points from the interval [1988-2010] and 30 from [2011-2023]. A detailed list of species used for the analysis can be found in Table 1.

Table 1 provides an overview of the species used in the analysis, their family affiliations, and the number of data points within the intervals [1988-2010] and [2011-2023] from herbarium specimens, as well as the number of data points for the intervals [1988-2010] and [2011-2023] from gardens.

Species	**Family**	**Datapoints per interval in herbaria [1988-2010] / [2011-2023]**	**Datapoints per interval in gardens [1988-2010] / [2011-2023]**
Anemone nemorosa	Ranunculaceae	4/1	7/3
Brunnera macrophylla	Boraginaceae	2/4	7/5
Convallaria majalis	Asparagaceae	6/1	7/2
Lathyrus vernus	Fabaceae	4/3	5/5
Muscari neglectum	Asparagaceae	7/8	6/5
Scilla siberica	Asparagaceae	2/2	6/5
Trollius europaeus	Ranunculaceae	1/9	3/5

Flowering day data

For the gardening school, only the flowering onset (FO) was clearly marked, hence the onset of flowering was used for analysis in the data set sourced from garden conditions. In contrast, only the day of the year (DOY) for flowering, labeled as the "flowering day," can be extracted from the JACQ database since herbarium specimens only indicate whether a species is in bloom or not.

Temperature data and distribution in time intervals

To determine a meaningful temperature trend in Vienna, temperature data from the Vienna monitoring station "Hohe Warte" were utilized, which are available at the link https://dataset.api.hub.geosphere.at/app/frontend/station/historical/klima-v1-1m. The "air temperature 2m monthly mean of observation dates" was extracted, from which the annual average temperature was subsequently calculated. Monthly average temperatures missing at the time of collection from the year 2023 were replaced with values from the previous year. After 2010, we noticed a change in the trend in the data, as there were no annual average temperatures close to the trend line (see Figure 2). The distribution of the data structure within the intervals

is shown in Figure 3. After 2013, the distance to the trend line is already significantly greater and as a result could also a possible temperature effect be greater. Therefore, we calculated the analyses also here. The results are available in Appendix 2.

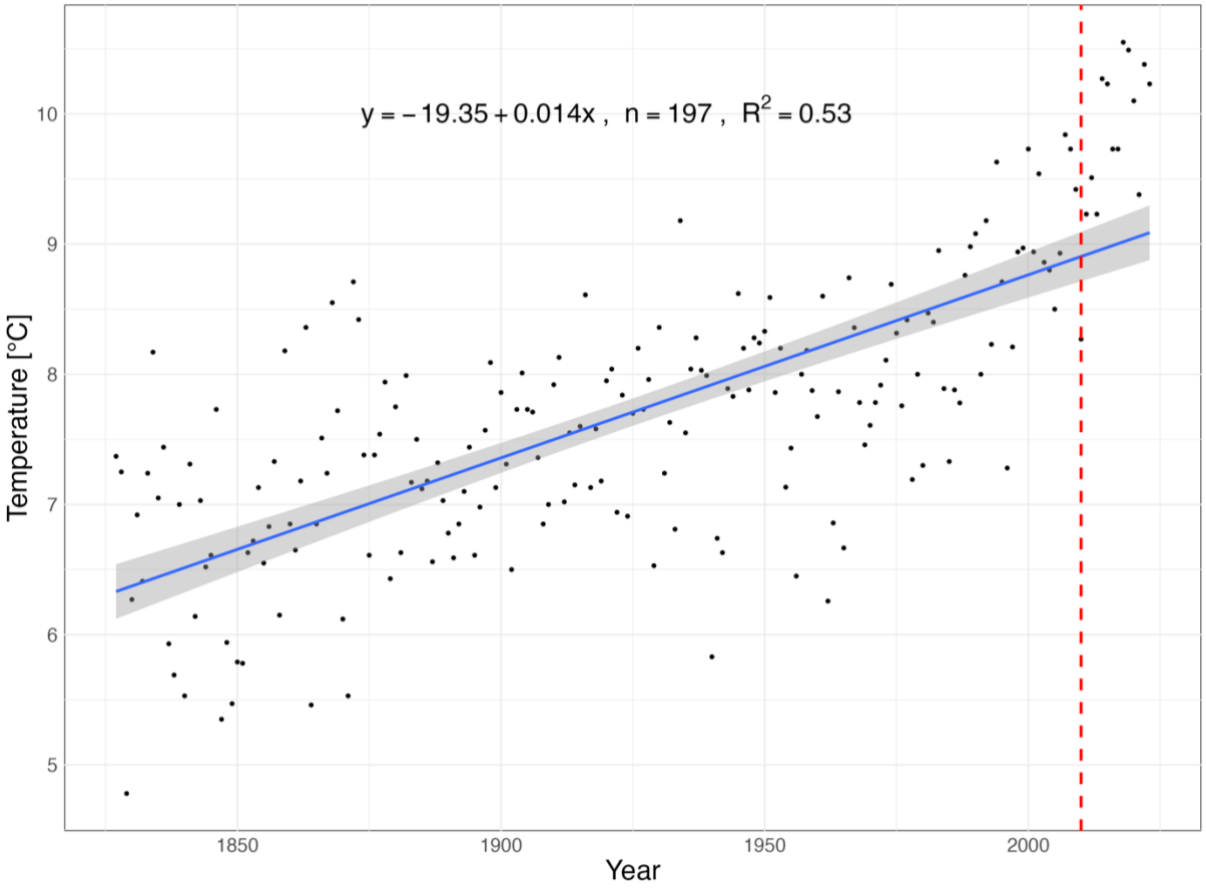

Figure 2 illustrates the trend in annual mean temperature since 1827 at the "Hohe Warte" weather station in Vienna. The dashed line indicates the separation between intervals at the year 2010.

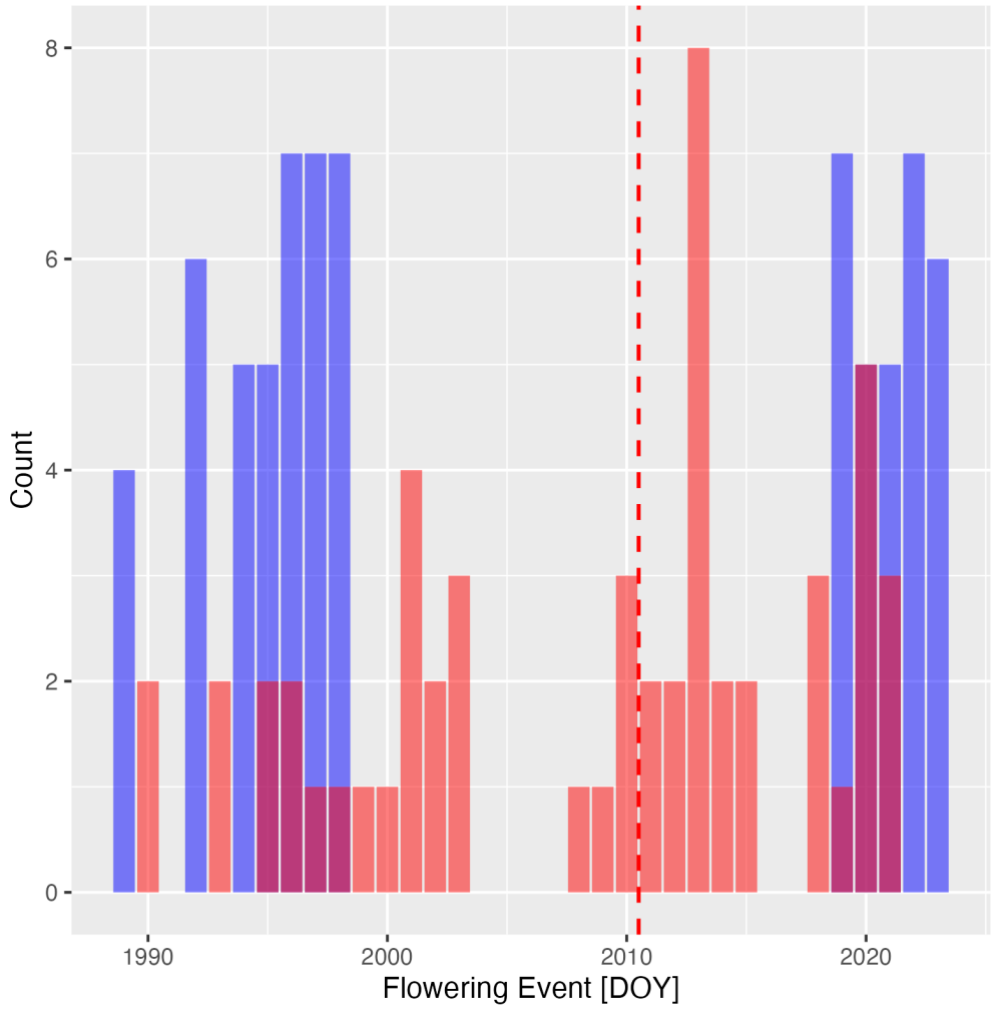

Figure 3 illustrates the distribution of herbarium data (blue) and data from gardens (red) over the years. The dashed line indicates the interval boundary. There are no data available from gardens between 2000 and 2018, whereas herbarium data are more evenly distributed.

Data analysis

The analyses were conducted using the R Studio program (version 2023.3.1.446). A linear mixed-effects model (LME model) from the "lmerTest" package was utilized for the analysis, distinguishing between fixed factors (interval, data source) and their interaction, as well as random factors (constant intercept, species membership) when estimating the regression coefficients. This approach was used to test whether the influence on the day of flowering differs between the intervals [1988-2010] and [2011-2023]. To make the absolute advancement of the flowering days comparable with the corresponding distribution in both methods, it was estimated using the “emmeans” package within the LME. Furthermore, the linear effect model was used to test if there are differences between the data sources herbarium and ground-based garden observations. The Conditional R^2 was calculated to assess the model's goodness of fit, while the Marginal R^2 was additionally computed to determine the proportion of explained

variance attributable to the fixed effects. Furthermore, the interclass correlation coefficient (ICC) was calculated to determine the proportion of variance explained by the species-membership in the sample.

2.3 Results

The analysis of the linear mixed model (LME) involving 7 species from both data sources did show a highly significant influence of the data source (LME: $F_{1,115} = 36.058$, $p < 0.000$). The conditional R^2 indicating that the linear mixed model explains 60.1% of the variance (LME: $cR^2 = 0.601$). The fixed effects account for 13.8% of this variance, as indicated by the marginal R^2 (LME: $mR^2 = 0.138$), likely attributable to the data source and the varying flowering events. Almost half of the random variation in flowering events is attributed to differences between species (LME: ICC = 0.537). The remainder occurs within species, reflecting the differences in flowering events.

The advancement of flowering time across both data sources shows a significant result (LME: $F_{1,116} = 6.623$, $p = 0.011$). Furthermore, there are no significant results regarding the advancement of flowering time in herbaria or the FO in ground-based gardens. However, there was found in both data sources and flowering events a homogeneous advancement. The estimate average day of FO from ground-based garden observations for the interval [1988-2010] was DOY 101.6 (SE: 7.58, df: 7.17), with an adjusted 95% confidence interval ranging from DOY 83.8 to 119. For the interval [2011- 2023], it was on DOY 93.9 (SE: 7.76, df: 7.87), with an adjusted 95% confidence interval ranging from DOY 76.0 to 112. The span of the confidence intervals is nearly the same in both intervals ([1988-2010]: 35.2, [2011-2023]: 36.0). In the herbarium data, the estimate average flowering event for the interval [1988-2010] was on the DOY 121.9 (SE: 7.89, df: 8.40), with an adjusted 95% confidence interval ranging from DOY 103.9 to 140, and for the interval [2011-2023] it was on the DOY 112.3 (SE: 7.89, df: 8.37), with an adjusted 95% confidence interval ranging from DOY 94.3 to 130. The adjusted confidence intervals for both intervals are almost the same ([1988-2010]: 36.1, [2011-2023]: 35.7). A comparison of both data sources therefore shows the homogeneous advancement in both data sources. Visualization of the similar results pattern of both data source is presented in Figure 4.

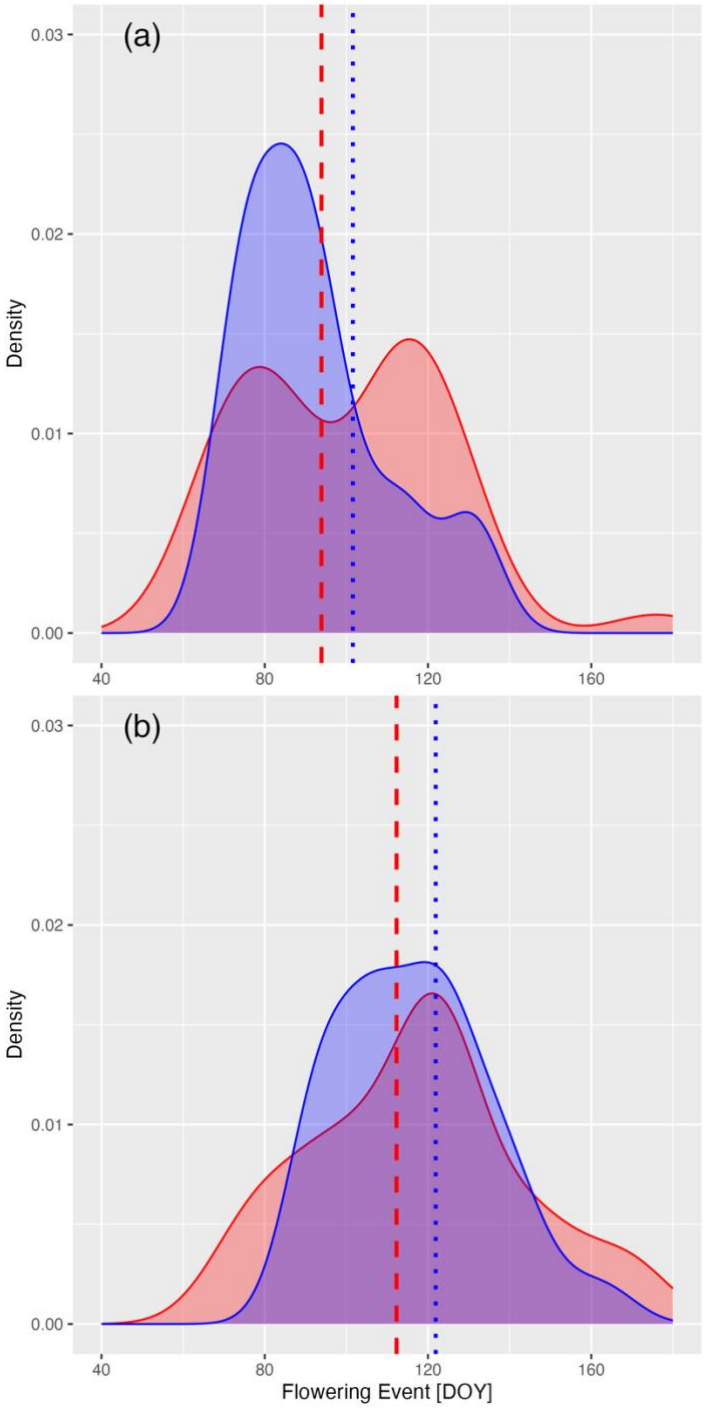

Figure 4 shows the (a) distribution of annual FO in gardens and (b) distribution of flowering events in herbarium specimens. The time intervals (red) [1989-2010] and (blue) [2011-2023] are color-coded. The dashed line (red) corresponds to the estimated average FO/flowering event from the linear mixed model for the [1989-2010] interval, and the dotted line (blue) for the [2011-2023] interval. The difference between the estimated average FO/flowering event for the two intervals is in (a) 7.5 days and in (b) 9.7 days.

2.4 Discussion

It is not surprising that the flowering time in herbaria is on average later due to the different flowering events (onset of flowering in the gardens vs. flowering time in herbarium data). As a result, a significant difference between data sources of herbarium and data of ground-based garden was found. Observing the flowering day of a species can be particularly associated with the peak of flowering, especially in short-flowering species. This is often used, although there is no way to verify this (Panchen et al., 2012). Since the correlation between the peak of flowering and FO, according to Sporbert et al. (2022) is very high at 0.923, it can be assumed as a prerequisite for our study that the different phenological stages do not affect the observed patterns.

Combining both data sources enhanced the statistical power of our study, as demonstrated by the significant shift observed only when the combined data set was analyzed. This is likely due to the small sample sizes within the individual data sets. Therefore, the importance of combining data to amplify statistical power for specific research questions was emphasized. Additionally, both data sources exhibit very homogeneous patterns in their distributions. For example, an advancement of 7.7 days in the FO was identified in gardens, and a shift of 9.7 days in flowering events was observed in herbarium specimens. This is consistent with other studies, such as those of Menzel et al., (2006), which describe a shift of 2.5 days per decade in spring/summer phenology since the 1970s. Additionally, the dispersion values show little difference between both data sources. This supports our assumption that the patterns between herbarium specimens and gardens are highly similar and that herbarium data, as suggested by Lang et al. (2019), are well fitting for studying phenological changes worldwide as well as botanical gardens (Primack & Miller-Rushing, 2009). Therefore, it suggests that both data sources exhibit high validity and can be used together to examine past phenological shifts. We suggest that future studies examining the timing of flowering or similar resource questions can use herbaria and ground-based observations together to create larger data sets.

It must be mentioned that the found patterns possibly arose because two different influencing factors balanced each other out. First, drought periods have significantly increased in recent years (Intergovernmental Panel On Climate Change (Ipcc), 2023) which likely contributed to a slightly greater advancement in FO of herbaceous species in herbarium than in garden specimens (Rauschkolb et al., 2022). In non-garden habitats where herbarium species were collected, the impact may be greater than in gardens, as droughts in gardens were largely offset by additional watering.

And second, the average annual temperatures recorded during data collection did not meet the same requirements. FO in gardens was exclusively recorded before 2000 or after 2019 (see Figure 3). Therefore, more frequent higher average annual temperatures in the [2011-2023] interval and more frequent lower average annual temperatures in the [1989-2010] interval (see Figure 2) have a strong effect on advancing FO (Menzel & Fabian, 1999; Rauschkolb et al., 2024). As a result, the greater temperature difference between the intervals may have favored the advancement of flowering onset in gardens compared to the flowering events in the herbarium data.

Future research should ensure that only flowering events of those years from herbarium specimens are used in comparison, in which ground-based observations were also made in gardens. Additionally, the linear mixed-effects model of our results would probably offer more explanation, if the specific year was used as the independent variable instead of the interval, which overlooks the steadily rises in temperature in Vienna (see Figure 2).The concrete year might connect the phenological event indirectly with the specific average temperature of each year, which has one of the greatest impacts on phenological shifts of flowering (Piao et al., 2019). Using different filtering methods for the data sets during these years could significantly increase the data set as well as other methods for adding data from a broader radius around Vienna. However, Vienna is well suited for such analyses, as it has been historically significant and therefore has a large amount of herbarium specimens, but also particularly well-documented temperature data. Furthermore, it can be assumed that the maintenance factors, such as the frequency of irrigation, soil type, weed control plan, availability of light and shade, and microclimatic conditions, may vary between gardens (Rauschkolb et al., 2024), but are possibly not fundamentally different. However, this assumption cannot be made in the field, where biotic and abiotic influencing factors can vary significantly between different locations. Additionally, it is worth mentioning the potential influence of human activities or livestock, such as substance inputs or footprints at some sites, which affect abiotic factors and, in a second step, directly impact the plants (Matyssek & Herppich, 2019).

Herbarium data represent an enormous resource for obtaining large data sets. Together with ground-based observations they could be used to large-scale studies to examine the phenology of additional species or to explore interconnections with other influencing factors on the herbaceous plant’s phenology. For example, Sporbert et al. (2022) emphasize the immense importance of species' life history in relation to phenology while Primack & Miller-Rushing, (2009) and Yang et al. (2021) argue that phenology is influenced by phylogenetic factors and plants traits. These effects were especially examined in botanical gardens, where

plants usually grow under favorable conditions (Rauschkolb et al., 2024). Using this connected data sets could investigate the significance of life history strategies, plant relatedness, or functional traits on phenology on a large scale in the field. These approaches could lead to valuable insights, allowing us to study how herbaceous plants respond to climate change in their natural environments.

3. Chapter II: A Comparative Analysis of Space-for-Time Substitution using ground-based data from gardens

3.1 Introduction:

Since the end of the Little Ice Age in the 19th century, the Earth's climate has warmed significantly from a relatively low level during the Holocene (Marcott et al., 2013). The increasing global temperatures are anthropologically driven and have a huge impact on all ecosystems (Hauck et al., 2019; Marcott et al., 2013). As a result, phenological shifts in plants have been observed more frequently in recent decades (Bolmgren et al., 2013; Huang et al., 2020; Primack, D. et al., 2004; Wittich & Liedtke, 2015).

Research has primarily concentrated on the impact of temporal variability on plant phenology, while influences of spatial variability in phenology remains poorly explored (Rauschkolb et al., 2024). Therefore, it is often assumed that correlations of the temporal variability in environmental parameters would be equal to those for spatial variability (Peaucelle et al., 2019). On the one hand, some evidence suggests that spatial variability in herbaceous plant phenology is primarily driven by temperature (Rauschkolb et al., 2024), similar to temporal variability (Liu & Zhang, 2020; Zhang et al., 2014). On the other hand, recent research indicates significant spatial variability in the temperature sensitivity of plant spring phenology (Cook et al., 2012; Q. Liu et al., 2019; Shen et al., 2015; Wolkovich et al., 2012; Z. Yang et al., 2021; Zohner et al., 2017). These studies suggest that spatial variations in environmental factors play a significant role in explaining plant phenology and should be considerate. For instance, factors such as the association of different continents (Zohner et al., 2017), variation in photoperiod (Rauschkolb et al., 2024) or differences in precipitation in arid regions (Du et al., 2020; Shen et al., 2015) have been identified as important influences.

To investigate and predict the development of herbaceous plants, temperature-based approaches spanning different temporal and spatial scales are often used (Cook et al., 2012; Pau et al., 2011). Long term studies use chronological data to observe plant phenology under the influence of external environmental factors at one site over an extended period (Blois et al., 2013). The linear regressions derived from these approaches can be used to make the most accurate predictions for future developments at that site (Damgaard, 2019; Liang, 2016; Montague et al., 2008). However, the data series required for this method need to be collected over many years to obtain statistically meaningful results (Damgaard, 2019). To circumvent this time consuming approach, alternative methods such as the Space-for-time Substitution

(SFT) have been developed, which assume that changes in space are equivalent to changes in time as long as the environmental influences of the spatial-climatic scale correspond to those of the temporal scale (Blois et al., 2013; Damgaard, 2019; Wogan & Wang, 2018). In phenology, this approach can be used to shorten decades of observations into a few years and make predictions about the influence of temperature based on specific data from other observation sites (Damgaard, 2019; Wittich & Liedtke, 2015). One of the biggest advantages of SFT is the ability to statistically test hypotheses on a larger scale (Damgaard, 2019). However, the drawback of this approach is the inability to confirm whether the tested hypotheses are indeed true (Damgaard, 2019). To evaluate the reliability of the SFT approach in studying the phenology of woody plants, Wittich & Liedtke (2015) compared it using chronological data– a rare consideration in phenological studies. Wittich & Liedtke (2015) discovered that in woody plants it is required to link temporal and spatial scales to use this approach and obtain meaningful results. These findings were confirmed by Damgaard (2019).

However, limited research has been conducted on phenological shifts in herbaceous plants (Huang et al., 2020; Matesanz & Ramírez-Valiente, 2019), and there is no known comparison of SFT and long term studies with chronological data, as studied by Wittich & Liedtke (2015) for woody plants. Based on the lack of testing SFT on the phenology of herbaceous plants, we hypothesized that a spatial scale can be utilized to approximate historical phenological shifts of herbaceous species of flowering onset (FO) at a specific location in Vienna.

3.2 Method

Data set

For the determination of FO, a sample was collected from 10 botanical gardens linked through the PhenObs network (see Nordt et al., 2021), as well as from the Horticultural School in Vienna (see Appendix 1). We used the PhenObs network data for the spatial temperature gradient, and the data from Horticultural School combined with PhenObs network data in Vienna for the temporal temperature gradient in Vienna. Since different individuals conducted the phenological observations and there was no test to verify the correlations between observers, compliance of protocol interpretation cannot be proven.

Data from the temporal gradient were adjusted to the local gradient by considering only flowering events occurring within Vienna's measured temperature range over the past 23 years. Subsequently, flowering events from both gradients underwent a filtering process to remove duplicate or missing values. Additionally, each species required a minimum of 7 data points per

temperature gradient. For avoiding mistakes in transcription, the remaining data sets were filtered for each species and temperature gradient using a variance threshold of <900. This threshold aligns with the rule proposed by Schaber & Badeck, (2002), providing a robust method for identifying outliers with a tolerance of +/- 30 days. Following this, both gradients were matched to retain only species present in both data sets.

After these filtering processes, the total sample size amounted to 966 from 35 different species spanning 19 families, with sample sizes per species ranging from 14 and 37. For the spatial gradient, 633 phenological data points of FO from 11 botanical gardens worldwide were utilized (Nordt et al., 2021). The average flowering event occurs on DOY 110 +/- 36 (20th April), with all data points ranging between DOY 5 (5th January) and 197 (16th July) (see Figure 5). The temporal gradient comprises a sample size of 333, sourced from two gardens within Vienna: data from the Horticultural School between 1989 and 1998 (see Appendix 1) and data from the botanical garden of the University of Vienna in the years 2019 and 2023 (Nordt et al., 2021). The average flowering event occurs on DOY 109 +/- 35 (18th April), with all data points ranging between DOY 14 (14th January) and 176 (25th June) (see Figure 5). A detailed breakdown of the data underlying the analyses is provided in Table 2.

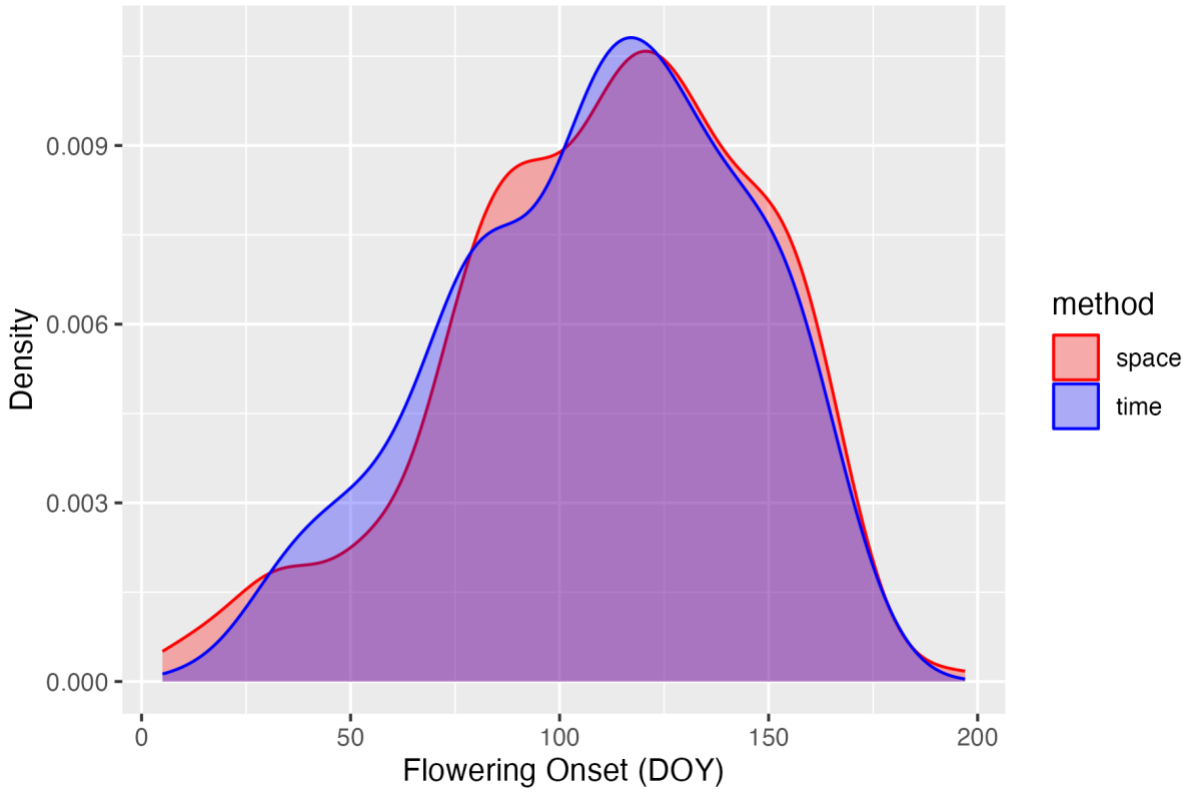

Figure 5 The annual distribution of FO across the local gradient and (blue) the annual distribution of FO based on the temporal gradient in Vienna exhibit a substantial overlap between the two distribution functions. The average flowering event on the spatial gradient occurs on DOY 110 +/- 36 (20th April), with all data points ranging between DOY 5 (5th January) and 197 (16th July). The average flowering event of the temporal gradient occurs on DOY 109 +/- 35 (18th April) with all data points ranging between DOY 14 (14th January) and 176 (25th June).

Table 2 The table provides an overview of all types that were examined in this chapter. It includes information about the respective city of origin, the country of origin (AU – Austria, CZ – Czech Republic, DE –Germany, IN – India), classification by type of garden (HS – horticultural school), precise coordinates of the location (latitude, longitude), year of collection, annual mean temperature, number of species, number of families, and the assignment of the used gradient.

Garden	Latitude	Longitude	Year of Collection	Annual mean of Temperature	Number of species	Number of Families	Gradient
Berlin (DE)	52.454	13.305	2019	11.492	27	16	space
Berlin (DE)	52.454	13.305	2020	11.575	27	16	space
Berlin (DE)	52.454	13.305	2021	10.317	28	16	space
Berlin (DE)	52.454	13.305	2022	11.408	28	16	space
Frankfurt (DE)	50.123	8.656	2020	11.675	17	10	space
Frankfurt (DE)	50.123	8.656	2021	10.125	16	10	space
Frankfurt (DE)	50.123	8.656	2022	11.758	15	9	space
Halle (DE)	51.488	11.960	2019	10.750	32	19	space
Halle (DE)	51.488	11.960	2020	10.867	28	18	space
Halle (DE)	51.488	11.960	2021	9.500	29	18	space
Halle (DE)	51.488	11.960	2022	10.808	27	17	space
Jena (DE)	50.930	11.585	2019	9.883	24	14	space
Jena (DE)	50.930	11.585	2020	9.942	27	18	space
Jena (DE)	50.930	11.585	2022	9.883	25	16	space
Leipzig (DE)	51.328	12.392	2019	11.050	9	8	space
Leipzig (DE)	51.328	12.392	2020	11.116	7	7	space
Leipzig (DE)	51.328	12.392	2021	9.767	10	9	space
Leipzig (DE)	51.328	12.392	2022	11.067	17	14	space
Potsdam (DE)	52.404	13.025	2021	10.316	25	17	space
Potsdam (DE)	52.404	13.025	2022	11.408	26	16	space
Prague (CZ)	50.121	14.413	2020	10.817	12	8	space
Prague (CZ)	50.121	14.413	2022	10.825	15	10	space

Srinagar (IN)	34.127	74.832	2021	11.375	1	1	space
Srinagar (IN)	34.127	74.832	2022	11.966	4	4	space
Tuebingen (DE)	48.539	9.035	2021	10.125	14	10	space
Tuebingen (DE)	48.539	9.035	2022	11.808	14	9	space
Vienna (AT), HS	48.179	16.310	1989	10.640	21	15	time
Vienna (AT), HS	48.179	16.310	1992	10.910	30	18	time
Vienna (AT), HS	48.179	16.310	1994	11.530	29	18	time
Vienna (AT), HS	48.179	16.310	1995	10.340	30	18	time
Vienna (AT), HS	48.179	16.310	1996	9.000	31	19	time
Vienna (AT), HS	48.179	16.310	1997	10.100	32	19	time
Vienna (AT), HS	48.179	16.310	1998	10.670	34	20	time
Vienna (AT)	48.192	16.380	2019	12.010	30	15	space/time
Vienna (AT)	48.192	16.380	2020	11.630	19	14	space/time
Vienna (AT)	48.192	16.380	2021	10.710	20	11	space/time
Vienna (AT)	48.192	16.380	2022	11.910	29	14	space/time
Vienna (AT)	48.192	16.380	2023*	11.910	27	15	space/time
Xixon (ESP)	43.545	-5.661	2022	11.910	5	5	space

*The missing annual temperature data was approximated by using data from the previous year. The difference between these years at Vienna's "Hohe Warte" was 0.5 degrees. This estimate might be replaced once the actual data for 2023 is available on the Global Climate Monitor.

Temperature data

Since standardized measurements of temperature were not conducted in individual gardens, the Global Climate Monitor available at the following link was utilized: https://www.globalclimatemonitor.org/. From this source, the monthly average temperature of the 0.5° grid cell for each garden was extracted. This data was then used to obtain the annual average temperature for each year and each garden separately (see Table 1). The missing annual temperature data in 2023 was approximated by using data from the previous year. The difference between the years 2022 and 2023 at Vienna's weather station "Hohe Warte" was 0.35 degrees as available at https://dataset.api.hub.geosphere.at/app/frontend/station/historical/klima-v1-1m. This estimate might be replaced once the actual data for 2023 is available on the Global Climate Monitor. Maintenance factors, including irrigation frequency, soil type, weed control plan, availability of light and shade, as well as microclimatic conditions, may vary from garden to garden.

Data analyses

The analyses were conducted using R Studio (version 2023.3.1.446). The consideration of distinguishing between fixed (temperature, methodology (gradient membership)) and random components (constant intercept, species identity) in estimating the regression coefficients led to the methodological approach of a linear mixed effect model (LME) from the package "lmerTest". This approach tests whether the influence of temperature on the day of FO differs between the spatial gradient across the botanical gardens and the temporal gradient in Vienna considering all species. To assess the quality of the model, the Conditional R^2 (cR^2) was calculated, and to determine the proportion of fixed effects in the explained variance, the Marginal R^2 (mR^2) was calculated. Additionally, the interclass correlation coefficient (ICC) was computed, which describes the proportion of variance explained by the group structure (species) of the random effects.

Assuming a linear relationship, linear regressions (LR) of the FO were also performed for each species and methodology as a function of temperature. This was done to identify possible overlaps in slope coefficients between the two scales and facilitate comparison by examining the slope and their confidence intervals.

To make significant interactions between methodologies visible and potentially identify intersections, multiple regressions (MR) were conducted for each species, with FO as the dependent variable, methodology, temperature, and their interaction as independent variables.

3.3 Results

The results underline the importance of the SFT method for examinations of increasing temperatures on phenological shifts in herbaceous species. The linear mixed-effect model (LME) used explains 84.8% of the total variance (cR^2 =0.848). Out of the explained variance, the random, species-specific effect accounts for 84.5% of the variation in the measured data, indicating significant differences between species, while the variation within each species remains relatively low (LME: ICC = 0.845). On the other hand, the fixed effects of temperature and methodology contribute only 2.1% to the explanation (see Figure 6, mR^2 = 0.021). Regarding methodology, no significant effect on the onset of flowering was observed (LME: $F_{1,928}$ = 0.920, p = 0.338, Figure 6). Furthermore, no significant interaction between temperature and methodology was detected (LME: $F_{1,928}$ = 0.778, p = 0.414, see Figure 6). However, temperature exhibited a highly significant influence (LME: $F_{1,928}$ = 119.676, p < 0.001, see Figure 6), which needs to be considered in the context of the low mR^2

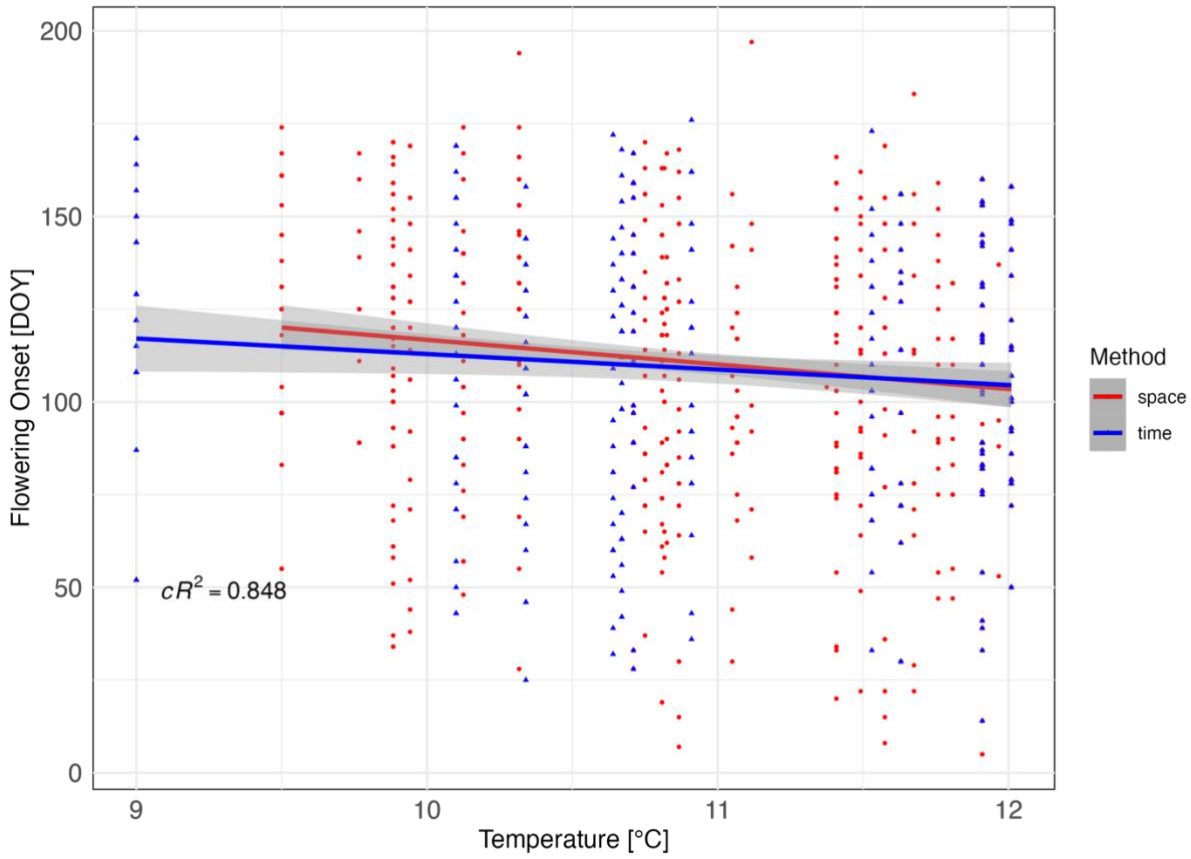

Figure 6 (red) shows the advancement of FO in relation to temperature across the local gradient and (blue) the advancement of FO in relation to temperature across the temporal gradient in Vienna. The gray area represents the 95% confidence interval for both linear regressions, overlapping across the entire possible range. The linear regressions run nearly parallel to each other, illustrating the similarity between both methods. The data points representing the spatial gradient are shown as red points, while the data points representing the temporal gradient are shown as blue triangles.

Table 3 The table presents the coefficients of the linear regression analyses for various plant species in comparison. The first column lists the species. The following three columns display the results of linear regressions for the spatial gradient in this order: F-values, degrees of freedom, p-values and estimated slope coefficients. Columns seven to ten contain the same metrics for the linear regression of the temporal gradient: F-value, degrees of freedom, p-values and estimated slope coefficients. Figure 7 shows a visual representation of these results with the corresponding confidence intervals. The last column indicates the significance of the interaction between temperature and method in the multiple regression for each species. Significant results are marked in bold.

Species	**Comparing results of the Linear Regression**								**Multiple Regression**
	Spatial gradient				Temporal gradient				Interaction between temperature and method
	F	df	p	slope coefficient	F	df	p	slope coefficient	p-value
Viola odorata	1.943	1,5	0.222	-13.742	4.342	1,5	0.092	-13.644	0.993
Vinca minor	0.296	1,20	0.592	-3.437	14.203	1,5	0.190	-14.203	0.387
Trollius europaeus	**15.730**	**1,15**	**0.001**	**-11.655**	3.170	1,6	0.125	-5.910	0.213
Silene coronaria	**6.897**	**1,17**	**0.017**	**-9.007**	**18.660**	**1,9**	**0.002**	**-6.461**	0.566
Scilla siberica	**11.060**	**1,5**	**0.021**	**-15.726**	2.866	1,9	0.125	-6.118	0.184
Saxifraga paniculata	0.098	1,19	0.758	-1.740	**37.180**	**1,5**	**0.002**	**-8.080**	0.456
Salvia nemorosa	**7.057**	**1,12**	**0.021**	**-10.165**	0.806	1,5	0.410	-3.731	0.338
Primula veris	2.586	1,12	0.134	-5.914	0.732	1,6	0.425	-6.227	0.966
Primula denticulata	0.833	1,21	0.372	-7.108	13.579	1,10	0.088	-12.960	0.610
Phlomis russeliana	1.931	1,16	0.184	-1.888	0.757	1,9	0.407	-2.369	0.861
Paeonia officinalis	3.906	1,15	0.067	-5.334	**8.704**	**1,8**	**0.018**	**-7.036**	0.655
Menyanthes trifoliata	6.732	1,19	0.178	-9.117	0.659	1,6	0.448	-3.088	0.285
Lunaria rediviva	**15.07**	**1,9**	**0.004**	**-6.801**	0.863	1,8	0.380	-2.600	0.221
Lathyrus vernus	**8.719**	**1,25**	**0.007**	**-10.722**	4.99	1,8	0.056	-10.017	0.908
Iris pseudacorus	0.010	1,17	0.923	-0.332	0.149	1,10	0.707	1.172	0.750
Iberis sempervirens	0.388	1,21	0.540	-4.509	4.444	1,10	0.061	-7.385	0.770

Table 3 - continued

Galium odoratum	**7.786**	**1,12**	**0.016**	**-10.170**	**18.450**	**1,7**	**0.004**	**-8.379**	0.690
Galega officinalis	**10.270**	**1,17**	**0.005**	**-4.433**	**5.927**	**1,9**	**0.038**	**-5.151**	0.764
Galanthus nivalis	0.530	1,13	0.480	-4.945	0.050	1,5	0.832	-0.698	0.666
Fragaria vesca	2.185	1,21	0.154	-11.712	**5.995**	**1,8**	**0.040**	**-7.649**	0.711
Eranthis hyemalis	0.6715	1,21	0.422	-3.092	1.100	1,10	0.319	-3.254	0.976
Dictamnus albus	**23.900**	**1,24**	**0.000**	**-7.267**	0.385	1,9	0.551	-1.251	**0.021**
Convallaria majalis	3.414	1,23	0.078	-6.473	0.119	1,7	0.740	-1.017	0.332
Clematis recta	3.540	1,19	0.075	-6.655	2.173	1,8	0.179	-4.177	0.629
Chelidonium majus	0.000	1,16	0.994	-0.064	0.018	1,5	0.899	-0.523	0.975
Centranthus ruber	**5.742**	**1,8**	**0.043**	**-15.64**	1.626	1,5	0.258	-8.159	0.457
Caltha palustris	**12.030**	**1,20**	**0.002**	**-13.895**	**30.560**	**1,9**	**0.000**	**-11.937**	0.706
Buphthalmum salicifolium	0.656	1,8	0.442	-5.582	0.586	1.7	0.469	1.541	0.302
Brunnera macrophylla	**5.925**	**1,16**	**0.027**	**-11.418**	**15.740**	**1,10**	**0.003**	**-9.317**	0.721
Aurinia saxatilis	0.123	1,6	0.738	-1.400	2.463	1,7	0.161	-9.184	0.161
Anemone nemorosa	**10.770**	**1,21**	**0.004**	**-7.041**	4.662	1,8	0.063	-9.684	0.535
Anemone hepatica	1.983	1,19	0.175	-7.517	1.923	1,10	0.196	-7.382	0.986
Allium ursinum	**6.955**	**1,24**	**0.014**	**-8.491**	5.531	1,5	0.065	-9.169	0.933
Adonis vernalis	2.537	1,16	0.131	-4.885	3.101	1,7	0.122	-7.675	0.585
Actaea spicata	0.720	1,11	0.414	1.775	0.8416	1,8	0.386	1.468	0.909

A comparison between the linear regressions of both gradients shows significant negative slope coefficients of different species between temperature increases and the advancement of FO (see Table 3, Figure 7). These negative slope coefficients were observed in 14 out of 35 plant species on the spatial gradient and 8 out of 29 plant species on the temporal gradient (see Table 3). No significant positive slope coefficient between temperature and FO was found for any species on either gradient (see Table 3).

The overlap of the 95% confidence intervals of the slope coefficients for all species (see Figure 7) suggests, together with the results of the linear mixed model, that there are no clear differences between both temperature gradients (see Figure 6). Furthermore, 34 out of the 35 species analyzed show no significant interaction between the spatial and the temporal gradient (see Table 1) with only *D. albus* showing a significant interaction (MR: $F_{3,33} = 11.16$, $p = 0.002$), as evident in Figure 7 by the minimal overlap of the confidence intervals between the two gradients. Finally, five species (*B. macrophylla*, *C. palustris*, *G. officinalis*, *G. odoratum*, *S. coronaria*) show significant slope coefficients on both gradients of the linear regressions, supporting the assumption of the lack of differences between the two gradients (see Table 3).

Although only 23 (32.86%) out of the total 70 conducted linear regressions can be considered statistically significant and hence informative (see Table 3), a pattern in the expression of the dispersion coefficients can be found (see Figure 7). All except one non-significant regression of species (*A. spicata*) from the spatial gradient and three non-significant species on the temporal gradient (*A. spicata*, *B. salicifolium and I. pseudacorus*) exhibit a negative slope coefficient. 20 (57.14%) of the 35 species are more negative on the temporal gradient than on the spatial gradient. Thus, no different trend related to the gradients can be observed.

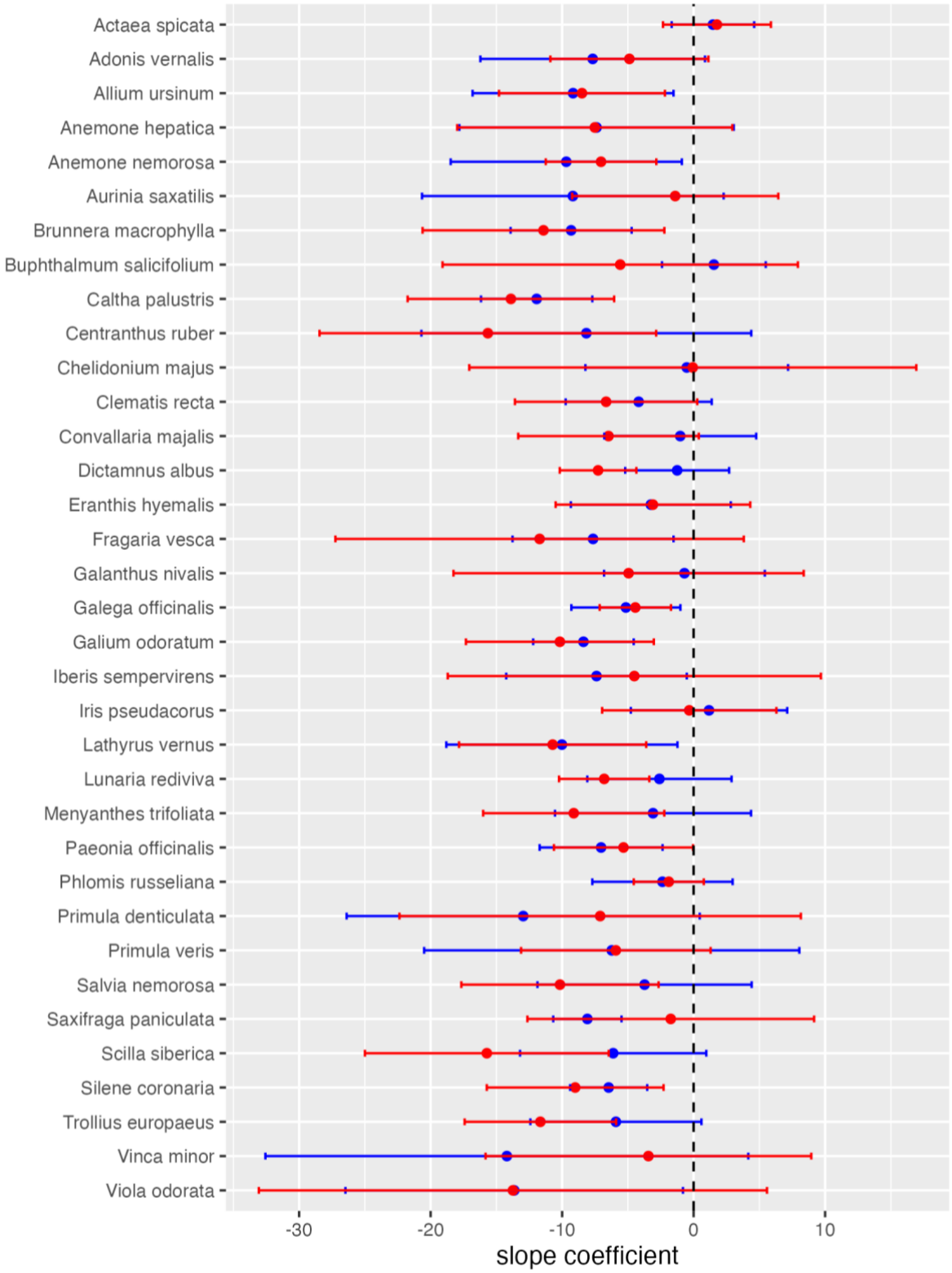

Figure 7 The illustration depicts the slope coefficients (points) along with their corresponding 95% confidence intervals (horizontal) of the linear regressions for each plant species, across the two gradients "space" (red) and "time" (blue). The overlap of the confidence intervals between the different methods provides insights into potential similarities or differences in the responses of plant species to the considered method. The dashed vertical line facilitates comparison with situations where no linear relationship exists. For consideration of the significance level, refer to Table 3.

3.4 Discussion

The results of our research suggest that the SFT method can be utilized to study phenological shifts in herbaceous plant species in response to rising temperatures of the actual climate change. This is proven by the fact that no significant differences were found in the effect of temperature on the onset of flowering across all species and only one significant interaction considering individual species. The significant interaction between the temperature sensitivity and the methodology of the multiple regression of *D. albus* is possibly due to the fact that only a single individual was observed on the temporal gradient both in the horticultural school and in the botanical garden of Vienna. Genetic differences and possible interactions with other organisms may have a greater influence on the annual FO of a single individual, as there is no averaging (Bustamante & Búrquez, 2008). This means that a possible outlier is weighted higher. In a larger population, in which the first flowering of a population is observed, these influences would possibly be smaller. Furthermore, there is no precise information on the site in the horticultural school, so additionally influences of external environmental factors such as moisture, light conditions as well as soil conditions could lead to a generally earlier or later annual FO of the individual in the horticultural school. Finally, similar slope patterns were observed on both gradients, indicating that the sensitivity of FO to temperature is comparable on both gradients.

A comparison with the previous study by Wittich & Liedtke (2015) shows differences between woody and herbaceous plants. In their study the temporal gradient of woody plants shows greater sensitivity to temperature, both in the spring response of "beginning of leaf unfolding" and in the summer response of "the date on which gooseberry fruits", compared to the spatial gradient of woody plant (Wittich & Liedtke, 2015). This contrasts with our results where the sensitivity to temperature on the FO on both gradients shows the same trend (see Figure 6). These difference observations are supported, for example, by Du et al. (2020), who suggest that herbaceous and woody plant assemblages respond differently to climate change, possibly due to the variability and stronger association of flowering and leaf phenology with functional traits in herbaceous compared to tree species (Horbach et al., 2023).

We found a significant impact of temperature on flowering day (DOY) revealed in our linear mixed effect model. As our plants flower, on average, around the 18th of April on both gradients (see Figure 5), this supports the existing research indicating the high sensitivity of early-flowering species to climate change (Forrest & Miller-Rushing, 2010; Rauschkolb et al., 2024; Wadgymar et al., 2018). However, it must be considered that the fixed effects in the linear-mixed effect model, where temperature is the only significant p-value, explain only 2.1%

of the explained variance. Therefore, this result should be interpreted with caution, as on its own is not sufficient to demonstrate high sensitivity of phenological development in herbaceous species.

The results of our study contribute to the considerations of Rauschkolb et al. (2022) and Sporbert et al. (2022), who suggest that botanical gardens belonging to the PhenObs network provide an adequately controlled environment for phenological research. This is confirmed from the temporal and spatial regressions from FO to temperature, which are almost parallel to each other (see Figure 6). The botanical gardens appear to be perfectly suited to transfer the SFT method to other contexts. As already observed by (Rauschkolb et al., 2024) the different influence of factors such as garden management, soil properties, irrigation, etc. in the botanical gardens had only a minor impact on the variability of phenological stages. Additionally, other influences from non-stationary environments and community ecosystems can also be limited. These are especially pronounced in the Anthropocene and have been identified as significant disturbances to the SFT method (Damgaard, 2019).

Our results suggest that there is no difference between the spatial and the temporal gradient which allows the combination of both gradients for future studies. Thus, it can make a meaningful contribution to predicting phenological responses of plant species in scientifically well-studied habitats such as the temperate zone, particularly in the context of the recently fast changing climate. However, many more influencing factors should be considered to adequately address community structure, ecosystem dynamics, and population-related processes. Comparisons between data sets from the field and individual botanical gardens (as for example examined in Chapter I) could be conducted to highlight underlying differences. These measures could eventually enable the transfer of the SFT method across various botanical gardens to field conditions. Future research could focus on further categorizations of herbaceous plants in relation to the validation of this method, such as according to life forms (such as phanerophytes, chamaephytes, hemicryptophytes, geophytes, therophytes), phylogenetic relationships, or plant communities. We propose that the observations of the botanical garden Vienna, initiated as part of this work, should be continued to add more species for comparison. Future applications of new statistical methods, larger databases with additional variables (functional traits, photoperiod, water availability), and a deeper understanding of the underlying mechanisms in phenology across both gradients could help to further optimize the validation the SFT method.

Conclusion

The present results provide valuable insights into the application and validity of phenological data sets from different sources and methods. First, the analysis of the SFT method shows that it is suitable for investigating phenological shifts in herbaceous plants in response to temperature changes. The results illustrate that both spatial and temporal gradients show similar temperature sensitivities in relation to flowering time, with differences within the species *D. albus* presumably due to a small number of observed individuals. These findings confirm the validity of the SFT method and the suitability of combination of both data sets from the spatial and temporal gradient, as well as the utility of botanical gardens as a controlled research environment for future phenological studies.

Secondly, the comparison of herbarium and garden data indicates that both combined data sources shows significant and homogeneously shift patterns in flowering time, despite significant differences in flowering events. No significant advancement was found within a single data source. This underscores the consistency and validity of both herbarium data and data from botanical garden for phenological studies, as well as the value of combining both data sets for future research. However, the results underlie some limitations, because there is no possibility to prove the exact phenological event in herbaria. Future research should ensure that only flowering events of those years from herbarium specimens are used in comparison, in which ground-based observations were also made in gardens.

Both Chapter illustrate that despite differences in data collections, consistent temperature sensitivity patterns of flowering events can be observed. The SFT method with data from ground-based garden observations and herbarium data complement each other in their ability to identify phenological trends and together provide a more comprehensive picture of plant responses to climate change. The combination of different approaches might lead to a deeper analysis and better understanding of the phenological responses of plants in different environmental scenarios. However, it should be borne in mind that there are also other influences on phenological events besides temperature that can affect individual results. Therefore, these factors should be included in the statistical models. We also emphasize that the temperature data must be consistent across all linked data. Taking these limitations into account, future research should therefore consider combining all validated data sources and methods to comprehensively assess and evaluate the impact of climate change on plant phenology.

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List of Tables

Appendix 1

The following appendix outlines the collection, documentation, and processing of data from the Horticultural School for integration into the existing research.

Data collection of Horticultural school's data

The phenological flowering observations were conducted once a week by DI Wolfgang Matzke in the garden of the Horticultural School in Vienna in the years from 1989 to 1998. The data is no longer fully available and does not match the required format, therefore unification and digitization are required. However, from the years 1989, 1992, 1994, 1995, 1996, 1997, and 1998, a total of 2157 data points from 316 different plant species are available. DI Wolfgang Matzke categorized these data as "shrubs," distinguishing them from "woody plants." Furthermore, lies the garden of the Horticultural School in the southwest of Vienna (48.179, 16.310). The flat garden is surrounded by fences and houses, providing limited wind protection where the various plant species were planted in suitable locations with appropriate soils, light conditions, and interspecific favorable conditions. DI Wolfgang Matzke maintained the garden accordingly.

During his observations, DI Wolfgang Matzke did not follow a fixed route but recorded all phenological events related to flowering that caught his attention. Consequently, it cannot be excluded that the locations of observed individuals, as well as the observed individuals themselves, may have slightly changed over the years in the gardening school. There was no clear definition of when a stage was recorded as a flowering event, although it can be assumed that he proceeded coherently due to his expertise.

Data Structure and Digitization of Horticultural school's data

During digitization, original, handwritten data were used whenever possible, otherwise, existing initial Excel documents were consulted. Both data sources had a similar structure: only the weeks of the observed event were indicated, without specific days. However, a clear distinction was made between the events flowering onset (FO) and full flowering (FF) with both events potentially lasting several weeks. Additionally, a significant difference concerned the data entry: Digitally captured data could include events in parentheses, which arose during the transfer to digital and likely indicated uncertainties. Therefore, they were not detected as a flowering event. If no FO was entered in the lists, the first date, with the event FF was designated as the FO.

For FO, the first described event was recorded, while for the peak of flowering (PF) the average of the available events was calculated and used for the current list. To improve comparability with data from PhenObs, a specific DOY was calculated, representing the indicated week. As DI Matzke conducted observations on weekdays, Wednesday was chosen as the reference point, as it lies in the middle of a workweek. Using a calendar for the corresponding year, the respective Wednesday was found, with a new week counted from Monday to Sunday. For example, if January 1st, 1989, was a Sunday, then the following Wednesday already corresponded to the 2nd week and was dated as day 4th. The summer was only partially observed due to vacation days. Observations in summer were limited due to vacation days, with partial resumption in the fall.

Appendix 2

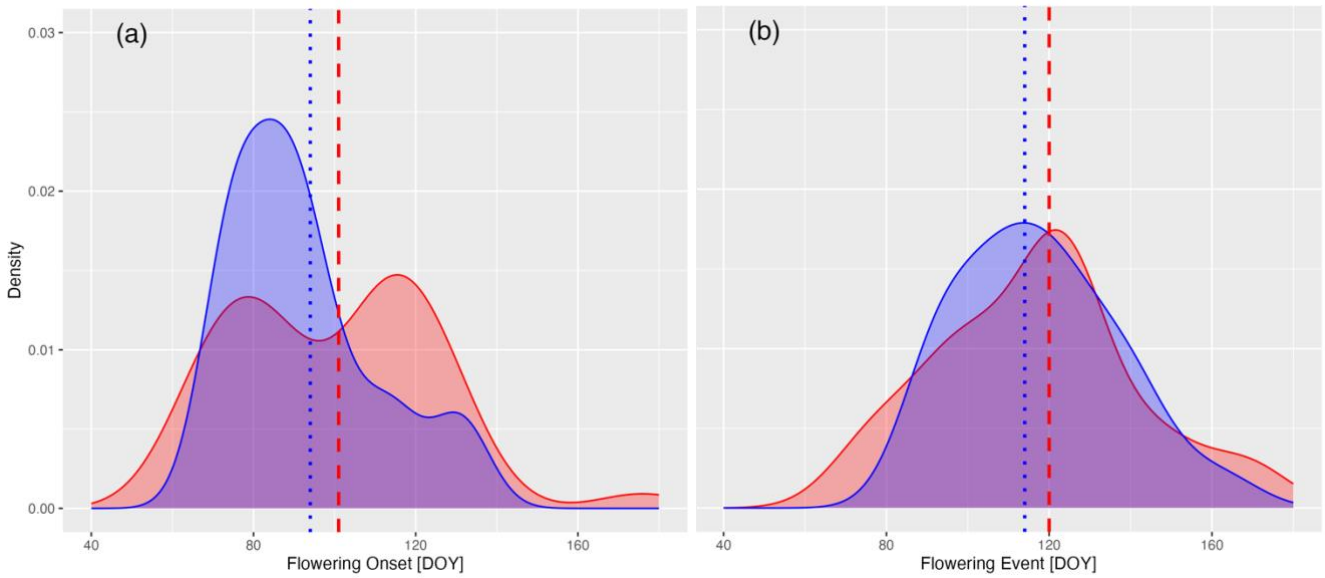

Figure 8 (a) Distribution of annual FO in gardens and (b) Distribution of flowering events in herbarium specimens. The time intervals (red) [1989-2013] and (blue) [2014-2023] are color-coded. The dashed line (red) corresponds to the estimated average event from the linear mixed model for the [1989-2013] interval, and the dotted line (blue) for the [2014-2023] interval. The difference between the estimated average event for the two intervals is 7 days in (a) and 6 days in (b).

Although the pattern in both data sources also shows with the interval boundary of 2013 some visible differences, they have a higher p-value (LME: $F_{1,\ 116} = 3.896$, $p = 0.051$) compared to the interval boundary in 2010 (LME: $F_{1,115} = 6.623$, $p = 0.\ 0.011$). This leads us to assume, that the boundary of 2010 is better usable to identify possibly differences. Consequently, distributions of the data are better illustrated within the intervals [1989-2010] and [2011-2023], as described in the presented work. For further details, the R script used for the analysis has been included.