The relationship between phenology and functional traits in herbaceous plants in the face of climate change and implications for pollinators

Dissertation

zur Erlangung des

Doktorgrades der Naturwissenschaften (Dr. rer. nat.)

der Naturwissenschaftlichen Fakultät I – Biowissenschaften

der Martin-Luther-Universität Halle-Wittenberg

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Verteidigt am 25.06.2025

“It is astonishing how soon and unexpectedly flowers appear, when the fields are scarcely tinged with green. Yesterday, for instance, you observed only the radical leaves of some plants; today you pluck a flower.”

Henry David Thoreau (Thoreau 1962)

"The art of life lies in a constant readjustment to our surroundings."

Kakuzō Okakura

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Summary

Phenology, the timing of recurring life cycle events, is widely observed to shift in response to climate change, serving as a “fingerprint of climate warming”. In plants, earlier spring phases (e.g. leaf out or flowering) and delayed autumn phenology (e.g. leaf senescence) are common but strongly vary across species and contexts, limiting broader generalizations. Thus, a key goal of phenological research is to deepen our understanding of species- and context-specific phenological patterns and their responses to a changing climate. Functional traits help explain these patterns, yet research has primarily focused on vegetative traits, overlooking floral traits despite their key role in pollination and reproduction. Additionally, floral traits related to nectar or pollen determine pollinator resource availability, making them crucial for both plant and pollinator fitness.

This thesis explores phenology-trait relationships across species and under climate change conditions to understand interspecific phenological variation and shifts, while also exploring the potential impacts of climate change on pollinators through alterations in floral resources.

In Chapter II, I linked year-round phenological observations with measurements of floral and vegetative traits in 68 herbaceous plant species across three German botanical gardens to assess the relative importance of floral compared to vegetative traits in explaining interspecific phenological variation. Vegetative traits were stronger predictors of phenological patterns than floral traits that had only minor influence. Plant height was a key trait, showing a strong positive relationship with both flowering and fruiting phenology while leaf senescence was more strongly explained by leaf dry matter content, highlighting plant growth and resource-use strategies as key determinants of phenological timing.

In Chapter III, I investigated interacting effects of climate change and land-use type (mowing or grazing) on the flowering phenology of 17 herbaceous plant species within the Global Change Experimental Facility and explored the role of functional traits in mediating phenological responses. Climate and land-use type influenced flowering phenology in a species-specific way, but not in interaction with each other, although microclimatic conditions in meadows and pastures were differentially modified by climatic changes. Phenological shifts under future climate were explained by traits related to an acquisitive growth strategy and the phenological niche. Acquisitive (e.g. with high specific leaf area, SLA), late, and long-flowering species showed reductions in flowering duration, suggesting a strategy of phenological drought escape.

To better understand direct and indirect effects of climate change on plant-pollinator interactions, in Chapter IV, I studied the impact of temperature and solar radiation on floral rewards and pollinator visitation rates in four herbaceous species with distinct floral traits in the botanical garden in Halle. Nectar volume decreased with increasing temperature or solar radiation across all four species, whereas other nectar properties responded more species-specifically to abiotic conditions. Although both nectar traits and flower visitation rates varied species-specifically with changes in temperature and solar radiation, pollinator visitation was largely unaffected by nectar properties and primarily driven by flower abundance.

This thesis contributes to our understanding of how climate change reshapes phenology and floral resource availability, which is crucial for predicting future ecosystem dynamics and potential disruptions in plant-pollinator networks. It highlights the dominant role of vegetative traits over floral traits in shaping phenological variation, with plant height emerging as a key predictor of interspecific differences in phenology. Phenological responses to climate change were mainly driven by growth strategy traits (e.g., the leaf economic spectrum) and the phenological niche, highlighting the role of resource-use strategies and intrinsic phenological traits in driving phenological shifts. Additionally, the findings suggest that future climatic conditions, depending on the context (e.g., land-use type), may result in declines in floral resources across multiple scales, including shifts in species-level phenology, species- and community-level flower abundances (Box 1, 2, 3 in Chapter V), and species-level nectar properties. While floral traits played a minor role in explaining phenological variation, they contribute to our understanding of the plant economic spectrum and highlight key aspects of floral rewards, which are essential for assessing the potential impacts of climate change on plant-pollinator interactions.

Zusammenfassung

Phänologie, der zeitliche Ablauf wiederkehrender Lebenszyklusereignisse, verschiebt sich aufgrund des Klimawandels bei vielen Organismen nachweislich. Diese klimabedingten phänologischen Verschiebungen werden daher auch als „Fingerabdruck der Klimaerwärmung“ bezeichnet. Bei Pflanzen tritt meist eine frühere Frühjahrs- (z.B. Blattaustrieb und Blüte) und verzögerte Herbstphänologie (z.B. Seneszenz) auf, deren Verschiebungen jedoch artspezifisch und kontextabhängig stark variieren, sodass es schwierig ist, verallgemeinernde Aussagen zu treffen. Ein zentrales Ziel der phänologischen Forschung ist es, diese art- und kontextspezifischen phänologischen Verschiebungen in Reaktion auf ein sich veränderndes Klima besser zu verstehen. Funktionelle Merkmale können zur Erklärung dieser Muster beitragen. Jedoch hat sich die bisherige Forschung in erster Linie auf vegetative Merkmale konzentriert und Blütenmerkmale, trotz ihrer Schlüsselrolle für die Bestäubung, Fortpflanzung und Bestäuberressourcen nicht berücksichtigt.

In dieser Arbeit werden Zusammenhänge zwischen Phänologie und funktionellen Merkmalen über verschiedene Pflanzenarten hinweg und unter Klimawandelbedingungen untersucht, um interspezifische phänologische Variation und Verschiebungen zu verstehen. Zudem werden die potenziellen Auswirkungen des Klimawandels auf Bestäuber im Kontext veränderter Bestäuberressourcen untersucht.

In Kapitel II habe ich ganzjährige phänologische Beobachtungen mit Messungen von Blüten- und vegetativen Merkmalen bei 68 krautigen Pflanzenarten in drei deutschen botanischen Gärten verknüpft, um die relative Bedeutung von Blütenmerkmalen im Vergleich zu vegetativen Merkmalen für die Erklärung interspezifischer phänologischer Variation zu untersuchen. Vegetative Merkmale waren stärkere Prädiktoren für interspezifische phänologische Muster als Blütenmerkmale, die nur einen geringen Einfluss hatten. Dabei war Wuchshöhe ein zentrales Merkmal, das einen ausgeprägten positiven Zusammenhang sowohl mit der Blüh- als auch der Fruchtphänologie aufwies, während die Blattseneszenz stärker durch den Trockenmasse-Gehalt der Blätter (LDMC) erklärt wurde, was zeigt, dass Wachstums- und Ressourcennutzungsstrategien die phänologischen Zeitpunkte wesentlich mitbestimmen.

In Kapitel III habe ich die interaktiven Effekte von Klimawandel und Landnutzungstyp (Mahd oder Beweidung) auf die Blühphänologie von 17 krautigen Pflanzenarten sowie die Rolle funktioneller Merkmale bei der Vermittlung phänologischer Reaktionen in der Global Change Experimental Facility untersucht. Klima und Landnutzungstyp beeinflussten die Blühphänologie artspezifisch, aber nicht in Interaktion miteinander, obwohl die

mikroklimatischen Bedingungen auf Wiesen und Weiden durch Klimaveränderung in verschiedener Weise modifiziert wurden. Phänologische Verschiebungen unter zukünftigen Klimabedingungen wurden durch Merkmale erklärt, die mit einer akquisitiven Wachstumsstrategie und der phänologischen Nische in Zusammenhang stehen. Arten mit einer akquisitiven Strategie (z.B. mit hoher spezifischer Blattfläche, SLA), spätem Blühbeginn und langer Blühdauer zeigten eine verkürzte Blühperiode, was auf eine Strategie zur phänologischen Trockenheitsvermeidung hindeutet.

Um die direkten und indirekten Auswirkungen des Klimawandels auf Pflanze-Bestäuber-Interaktionen besser zu verstehen, habe ich in Kapitel IV den Einfluss von Temperatur und Sonneneinstrahlung auf Blütenressourcen und Blütenbesuchsraten von vier krautigen Arten mit unterschiedlichen Blütenmerkmalen im Botanischen Garten in Halle untersucht. Das Nektarvolumen nahm bei allen vier Arten mit steigender Temperatur oder Sonneneinstrahlung ab, während andere Nektareigenschaften eher artspezifisch auf Veränderungen abiotischer Bedingungen reagierten. Obwohl sowohl Nektareigenschaften als auch Blütenbesuchsraten artspezifisch auf Veränderungen der Temperatur und Sonneneinstrahlung reagierten, war die Bestäuberbesuchsrate kaum von den Nektareigenschaften beeinflusst, sondern wurde hauptsächlich durch die Blütenanzahl bestimmt.

Diese Arbeit leistet einen Beitrag zu unserem Verständnis darüber, wie der Klimawandel die Phänologie von Pflanzen sowie die Verfügbarkeit von Bestäuberressourcen verändert, und beleuchtet damit wichtige Aspekte, die zum Verständnis zukünftiger Ökosystemdynamiken und potenzieller Störungen in Pflanze-Bestäuber-Netzwerken beitragen. Sie hebt die übergeordnete Rolle vegetativer Merkmale gegenüber Blütenmerkmalen bei der Erklärung phänologischer Variation hervor, wobei die Wuchshöhe als zentraler Prädiktor für interspezifische Unterschiede in der Phänologie identifiziert wurde. Phänologische Verschiebungen als Reaktion auf Klimaveränderungen wurden vor allem durch Wachstumsstrategie-Merkmale (z.B. das blattökonomische Spektrum) und die phänologische Nische bestimmt, was die Rolle von Ressourcennutzung und intrinsischen phänologischen Merkmalen betont. Darüber hinaus deuten die Ergebnisse darauf hin, dass zukünftige klimatische Bedingungen, abhängig vom Kontext (z.B. Landnutzungstyp), auf verschiedenen Ebenen zu einem Rückgang der bestäuberrelevanten Blütenressourcen führen können. Dazu gehören artspezifische phänologische Verschiebungen, Veränderungen der Blütenhäufigkeit auf Art- und Gemeinschaftsebene (Box 1, 2, 3 in Kapitel V), sowie Veränderungen der Nektareigenschaften auf Art-Ebene. Während Blütenmerkmale eine untergeordnete Rolle bei der Erklärung phänologischer Variation spielten, tragen sie zu unserem Verständnis des pflanzenökonomischen Spektrums bei und beschreiben wichtige Aspekte im Zusammenhang mit Bestäuberressourcen, die für die Einschätzung potenzieller Auswirkungen des Klimawandels auf Pflanze-Bestäuber-Interaktionen von Bedeutung sind.

Chapter I

General Introduction

Phenology and impacts of global change

Phenology refers to the timing of recurring life cycle events such as flowering of plants or emergence of bees in spring and plays a crucial role in shaping ecosystems, influencing biodiversity, and determining species interactions (Forrest and Miller-Rushing, 2010). Phenological events like leaf emergence, flowering or fruiting strongly relate to the species resource acquisition, reproductive success and mediate biotic interactions like herbivory or pollination (Elzinga et al., 2007; Heberling et al., 2019; Kudo and Cooper, 2019; Nord and Lynch, 2009). Plant phenology is primarily determined by daylength, precipitation and temperature making it sensitive to climate change, which is associated with increasing temperatures, increased variability of precipitation and a higher frequency of weather extremes (Calvin et al., 2023; Forrest and Miller-Rushing, 2010).

Research on phenology and how it is influenced by seasonal and interannual variations in climate has a long tradition (e.g., Miller-Rushing and Primack, 2008). Observations of the cherry blossom related to the cherry blossom festival in Japan, for example, dating back to the 9th century, revealing advanced flowering of cherry trees in association with increasing spring temperatures in recent years (Aono and Omoto, 1994; Primack et al., 2009). According to progressing climate change phenological shifts have been documented across a wide range of organisms and can be considered as “fingerprints of climate warming” (Hassan et al., 2023; Menzel et al., 2020; Menzel and Fabian, 1999; Parmesan and Yohe, 2003; Root et al., 2003). Shifts in plant phenology are usually associated with advanced spring phenology (e.g., earlier leaf out and flowering), delayed senescence and thus longer growing seasons (Ahas et al., 2002; Bock et al., 2014; Büntgen et al., 2022; Ge et al., 2015; Hassan et al., 2023; Menzel and Fabian, 1999; Parmesan and Yohe, 2003; Piao et al., 2019). However, across studies phenological shifts are reported to be highly species-specific, showing advances, delays and no shifts in response to changing climate, not allowing broad generalizations (Bock et al., 2014; Cook et al., 2012; Fitter and Fitter, 2002; Jentsch et al., 2009; König et al., 2018; Piao et al., 2019; Root et al., 2003).

Phenological shifts can influence biotic interactions critical to ecosystem functioning, such as herbivory (Meineke et al., 2021), pollination (Gérard et al., 2020; Kudo and Cooper, 2019; Kudo and Ida, 2013), and interspecific competition (Carter and Rudolf, 2019; Rudolf, 2019; Vitasse, 2013), potentially leading to cascading effects on populations, communities (Fabina et al., 2010; Nakazawa and Doi, 2012; Post et al., 2008; Wolkovich and Cleland, 2011), and ecosystems (Forrest and Miller-Rushing, 2010) (see also paragraph on *Plant-pollinator Mismatches* below).

While phenological research traditionally focused on woody or crop plants (Estrella et al., 2007; Panchen et al., 2014; Rauschkolb et al., 2024; Vitasse et al., 2011), phenological research on herbaceous species is still underrepresented, although they represent more than 85 percent of the species found in temperate ecosystems (Ellenberg and Leuschner, 2010; Hassan et al., 2023). A growing body of literature in recent years, however, revealed distinct phenological climate change responses of herbaceous compared to woody plant species that remain to be understood better (Büntgen et al., 2022; Ge et al., 2015; König et al., 2018).

Interacting effects of global change drivers on phenology

Interacting global environmental change factors such as warming, precipitation changes, elevated CO_2 and nitrogen deposition cause diverse and interactive phenological responses (Cleland et al., 2006; Zhou et al., 2023) indicating that a comprehensive understanding of phenological shifts in response to climate change requires consideration of multiple factors. The intensity and direction of phenological responses to climate further strongly depends on the overall context such as community composition, location of the study or habitat type (Bucher et al., 2018; Jentsch et al., 2009; König et al., 2018), indicating that biotic interactions are further shaping phenological shifts. Biotic interactions such as herbivory (Lemoine et al., 2017; Ulrich et al., 2020), pollination (Rafferty and Ives, 2011) and competition (Dumandan et al., 2023) have been shown to alter phenological patterns directly or modulate responses to climatic factors. Land-use practices such as mowing, grazing, and fertilization can further affect phenological patterns of plant communities by altering the availability of resources (e.g., light and nutrients), modifying microclimates, and shifting competitive dynamics (Reisch and Poschlod, 2009; Tadey, 2020; Völler et al., 2013).

Thus, global changes, beyond climate change, such as land-use changes and biodiversity loss, can influence plant phenology (Buyantuyev and Wu, 2012; Romo-Leon et al., 2016; Ulrich et al., 2020; Wolf et al., 2017; Zhang et al., 2019), potentially interacting with climate change in shaping phenological shifts. Despite their importance, research examining how several global change drivers interact to shape phenological shifts remains scarce (but see Cleland et al., 2006; Zhou et al., 2023). This gap emphasizes the necessity of integrating multiple interacting drivers into phenological studies to better understand the complex mechanisms underlying plant responses to global environmental change.

Given that phenological shifts in response to global change drivers are highly species- and context-specific, predictions on future phenological shifts and their consequences for ecosystems remain challenging (Cleland et al., 2006; Jentsch et al., 2009; Zhou et al., 2023). However, understanding why some species respond to climate change while others showing different or no responses is crucial to evaluate ecological consequences and can help to inform conservation and restoration strategies.

Understanding phenological patterns through functional traits

One major aim of phenological research is to better understand species- and context-specific phenological patterns and responses to changing climate. On the one hand, plant phenology as well as phenological climate responses can be partly explained by shared phylogenetic history, meaning that closely related species show a more synchronized phenology and tend to similarly respond to changing environmental conditions (Davies et al., 2013; Davis et al., 2010). This is likely a consequence of evolutionarily conserved responses to environmental cues (Davies et al., 2013). Phylogeny, while crucial to consider, nevertheless does not fully explain phenological patterns suggesting that other aspects are likewise involved (König et al., 2018).

Over the last two decades, research on functional traits has become a cornerstone of ecological studies, integrating across ecosystems to better understand biodiversity-ecosystem function relationships (Díaz and Cabido, 2001; Nock et al., 2016; Violle et al., 2007). Functional traits are defined as morphological, physiological or phenological features measurable at the individual level, which impact fitness indirectly via their effects on individual performance, i.e. growth, reproduction and survival (Violle et al., 2007). In contrast to phylogenetic relatedness, traits can be similar across phylogenetically unrelated species or different across closely related species, thus better covering the functional space of species (Díaz et al., 2016).

Plant functional traits have been shown to be promising tools for understanding phenological patterns and shifts (Bucher et al., 2018; Bucher and Römermann, 2021; Horbach et al., 2023; König et al., 2018; Liu et al., 2021; Sporbert et al., 2022; Wang et al., 2021). Across studies plant height seems to be a key trait mediating plant phenology and phenological responses, with taller species being associated to generally later flowering and stronger phenological advances in response to warming (Bolmgren and D. Cowan, 2008; Huang et al., 2018; König et al., 2018; Liu et al., 2021; Sporbert et al., 2022). Leaf traits associated to the plant economic spectrum (Díaz et al., 2016; Wright et al., 2004) showed further explanatory power in explaining phenological patterns. Specific leaf area (SLA), related to growth rate and competitive ability (Pérez-Harguindeguy et al., 2016; Wright et al., 2004), is positively related to later flowering (Sun and Frelich, 2011), earlier leaf senescence (Bucher and Römermann, 2021) and stronger shifts in flowering phenology (König et al., 2018). Leaf dry matter content (LDMC) related to resistance to physical hazards (Pérez-Harguindeguy et al., 2016) is positively associated to later leaf senescence (Bucher and Römermann, 2021), while leaf area, associated to productivity, light interception, leaf energy and water balance (Díaz et al., 2016), is positively related to later leaf out (Sun et al., 2006) and shorter flowering (Sporbert et al., 2022). Furthermore, plants appear to exhibit varying levels of phenological sensitivity to climate change, depending on their phenological niche. A commonly observed pattern is that early-flowering species experience more pronounced phenological advancements in response to climate warming compared to species that flower later (Dunne et al., 2003; Fitter and Fitter, 2002; Lesica and Kittelson, 2010; Menzel et al., 2006; Pareja-Bonilla et al., 2023).

Compared to whole-plant or leaf traits, reproductive especially floral traits are mostly neglected in functional ecology research (E-Vojtkó et al., 2020) and their role in mediating plant phenology is largely unclear (but see E-Vojtkó et al., 2022). This is surprising as reproductive traits directly influence plant fitness, by mediating plant-pollinator interactions and thus influence pollination. A recent study first revealed associations between flowering phenology and floral traits and has begun to advance our understanding of the role of reproductive traits within the plant economic spectrum: E-Vojtkó et al. (2022) showed that floral traits are an independent dimension within the plant economic spectrum being largely independent from vegetative traits. However, comprehensive knowledge on the role of floral traits for explaining the year-round phenology of plants (from initial growth, over flowering, to senescence) considering also rarely measured pollen and nectar traits is still lacking and will be one focus of this thesis.

There are mainly two reason why floral traits being neglected in functional ecology studies and studies on phenology-trait relationships in particular: 1) To date there are no standardized and widely accepted protocols on how to comprehensively measure floral traits and which traits should be focused on (E-Vojtkó et al., 2020), as it exists for vegetative traits (and few seed traits) (Pérez-Harguindeguy et al., 2016). However, there are recent attempts for a standardized way of measuring floral traits, at least for those traits related to the newly proposed flower economic spectrum (Roddy et al., 2021). 2) The measurement of floral traits, including nectar and pollen characteristics, is often time-consuming and laborious and measurement or sampling techniques need to be adjusted for different plant species depending on the flower morphology. Despite extensive efforts by databases such as BiolFlor (Klotz et al., 2002) to compile categorical reproductive traits from ‘grey’ literature, quantitative floral trait data remain scarce in global trait databases like TRY or LEDA (Kattge et al., 2020; Kleyer et al., 2008). This limitation hinders a more comprehensive understanding of floral traits in mediating ecological processes such as phenology or community assembly (E-Vojtkó et al., 2020).

Significance of floral traits in mediating plant and pollinator fitness

Floral traits are central to plant-pollinator interactions, directly influencing reproductive success in animal-pollinated plants. Key traits such as flower size, floral display (i.e., flower size x number of flowers), color, and scent enhance pollinator attraction and recognition while mediating competition for pollinators (Willmer, 2011a, 2011b). Morphological traits, including flower shape and corolla tube depth, determine pollinator specificity by restricting access to floral resources to particular pollinator groups (Kugler, 1970; Willmer, 2011c). For instance, flowers with deep, narrow corollas can only be accessed by pollinators with sufficiently long proboscises (Inouye, 1980).

Beyond attraction, floral rewards such as nectar and pollen provide essential nutrients, including sugars, amino acids, and proteins, which directly influence pollinator survival and reproductive success (Pacini and Nicolson, 2007; Taha et al., 2019; Willmer, 2011d, 2011e, p. 2). While nectar primarily serves as a reward, pollen plays a dual role in plant reproduction and pollinator nutrition. Effective pollen transport requires traits that enhance attachment to pollinators while also protecting the male gamete until fertilization (Edlund et al., 2004). Additionally, pollen fluorescence has been suggested to contribute to pollinator attraction (Mori et al., 2018). Despite the vast diversity in pollen morphology and surface structures, their functional significance remains poorly understood, particularly in the context of the plant economic spectrum (Williams and Mazer, 2016; Willmer, 2011d). Advanced analytical techniques, such as multispectral imaging flow cytometry, now enable detailed pollen trait measurements, offering new opportunities to explore their ecological and evolutionary roles (Dunker et al., 2021; Hornick et al., 2022).

Given the critical role of floral traits in plant reproduction and pollinator fitness, a deeper understanding of phenology-trait relationships—particularly the contribution of floral traits—will enhance our ability to predict how climate change may disrupt plant-pollinator interactions, with implications for biodiversity and ecosystem stability.

Plant-pollinator mismatches

A main concern regarding climate induced phenological changes are potential mismatches among interacting species, which occur when phenological shifts are not synchronized across organism groups (Visser and Gienapp, 2019). In plants, the disruption of plant–pollinator interactions (i.e. plant-pollinator mismatches) is discussed (Gérard et al., 2020; Memmott et al., 2007; Miller-Struttmann et al., 2015; Petanidou et al., 2014; Stemkovski et al., 2020). Such temporal mismatches can occur when plants flower earlier in the season before their pollinators emerge, or when pollinators become active before floral resources are available. Changes in plant phenology alter the temporal availability of floral resources, such as nectar and pollen, which can reduce pollination success and reproductive output in plants while also limiting food availability for pollinators, ultimately impacting their fitness (Memmott et al., 2007). Studies to date suggest that generalist species might be better able to compensate for temporal mismatches by shifting to alternative interaction partners (Bartomeus et al., 2011; Gérard et al., 2020; Hegland et al., 2009), whereas more specialized species are more vulnerable to these disruptions (Kudo and Cooper, 2019; Kudo and Ida, 2013).

Plant-pollinator mismatches can occur not only on the temporal scale outlined above but also on the morphological and recognition scale (Gérard et al., 2020). Floral traits are directly affected by changing environmental conditions (e.g., temperature and precipitation) and are thus sensitive to climate change. Increased temperatures and decreased water-availability, for instance, can result in reduced nectar production, smaller or fewer flowers (Descamps et al., 2021, 2018; Rering et al., 2020; Scaven and Rafferty, 2013; Takkis et al., 2018), leading to reduced pollinator attractiveness and pollination success (i.e. seed set) and decreased pollinator resources (Phillips et al., 2018; Rering et al., 2020). Thus, not only the shift in flowering timing but also the altered amounts of resources like nectar and pollen or changes in the flower morphology, will potentially negatively influence plant-pollinator interactions under climate change.

Phenological shifts in plants and pollinators are highly species-specific and it is largely unclear how climate change affects the resource availability for pollinators (i.e., the quantity and quality of nectar and pollen) across different plant species throughout the flowering season (but see Baude et al. (2016) for data from Great Britain). Therefore, investigating the interplay between floral traits, phenology, and the influence of abiotic conditions on floral resources will enhance our understanding of plant-pollinator mismatches and associated risks to ecosystem functioning. To better understand the consequences of climate change for pollinators and pollination it is essential to simultaneously investigate the direct effects of environmental conditions on both floral rewards and pollinator behavior.

Thesis objectives

This thesis aimed to advance our understanding of the relationship between plant phenology and functional traits in the context of climate change. By incorporating floral rewards, it further seeks to elucidate how shifting climatic conditions may impact pollinators and their interactions with flowering plants. Figure I.1 provides an overview of the drivers (climate, abiotic conditions, and land use) and variables (phenology, traits, and pollinators) investigated in this thesis, along with the proposed and tested relationships examined in each chapter.

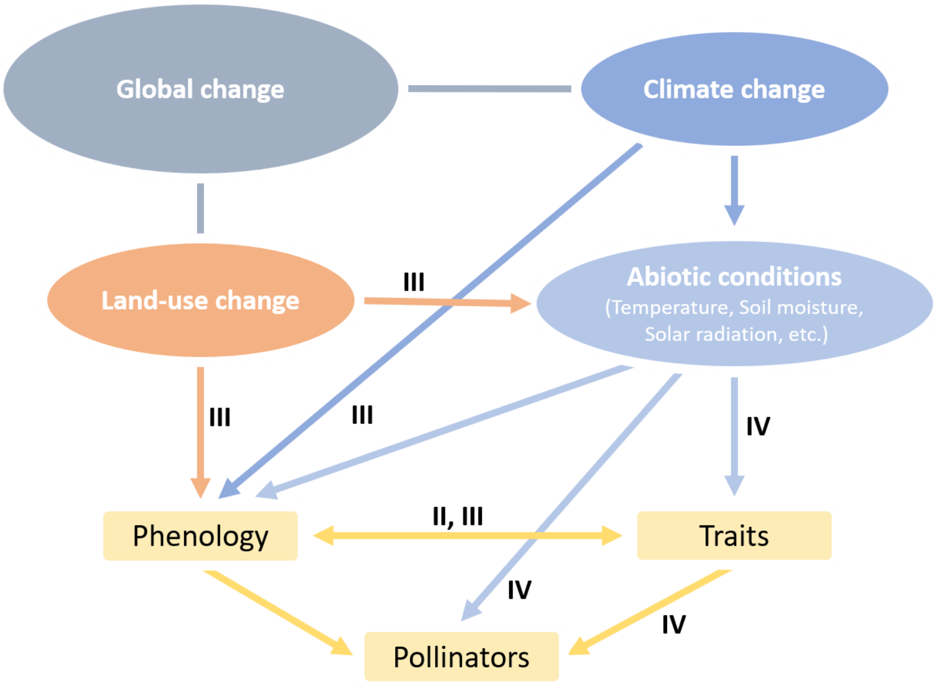


Figure I.1: Overview of drivers and variables investigated in this thesis. Arrows indicate influences of drivers on variables and relationships among variables as outlined above. Roman numerals refer to the chapters in which the respective effect or relationship was investigated.

Research on phenology-trait relationships has largely focused on vegetative traits, which are well-documented in global trait databases (e.g., TRY; Kattge et al., 2020), while the role of floral traits remains understudied as outlined above. Given their distinct functions—pollinator attraction and reproduction versus growth and competition—floral traits may influence phenology in ways that differ from vegetative traits. However, their interrelationships remain insufficiently understood (but see E-Vojtkó et al., 2022) and are the primary subject of Chapter II.

Global change drivers interactively shape plant phenology (Cleland et al., 2006), yet it is unclear how climate influences phenology across different land-use types (e.g., mowing, grazing) and how functional traits mediate these responses. Chapter III explores these interactions, focusing on the role of traits in phenological shifts under climate change in different land uses.

Temperature fluctuations influence both floral rewards and pollinator activity, with nectar availability and quality playing a key role in shaping pollinator behavior. To better understand the effects of climate warming on plant-pollinator interactions, Chapter IV investigates the impact of abiotic conditions on floral rewards and pollinator visitation patterns.

The specific objectives of this thesis can be grouped in three research topics aiming at understanding phenology-trait relationships in the face of climate change (Figure I.2):

Chapter II: Relationship between functional traits and phenological variation (“Patterns”)

This chapter investigates how floral and vegetative traits relate to plant phenology, with a particular focus on the role of floral traits in mediating year-round phenological variation. The study monitored the vegetative (e.g., leaf-out and senescence) and reproductive phenology (e.g., flowering and fruiting) of 68 herbaceous plant species in three German botanical gardens (Halle, Jena, Berlin) as part of the PhenObs network (Nordt et al., 2021). Floral traits—including flower dimensions, flower number, and rarely studied pollen (size, shape, surface structure, and fluorescence) and nectar traits (volume, sucrose concentration, total sucrose mass)—were measured in parallel with commonly used vegetative traits (e.g., plant height, leaf area, SLA, and LDMC). The three gardens, while representing different microclimates and maintenance regimes, share comparable macroclimatic conditions, allowing for an assessment of the consistency of phenology-trait relationships.

Principal component analysis (PCA) and Pearson’s correlation analysis were used to identify trait correlation structures and potential trade-offs among floral and vegetative traits. Boosted regression tree analysis assessed the relative importance of these traits in explaining phenological stages across the year. To account for phylogenetic relatedness, phylogenetic eigenvectors were included in the analysis.

Chapter III: Interactive effects of climate change and land-use type on phenology and the role of functional traits (“Trends”)

This chapter explores how climate change and land-use type (mowing vs. grazing) interactively influence the flowering phenology of herbaceous plants in extensively managed grasslands. The study was conducted in the Global Change Experimental Facility (GCEF) in Bad Lauchstädt, Germany, in 2020. Phenological observations (including flowering start, peak, end, and duration) were conducted under experimental climate treatments simulating future conditions, with a mean temperature increase of 0.55 °C and altered precipitation patterns (Schädler et al., 2019). These were compared to control plots under ambient climate conditions. The experiment also compared two extensive grassland management regimes: mowing (once per year) and sheep grazing (twice per year) in a split-plot design with five repetitions of each treatment combination.

Seventeen species that were evenly distributed across all treatments were selected for further analysis. Generalized linear mixed-effects models assessed the effects of climate, land use, species identity, and their interactions on flowering phenology. To understand species- and land-use specific phenological responses, functional traits—retrieved from the TRY database (Kattge et al., 2020), BiolFlor (Klotz et al., 2002), and *in situ* observations—were linked to species-specific phenological climate responses (log response ratios) within each land-use type to identify potential trait-mediated shifts in phenology.

Chapter IV: Environmental influences on floral rewards and pollinator behavior ("Pollinators")

This chapter investigates how abiotic environmental factors, specifically temperature and solar radiation, influence nectar quantity and quality as well as flower visitation rates, to better understand the potential impacts of climate warming on plant-pollinator interactions. A case study was conducted in the botanical garden in Halle, selecting four herbaceous plant species with distinct floral morphologies and colors. Pollinator observations and nectar measurements were performed simultaneously and linked to environmental data on temperature and solar radiation. Nectar traits—including nectar volume, sucrose concentration, and total sucrose mass—and flower visitation rates were assessed throughout the flowering period and across different times of the day.

To analyze these relationships, linear mixed-effects models were applied to assess the influence of abiotic factors on nectar characteristics, while generalized linear mixed-effects models evaluated the effects of temperature and solar radiation on flower visitation rates. Additionally, Pearson's correlation analysis explored associations between nectar traits and pollinator visitation rates.

Chapter V: Synthesis and Outlook

The final chapter synthesizes the findings from Chapters II–IV, discussing their implications for our understanding of phenology-trait relationships, plant responses to climate and land-use change, and the broader ecological consequences for plant-pollinator interactions, while also offering recommendations for future research.

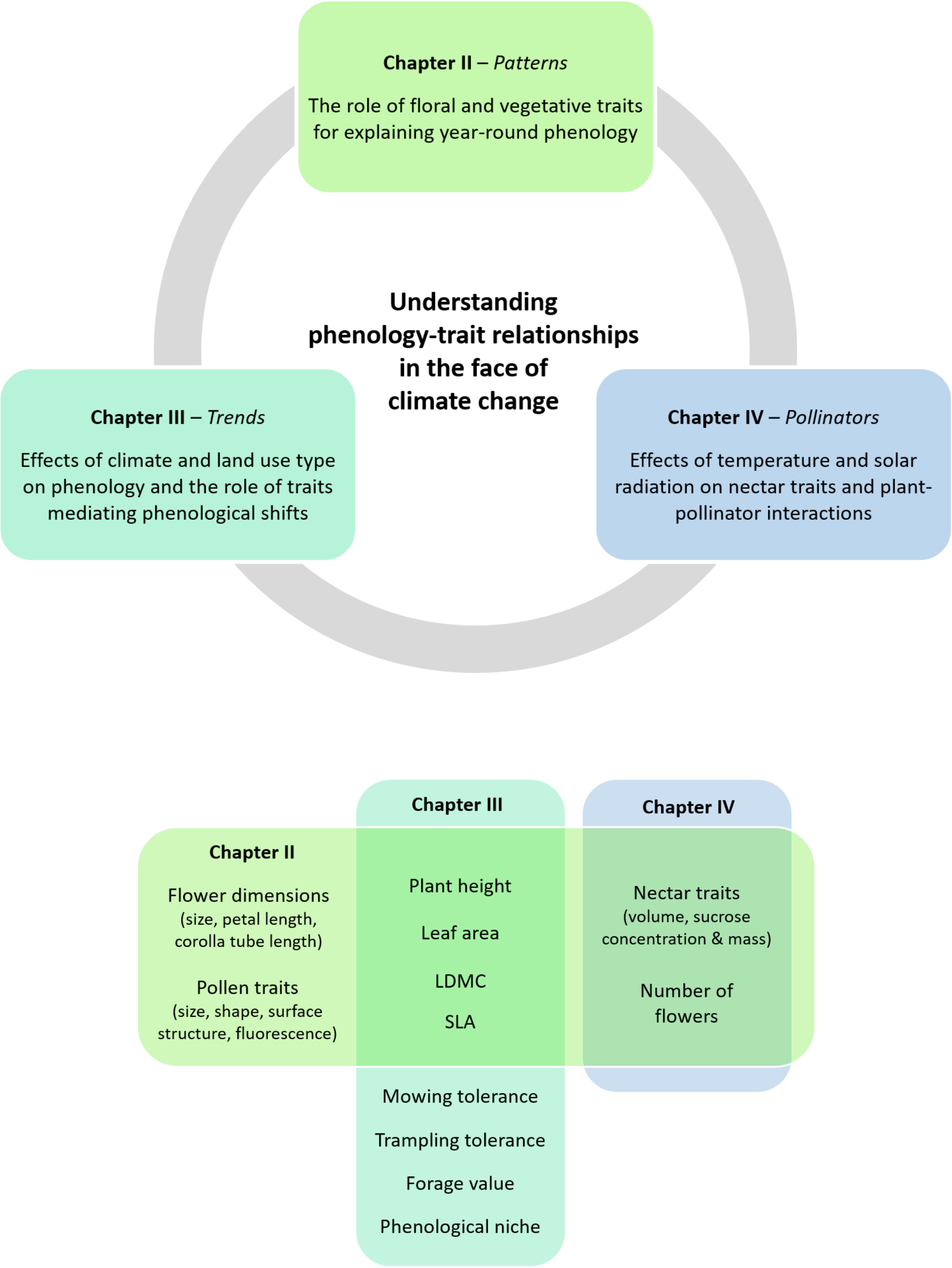


Figure I.2: Overview of the three objectives investigated in Chapters II to IV in this thesis (top), along with an overview of the functional traits that were investigated in each of the chapters (bottom). Abbreviations: LDMC – Leaf dry matter content, SLA – specific leaf area.

References

Ahas, R., Aasa, A., Menzel, A., Fedotova, V.G., Scheifinger, H., 2002. Changes in European spring phenology. International Journal of Climatology 22, 1727–1738. https://doi.org/10.1002/joc.818

Aono Y., Omoto Y., 1994. Estimation of Temperature at Kyoto since the 11th Century. Using Flowering Data of Cherry Trees in Old Documents. J. Agric. Meteorol. 49, 263–272. https://doi.org/10.2480/agrmet.49.263

Bartomeus, I., Ascher, J.S., Wagner, D., Danforth, B.N., Colla, S., Kornbluth, S., Winfree, R., 2011. Climate-associated phenological advances in bee pollinators and bee-pollinated plants. Proceedings of the National Academy of Sciences 108, 20645–20649. https://doi.org/10.1073/pnas.1115559108

Bartoń, K., 2023. MuMIn: Multi-Model Inference.

Baude, M., Kunin, W.E., Boatman, N.D., Conyers, S., Davies, N., Gillespie, M.A.K., Morton, R.D., Smart, S.M., Memmott, J., 2016. Historical nectar assessment reveals the fall and rise of floral resources in Britain. Nature 530, 85–88. https://doi.org/10.1038/nature16532

Blumenthal, D.M., Mueller, K.E., Kray, J.A., Ocheltree, T.W., Augustine, D.J., Wilcox, K.R., 2020. Traits link drought resistance with herbivore defence and plant economics in semi-arid grasslands: The central roles of phenology and leaf dry matter content. Journal of Ecology 108, 2336–2351. https://doi.org/10.1111/1365-2745.13454

Bock, A., Sparks, T.H., Estrella, N., Jee, N., Casebow, A., Schunk, C., Leuchner, M., Menzel, A., 2014. Changes in first flowering dates and flowering duration of 232 plant species on the island of Guernsey. Global Change Biology 20, 3508–3519. https://doi.org/10.1111/gcb.12579

Bolmgren, K., D. Cowan, P., 2008. Time – size tradeoffs: a phylogenetic comparative study of flowering time, plant height and seed mass in a north-temperate flora. Oikos 117, 424–429. https://doi.org/10.1111/j.2007.0030-1299.16142.x

Bucher, S.F., König, P., Menzel, A., Migliavacca, M., Ewald, J., Römermann, C., 2018. Traits and climate are associated with first flowering day in herbaceous species along elevational gradients. Ecology and Evolution 8, 1147–1158. https://doi.org/10.1002/ece3.3720

Bucher, S.F., Römermann, C., 2021. The timing of leaf senescence relates to flowering phenology and functional traits in 17 herbaceous species along elevational gradients. Journal of Ecology 109, 1537–1548. https://doi.org/10.1111/1365-2745.13577

Büntgen, U., Piermattei, A., Krusic, P.J., Esper, J., Sparks, T., Crivellaro, A., 2022. Plants in the UK flower a month earlier under recent warming. Proceedings of the Royal Society B: Biological Sciences 289, 20212456. https://doi.org/10.1098/rspb.2021.2456

Buyantuyev, A., Wu, J., 2012. Urbanization diversifies land surface phenology in arid environments: Interactions among vegetation, climatic variation, and land use pattern in the Phoenix metropolitan region, USA. Landscape and Urban Planning 105, 149–159. https://doi.org/10.1016/j.landurbplan.2011.12.013

Calvin, K., Dasgupta, D., Krinner, G., Mukherji, A., Thorne, P.W., Trisos, C., Romero, J., Aldunce, P., Barrett, K., Blanco, G., Cheung, W.W.L., Connors, S., Denton, F., Diongue-Niang, A., Dodman, D., Garschagen, M., Geden, O., Hayward, B., Jones, C., Jotzo, F., Krug, T., Lasco, R., Lee, Y.-Y., Masson-Delmotte, V., Meinshausen, M., Mintenbeck, K., Mokssit, A., Otto, F.E.L., Pathak, M., Pirani, A., Poloczanska, E., Pörtner, H.-O., Revi, A., Roberts, D.C., Roy, J., Ruane, A.C., Skea, J., Shukla, P.R., Slade, R., Slangen, A., Sokona, Y., Sörensson, A.A., Tignor, M., Van Vuuren, D., Wei, Y.-M., Winkler, H., Zhai, P., Zommers, Z., Hourcade, J.-C., Johnson, F.X., Pachauri, S., Simpson, N.P., Singh, C., Thomas, A., Totin, E., Arias, P., Bustamante, M., Elgizouli, I., Flato, G., Howden, M., Méndez-Vallejo, C., Pereira, J.J., Pichs-Madruga, R., Rose, S.K., Saheb, Y., Sánchez Rodríguez, R., Ürge-Vorsatz, D., Xiao, C., Yassaa, N., Alegría, A., Armour, K., Bednar-Friedl, B., Blok, K., Cissé, G., Dentener, F., Eriksen, S., Fischer, E., Garner, G., Guivarch, C., Haasnoot, M., Hansen, G., Hauser, M., Hawkins, E., Hermans, T., Kopp, R., Leprince-Ringuet, N., Lewis, J., Ley, D., Ludden, C., Niamir, L., Nicholls, Z., Some, S., Szopa, S., Trewin, B., Van Der Wijst, K.-I., Winter, G., Witting, M., Birt, A., Ha, M., Romero, J., Kim, J., Haites, E.F., Jung, Y., Stavins, R., Birt, A., Ha, M., Orendain, D.J.A., Ignon, L., Park, S., Park, Y., Reisinger, A., Cammaramo, D., Fischlin, A., Fuglestvedt, J.S., Hansen, G., Ludden, C., Masson-Delmotte, V., Matthews, J.B.R., Mintenbeck, K., Pirani, A., Poloczanska, E., Leprince-Ringuet, N., Péan, C., 2023. IPCC, 2023: Climate Change 2023: Synthesis Report. Contribution of Working Groups I, II and III to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, H. Lee and J. Romero (eds.)]. IPCC, Geneva, Switzerland. Intergovernmental Panel on Climate Change (IPCC). https://doi.org/10.59327/IPCC/AR6-9789291691647

Carter, S.K., Rudolf, V.H.W., 2019. Shifts in phenological mean and synchrony interact to shape competitive outcomes. Ecology 100, e02826. https://doi.org/10.1002/ecy.2826

Cleland, E.E., Chiariello, N.R., Loarie, S.R., Mooney, H.A., Field, C.B., 2006. Diverse responses of phenology to global changes in a grassland ecosystem. PNAS 103, 13740–13744. https://doi.org/10.1073/pnas.0600815103

Cook, B.I., Wolkovich, E.M., Parmesan, C., 2012. Divergent responses to spring and winter warming drive community level flowering trends. Proceedings of the National Academy of Sciences 109, 9000–9005. https://doi.org/10.1073/pnas.1118364109

Davies, T.J., Wolkovich, E.M., Kraft, N.J.B., Salamin, N., Allen, J.M., Ault, T.R., Betancourt, J.L., Bolmgren, K., Cleland, E.E., Cook, B.I., Crimmins, T.M., Mazer, S.J., McCabe, G.J., Pau, S., Regetz, J., Schwartz, M.D., Travers, S.E., 2013. Phylogenetic conservatism in plant phenology. Journal of Ecology 101, 1520–1530. https://doi.org/10.1111/1365-2745.12154

Davis, C.C., Willis, C.G., Primack, R.B., Miller-Rushing, A.J., 2010. The importance of phylogeny to the study of phenological response to global climate change. Philosophical Transactions of the Royal Society B: Biological Sciences 365, 3201–3213. https://doi.org/10.1098/rstb.2010.0130

Descamps, C., Jambrek, A., Quinet, M., Jacquemart, A.-L., 2021. Warm Temperatures Reduce Flower Attractiveness and Bumblebee Foraging. Insects 12, 493. https://doi.org/10.3390/insects12060493

Descamps, C., Quinet, M., Baijot, A., Jacquemart, A.-L., 2018. Temperature and water stress affect plant–pollinator interactions in Borago officinalis (Boraginaceae). Ecology and Evolution 8, 3443–3456. https://doi.org/10.1002/ece3.3914

Díaz, S., Kattge, J., Cornelissen, J.H.C., Wright, I.J., Lavorel, S., Dray, S., Reu, B., Kleyer, M., Wirth, C., Colin Prentice, I., Garnier, E., Bönisch, G., Westoby, M., Poorter, H., Reich, P.B., Moles, A.T., Dickie, J., Gillison, A.N., Zanne, A.E., Chave, J., Joseph Wright, S., Sheremet'ev, S.N., Jactel, H., Baraloto, C., Cerabolini, B., Pierce, S., Shipley, B., Kirkup, D., Casanoves, F., Joswig, J.S., Günther, A., Falczuk, V., Rüger, N., Mahecha, M.D., Gorné, L.D., 2016. The global spectrum of plant form and function. Nature 529, 167–171. https://doi.org/10.1038/nature16489

Díaz, S., Cabido, M., 2001. Vive la différence: plant functional diversity matters to ecosystem processes. Trends in Ecology & Evolution 16, 646–655. https://doi.org/10.1016/S0169-5347(01)02283-2

Dumandan, P.K.T., Yenni, G.M., Ernest, S.K.M., 2023. Shifts in competitive structures can drive variation in species' phenology. Ecology 104, e4160. https://doi.org/10.1002/ecy.4160

Dunker, S., Motivans, E., Rakosy, D., Boho, D., Mäder, P., Hornick, T., Knight, T.M., 2021. Pollen analysis using multispectral imaging flow cytometry and deep learning. New Phytologist 229, 593–606. https://doi.org/10.1111/nph.16882

Dunne, J.A., Harte, J., Taylor, K.J., 2003. Subalpine Meadow Flowering Phenology Responses to Climate Change: Integrating Experimental and Gradient Methods. Ecological Monographs 73, 69–86. https://doi.org/10.1890/0012-9615(2003)073[0069:SMFPRT]2.0.CO;2

Edlund, A.F., Swanson, R., Preuss, D., 2004. Pollen and Stigma Structure and Function: The Role of Diversity in Pollination. The Plant Cell 16, S84–S97. https://doi.org/10.1105/tpc.015800

Ellenberg, H., Leuschner, C., 2010. Vegetation Mitteleuropas mit den Alpen: in ökologischer, dynamischer und historischer Sicht. Ulmer Verlag, Stuttgart, Germany.

Elzinga, J.A., Atlan, A., Biere, A., Gigord, L., Weis, A.E., Bernasconi, G., 2007. Time after time: flowering phenology and biotic interactions. Trends in Ecology & Evolution 22, 432–439. https://doi.org/10.1016/j.tree.2007.05.006

Estrella, N., Sparks, T.H., Menzel, A., 2007. Trends and temperature response in the phenology of crops in Germany. Global Change Biology 13, 1737–1747. https://doi.org/10.1111/j.1365-2486.2007.01374.x

E-Vojtkó, A., Bello, F., Durka, W., Kühn, I., Götzenberger, L., 2020. The neglected importance of floral traits in trait-based plant community assembly. J Veg Sci 31, 529–539. https://doi.org/10.1111/jvs.12877

E-Vojtkó, A., Junker, R.R., de Bello, F., Götzenberger, L., 2022. Floral and reproductive traits are an independent dimension within the plant economic spectrum of temperate central Europe. New Phytologist 236, 1964–1975. https://doi.org/10.1111/nph.18386

Fabina, N.S., Abbott, K.C., Gilman, R.T., 2010. Sensitivity of plant–pollinator–herbivore communities to changes in phenology. Ecological Modelling 221, 453–458. https://doi.org/10.1016/j.ecolmodel.2009.10.020

Fitter, A.H., Fitter, R.S.R., 2002. Rapid Changes in Flowering Time in British Plants. Science 296, 1689–1691. https://doi.org/10.1126/science.1071617

Flynn, D.F.B., Wolkovich, E.M., 2018. Temperature and photoperiod drive spring phenology across all species in a temperate forest community. New Phytologist 219, 1353–1362. https://doi.org/10.1111/nph.15232

Forrest, J., Miller-Rushing, A.J., 2010. Toward a synthetic understanding of the role of phenology in ecology and evolution. Philosophical Transactions of the Royal Society B: Biological Sciences 365, 3101–3112. https://doi.org/10.1098/rstb.2010.0145

Ge, Q., Wang, H., Rutishauser, T., Dai, J., 2015. Phenological response to climate change in China: a meta-analysis. Global Change Biology 21, 265–274. https://doi.org/10.1111/gcb.12648

Gérard, M., Vanderplanck, M., Wood, T., Michez, D., 2020. Global warming and plant–pollinator mismatches. Emerging Topics in Life Sciences 4, 77–86. https://doi.org/10.1042/ETLS20190139

Griffin-Nolan, R.J., Blumenthal, D.M., Collins, S.L., Farkas, T.E., Hoffman, A.M., Mueller, K.E., Ocheltree, T.W., Smith, M.D., Whitney, K.D., Knapp, A.K., 2019. Shifts in plant functional composition following long-term drought in grasslands. Journal of Ecology 107, 2133–2148. https://doi.org/10.1111/1365-2745.13252

Hassan, T., Gulzar, R., Hamid, M., Ahmad, R., Waza, S.A., Khuroo, A.A., 2023. Plant phenology shifts under climate warming: a systematic review of recent scientific literature. Environ Monit Assess 196, 36. https://doi.org/10.1007/s10661-023-12190-w

Heberling, J.M., McDonough MacKenzie, C., Fridley, J.D., Kalisz, S., Primack, R.B., 2019. Phenological mismatch with trees reduces wildflower carbon budgets. Ecology Letters 22, 616–623. https://doi.org/10.1111/ele.13224

Hegland, S.J., Nielsen, A., Lázaro, A., Bjerknes, A.-L., Totland, Ø., 2009. How does climate warming affect plant-pollinator interactions? Ecology Letters 12, 184–195. https://doi.org/10.1111/j.1461-0248.2008.01269.x

Horbach, S., Rauschkolb, R., Römermann, C., 2023. Flowering and leaf phenology are more variable and stronger associated to functional traits in herbaceous compared to tree species. Flora 300, 152218. https://doi.org/10.1016/j.flora.2023.152218

Hornick, T., Richter, A., Harpole, W.S., Bastl, M., Bohlmann, S., Bonn, A., Bumberger, J., Dietrich, P., Gemeinholzer, B., Grote, R., Heinold, B., Keller, A., Luttkus, M.L., Mäder, P., Motivans Švara, E., Passonneau, S., Punyasena, S.W., Rakosy, D., Richter, R., Sickel, W., Steffan-Dewenter, I., Theodorou, P., Treudler, R., Werchan, B., Werchan, M., Wolke, R., Dunker, S., 2022. An integrative environmental pollen diversity assessment and its importance for the Sustainable Development Goals. PLANTS, PEOPLE, PLANET 4, 110–121. https://doi.org/10.1002/ppp3.10234

Huang, L., Koubek, T., Weiser, M., Herben, T., 2018. Environmental drivers and phylogenetic constraints of growth phenologies across a large set of herbaceous species. Journal of Ecology 106, 1621–1633. https://doi.org/10.1111/1365-2745.12927

Inouye, D.W., 1980. The effect of proboscis and corolla tube lengths on patterns and rates of flower visitation by bumblebees. Oecologia 45, 197–201. https://doi.org/10.1007/BF00346460

Jentsch, A., Kreyling, J., Boettcher-Treschkow, J., Beierkuhnlein, C., 2009. Beyond gradual warming: extreme weather events alter flower phenology of European grassland and heath species. Global Change Biology 15, 837–849. https://doi.org/10.1111/j.1365-2486.2008.01690.x

Kattge, J., Bönisch, G., Díaz, S., Lavorel, S., Prentice, I.C., Leadley, P., Tautenhahn, S., Werner, G.D.A., Aakala, T., Abedi, M., Acosta, A.T.R., Adamidis, G.C., Adamson, K., Aiba, M., Albert, C.H., Alcántara, J.M., Alcázar C, C., Aleixo, I., Ali, H., Amiaud, B., Ammer, C., Amoroso, M.M., Anand, M., Anderson, C., Anten, N., Antos, J., Apgaua, D.M.G., Ashman, T.-L., Asmara, D.H., Asner, G.P., Aspinwall, M., Atkin, O., Aubin, I., Baastrup-Spohr, L., Bahalkeh, K., Bahn, M., Baker, T., Baker, W.J., Bakker, J.P., Baldocchi, D., Baltzer, J., Banerjee, A., Baranger, A., Barlow, J., Barneche, D.R., Baruch, Z., Bastianelli, D., Battles, J., Bauerle, W., Bauters, M., Bazzato, E., Beckmann, M., Beeckman, H., Beierkuhnlein, C., Bekker, R., Belfry, G., Belluau, M., Beloiu, M., Benavides, R., Benomar, L., Berdugo-Lattke, M.L., Berenguer, E., Bergamin, R., Bergmann, J., Bergmann Carlucci, M., Berner, L., Bernhardt-Römermann, M., Bigler, C., Bjorkman, A.D., Blackman, C., Blanco, C., Blonder, B., Blumenthal, D., Bocanegra-González, K.T., Boeckx, P., Bohlman, S., Böhning-Gaese, K., Boisvert-Marsh, L., Bond, W., Bond-Lamberty, B., Boom, A., Boonman, C.C.F., Bordin, K., Boughton, E.H., Boukili, V., Bowman, D.M.J.S., Bravo, S., Brendel, M.R., Broadley, M.R., Brown, K.A., Bruelheide, H., Brumnich, F., Bruun, H.H., Bruy, D., Buchanan, S.W., Bucher, S.F., Buchmann, N., Buitenwerf, R., Bunker, D.E., Bürger, J., Burrascano, S., Burslem, D.F.R.P., Butterfield, B.J., Byun, C., Marques, M., Scalon, M.C., Caccianiga, M., Cadotte, M., Cailleret, M., Camac, J., Camarero, J.J., Campany, C., Campetella, G., Campos, J.A., Cano-Arboleda, L., Canullo, R., Carbognani, M., Carvalho, F., Casanoves, F., Castagneyrol, B., Catford, J.A., Cavender-Bares, J., Cerabolini, B.E.L., Cervellini, M., Chacón-Madrigal, E., Chapin, K., Chapin, F.S., Chelli, S., Chen, S.-C., Chen, A., Cherubini, P., Chianucci, F., Choat, B., Chung, K.-S., Chytrý, M., Ciccarelli, D., Coll, L., Collins, C.G., Conti, L., Coomes, D., Cornelissen, J.H.C., Cornwell, W.K., Corona, P., Coyea, M., Craine, J., Craven, D., Cromsigt, J.P.G.M., Csecserits, A., Cufar, K., Cuntz, M., da Silva, A.C., Dahlin, K.M., Dainese, M., Dalke, I., Dalle Fratte, M., Dang-Le, A.T., Danihelka, J., Dannoura, M., Dawson, S., de Beer, A.J., De Frutos, A., De Long, J.R., Dechant, B., Delagrange, S., Delpierre, N., Derroire, G., Dias, A.S., Diaz-Toribio, M.H., Dimitrakopoulos, P.G., Dobrowolski, M., Doktor, D., Dřevojan, P., Dong, N., Dransfield, J., Dressler, S., Duarte, L., Ducouret, E., Dullinger, S., Durka, W., Duursma, R., Dymova, O., E-Vojtkó, A., Eckstein, R.L., Ejtehadi, H., Elser, J., Emilio, T., Engemann, K., Erfanian, M.B., Erfmeier, A., Esquivel-Muelbert, A., Esser, G., Estiarte, M., Domingues, T.F., Fagan, W.F., Fagúndez, J., Falster, D.S., Fan, Y., Fang, J., Farris, E., Fazlioglu, F., Feng, Y., Fernandez-Mendez, F., Ferrara, C., Ferreira, J., Fidelis, A., Finegan, B., Firn, J., Flowers, T.J., Flynn, D.F.B., Fontana, V., Forey, E., Forgiarini, C., François, L., Frangipani, M., Frank, D., Frenette-Dussault, C., Freschet, G.T., Fry, E.L., Fyllas, N.M., Mazzochini, G.G., Gachet, S., Gallagher, R., Ganade, G., Ganga, F., García-Palacios, P., Gargaglione, V., Garnier, E., Garrido, J.L., de Gasper, A.L., Gea-Izquierdo, G., Gibson, D., Gillison, A.N., Giroldo, A., Glasenhardt, M.-C., Gleason, S., Gliesch, M., Goldberg, E., Göldel, B., Gonzalez-Akre, E., Gonzalez-Andujar, J.L., González-Melo, A., González-Robles, A., Graae, B.J., Granda, E., Graves, S., Green, W.A., Gregor, T., Gross, N., Guerin, G.R., Günther, A., Gutiérrez, A.G., Haddock, L., Haines, A., Hall, J., Hambuckers, A., Han, W., Harrison, S.P., Hattingh, W., Hawes, J.E., He, T., He, P., Heberling, J.M., Helm, A., Hempel, S., Hentschel, J., Hérault, B., Hereş, A.-M., Herz, K., Heuertz, M., Hickler, T., Hietz, P., Higuchi, P., Hipp, A.L., Hirons, A., Hock, M., Hogan, J.A., Holl, K., Honnay, O., Hornstein, D., Hou, E., Hough-Snee, N., Hovstad, K.A., Ichie, T., Igić, B., Illa, E., Isaac, M., Ishihara, M., Ivanov, L., Ivanova, L., Iversen, C.M., Izquierdo, J., Jackson, R.B., Jackson, B., Jactel, H., Jagodzinski, A.M., Jandt, U., Jansen, S., Jenkins, T., Jentsch, A., Jespersen, J.R.P., Jiang, G.-F., Johansen, J.L., Johnson, D., Jokela, E.J., Joly, C.A., Jordan, G.J., Joseph, G.S., Junaedi, D., Junker, R.R., Justes, E., Kabzems, R., Kane, J., Kaplan, Z., Kattenborn, T., Kavelenova, L., Kearsley, E., Kempel, A., Kenzo, T., Kerkhoff, A., Khalil, M.I., Kinlock, N.L., Kissling, W.D., Kitajima, K., Kitzberger, T., Kjøller, R., Klein, T., Kleyer, M., Klimešová, J., Klipel, J., Kloeppel, B., Klotz, S., Knops, J.M.H., Kohyama, T., Koike, F., Kollmann, J., Komac, B., Komatsu, K., König, C., Kraft, N.J.B., Kramer, K., Kreft, H., Kühn, I., Kumarathunge, D., Kuppler, J., Kurokawa, H., Kurosawa, Y., Kuyah, S., Laclau, J.-P., Lafleur, B., Lallai, E., Lamb, E., Lamprecht, A., Larkin, D.J., Laughlin, D., Le Bagousse-Pinguet, Y., le Maire, G., le Roux, P.C., le Roux, E., Lee, T., Lens, F., Lewis, S.L., Lhotsky, B., Li, Y., Li, X., Lichstein, J.W., Liebergesell, M., Lim, J.Y., Lin, Y.-S., Linares, J.C., Liu, C., Liu, D., Liu, U., Livingstone, S., Llusià, J., Lohbeck, M., López-García, Á., Lopez-Gonzalez, G., Lososová, Z., Louault, F., Lukács, B.A., Lukeš, P., Luo, Y., Lussu, M., Ma, S., Maciel Rabelo Pereira, C., Mack, M., Maire, V., Mäkelä, A., Mäkinen, H., Malhado, A.C.M., Mallik, A., Manning, P., Manzoni, S., Marchetti, Z., Marchino, L., Marcilio-Silva, V., Marcon, E., Marignani, M., Markesteijn, L., Martin, A., Martínez-Garza, C., Martínez-Vilalta, J., Mašková, T., Mason, K., Mason, N., Massad, T.J., Masse, J., Mayrose, I., McCarthy, J., McCormack, M.L., McCulloh, K., McFadden, I.R., McGill, B.J., McPartland, M.Y., Medeiros, J.S., Medlyn, B., Meerts, P., Mehrabi, Z., Meir, P., Melo, F.P.L., Mencuccini, M., Meredieu, C., Messier, J., Mészáros, I., Metsaranta, J., Michaletz, S.T., Michelaki, C., Migalina, S., Milla, R., Miller, J.E.D., Minden, V., Ming, R., Mokany, K., Moles, A.T., Molnár V, A., Molofsky, J., Molz, M., Montgomery, R.A., Monty, A., Moravcová, L., Moreno-Martínez, A., Moretti, M., Mori, A.S., Mori, S., Morris, D., Morrison, J., Mucina, L., Mueller, S., Muir, C.D., Müller, S.C., Munoz, F., Myers-Smith, I.H., Myster, R.W., Nagano, M., Naidu, S., Narayanan, A., Natesan, B., Negoita, L., Nelson, A.S., Neuschulz, E.L., Ni, J., Niedrist, G., Nieto, J., Niinemets, Ü., Nolan, R., Nottebrock, H., Nouvellon, Y., Novakovskiy, A., Network, T.N., Nystuen, K.O., O'Grady, A., O'Hara, K., O'Reilly-Nugent, A., Oakley, S., Oberhuber, W., Ohtsuka, T., Oliveira, R., Öllerer, K., Olson, M.E., Onipchenko, V., Onoda, Y., Onstein, R.E., Ordonez, J.C., Osada, N., Ostonen, I., Ottaviani, G., Otto, S., Overbeck, G.E., Ozinga, W.A., Pahl, A.T., Paine, C.E.T., Pakeman, R.J., Papageorgiou, A.C., Parfionova, E., Pärtel, M., Patacca, M., Paula, S., Paule, J., Pauli, H., Pausas, J.G., Peco, B., Penuelas, J., Perea, A., Peri, P.L., Petisco-Souza, A.C., Petraglia, A., Petritan, A.M., Phillips, O.L., Pierce, S., Pillar, V.D., Pisek, J., Pomogaybin, A., Poorter, H., Portsmuth, A., Poschlod, P., Potvin, C., Pounds, D., Powell, A.S., Power, S.A., Prinzing, A., Puglielli, G., Pyšek, P., Raevel, V., Rammig, A., Ransijn, J., Ray, C.A., Reich, P.B., Reichstein, M., Reid, D.E.B., Réjou-Méchain, M., de Dios, V.R., Ribeiro, S., Richardson, S., Riibak, K., Rillig, M.C., Riviera, F., Robert, E.M.R., Roberts, S., Robroek, B., Roddy, A., Rodrigues, A.V., Rogers, A., Rollinson, E., Rolo, V., Römermann, C., Ronzhina, D., Roscher, C., Rosell, J.A., Rosenfield, M.F., Rossi, C., Roy, D.B., Royer-Tardif, S., Rüger, N., Ruiz-Peinado, R., Rumpf, S.B., Rusch, G.M., Ryo, M., Sack, L., Saldaña, A., Salgado-Negret, B., Salguero-Gomez, R., Santa-Regina, I., Santacruz-García, A.C., Santos, J., Sardans, J., Schamp, B., Scherer-Lorenzen, M., Schleuning, M., Schmid, B., Schmidt, M., Schmitt, S., Schneider, J.V., Schowanek, S.D., Schrader, J., Schrodt, F., Schuldt, B., Schurr, F., Selaya Garvizu, G., Semchenko, M., Seymour, C., Sfair, J.C., Sharpe, J.M., Sheppard, C.S., Sheremetiev, S., Shiodera, S., Shipley, B., Shovon, T.A., Siebenkäs, A., Sierra, C., Silva, V., Silva, M., Sitzia, T., Sjöman, H., Slot, M., Smith, N.G., Sodhi, D., Soltis, P., Soltis, D., Somers, B., Sonnier, G., Sørensen, M.V., Sosinski Jr, E.E., Soudzilovskaia, N.A., Souza, A.F., Spasojevic, M., Sperandii, M.G., Stan, A.B., Stegen, J., Steinbauer, K., Stephan, J.G., Sterck, F., Stojanovic, D.B., Strydom, T., Suarez, M.L., Svenning, J.-C., Svitková, I., Svitok, M., Svoboda, M., Swaine, E., Swenson, N., Tabarelli, M., Takagi, K., Tappeiner, U., Tarifa, R., Tauugourdeau, S., Tavsanoglu, C., te Beest, M., Tedersoo, L., Thiffault, N., Thom, D., Thomas, E., Thompson, K., Thornton, P.E., Thuiller, W., Tichý, L., Tissue, D., Tjoelker, M.G., Tng, D.Y.P., Tobias, J., Török, P., Tarin, T., Torres-Ruiz, J.M., Tóthmérész, B., Treurnicht, M., Trivellone, V., Trolliet, F., Trotsiuk, V., Tsakalos, J.L., Tsiripidis, I., Tysklind, N., Umehara, T., Usoltsev, V., Vadeboncoeur, M., Vaezi, J., Valladares, F., Vamosi, J., van Bodegom, P.M., van Breugel, M., Van Cleemput, E., van de Weg, M., van der Merwe, S., van der Plas, F., van der Sande, M.T., van Kleunen, M., Van Meerbeek, K., Vanderwel, M., Vanselow, K.A., Vårhammar, A., Varone, L., Vasquez Valderrama, M.Y., Vassilev, K., Vellend, M., Veneklaas, E.J., Verbeeck, H., Verheyen, K., Vibrans, A., Vieira, I., Villacís, J., Violle, C., Vivek, P., Wagner, K., Waldram, M., Waldron, A., Walker, A.P., Waller, M., Walther, G., Wang, H., Wang, F., Wang, W., Watkins, H., Watkins, J., Weber, U., Weedon, J.T., Wei, L., Weigelt, P., Weiher, E., Wells, A.W., Wellstein, C., Wenk, E., Westoby, M., Westwood, A., White, P.J., Whitten, M., Williams, M., Winkler, D.E., Winter, K., Womack, C., Wright, I.J., Wright, S.J., Wright, J., Pinho, B.X., Ximenes, F., Yamada, T., Yamaji, K., Yanai, R., Yankov, N., Yguel, B., Zanini, K.J., Zanne, A.E., Zelený, D., Zhao, Y.-P., Zheng, Jingming, Zheng, Ji, Ziemińska, K., Zirbel, C.R., Zizka, G., Zo-Bi, I.C., Zotz, G., Wirth, C., 2020. TRY plant trait database – enhanced coverage and open access. Global Change Biology 26, 119–188. https://doi.org/10.1111/gcb.14904

Kleyer, M., Bekker, R. m., Knevel, I. c., Bakker, J. p., Thompson, K., Sonnenschein, M., Poschlod, P., Van Groenendael, J. m., Klimeš, L., Klimešová, J., Klotz, S., Rusch, G. m., Hermy, M., Adriaens, D., Boedeltje, G., Bossuyt, B., Dannemann, A., Endels, P., Götzenberger, L., Hodgson, J. g., Jackel, A.-K., Kühn, I., Kunzmann, D., Ozinga, W. a., Römermann, C., Stadler, M., Schlegelmilch, J., Steendam, H. j., Tackenberg, O., Wilmann, B., Cornelissen, J. h. c., Eriksson, O., Garnier, E., Peco, B., 2008. The LEDA Traitbase: a database of life-history traits of the Northwest European flora. Journal of Ecology 96, 1266–1274. https://doi.org/10.1111/j.1365-2745.2008.01430.x

Klotz, S., Kühn, I., Durka, W., 2002. BiolFlor: Eine Datenbank mit biologisch-ökologischen Merkmalen zur Flora von Deutschland. Schriftenreihe für Vegetationskunde, Bonn: Bundesamt für Naturschutz.

König, P., Tautenhahn, S., Cornelissen, J.H.C., Kattge, J., Bönisch, G., Römermann, C., 2018. Advances in flowering phenology across the Northern Hemisphere are explained by functional traits. Global Ecology and Biogeography 27, 310–321. https://doi.org/10.1111/geb.12696

Kudo, G., Cooper, E.J., 2019. When spring ephemerals fail to meet pollinators: mechanism of phenological mismatch and its impact on plant reproduction. Proceedings of the Royal Society B: Biological Sciences 286, 20190573. https://doi.org/10.1098/rspb.2019.0573

Kudo, G., Ida, T.Y., 2013. Early onset of spring increases the phenological mismatch between plants and pollinators. Ecology 94, 2311–2320. https://doi.org/10.1890/12-2003.1

Kugler, H., 1970. Blütenökologie, 2. Auflage. ed. Gustav Fischer Verlag, Jena.

Lemoine, N.P., Doublet, D., Salminen, J.-P., Burkepile, D.E., Parker, J.D., 2017. Responses of plant phenology, growth, defense, and reproduction to interactive effects of warming and insect herbivory. Ecology 98, 1817–1828. https://doi.org/10.1002/ecy.1855

Lesica, P., Kittelson, P.M., 2010. Precipitation and temperature are associated with advanced flowering phenology in a semi-arid grassland. Journal of Arid Environments 74, 1013–1017. https://doi.org/10.1016/j.jaridenv.2010.02.002

Liu, Y., Li, G., Wu, X., Niklas, K.J., Yang, Z., Sun, S., 2021. Linkage between species traits and plant phenology in an alpine meadow. Oecologia 195, 409–419. https://doi.org/10.1007/s00442-020-04846-y

Meineke, E.K., Davis, C.C., Davies, T.J., 2021. Phenological sensitivity to temperature mediates herbivory. Global Change Biology 27, 2315–2327. https://doi.org/10.1111/gcb.15600

Memmott, J., Craze, P.G., Waser, N.M., Price, M.V., 2007. Global warming and the disruption of plant–pollinator interactions. Ecology Letters 10, 710–717. https://doi.org/10.1111/j.1461-0248.2007.01061.x

Meng, L., Zhou, Y., Gu, L., Richardson, A.D., Peñuelas, J., Fu, Y., Wang, Y., Asrar, G.R., De Boeck, H.J., Mao, J., Zhang, Y., Wang, Z., 2021. Photoperiod decelerates the advance of spring phenology of six deciduous tree species under climate warming. Global Change Biology 27, 2914–2927. https://doi.org/10.1111/gcb.15575

Menzel, A., Fabian, P., 1999. Growing season extended in Europe. Nature 397, 659. https://doi.org/10.1038/17709

Menzel, A., Sparks, T.H., Estrella, N., Koch, E., Aasa, A., Ahas, R., Alm-Kübler, K., Bissolli, P., Braslavská, O., Briede, A., Chmielewski, F.M., Crepinsek, Z., Curnel, Y., Dahl, Å., Defila, C., Donnelly, A., Filella, Y., Jatczak, K., Måge, F., Mestre, A., Nordli, Ø., Peñuelas, J., Pirinen, P., Remišová, V., Scheifinger, H., Striz, M., Susnik, A., Van Vliet, A.J.H., Wielgolaski, F.-E., Zach, S., Zust, A., 2006. European phenological response to climate change matches the warming pattern. Global Change Biology 12, 1969–1976. https://doi.org/10.1111/j.1365-2486.2006.01193.x

Menzel, A., Yuan, Y., Matiu, M., Sparks, T., Scheifinger, H., Gehrig, R., Estrella, N., 2020. Climate change fingerprints in recent European plant phenology. Global Change Biology 26, 2599–2612. https://doi.org/10.1111/gcb.15000

Miller-Rushing, A.J., Primack, R.B., 2008. Global Warming and Flowering Times in Thoreau's Concord: A Community Perspective. Ecology 89, 332–341. https://doi.org/10.1890/07-0068.1

Miller-Struttmann, N.E., Geib, J.C., Franklin, J.D., Kevan, P.G., Holdo, R.M., Ebert-May, D., Lynn, A.M., Kettenbach, J.A., Hedrick, E., Galen, C., 2015. Functional mismatch in a bumble bee pollination mutualism under climate change. Science 349, 1541–1544. https://doi.org/10.1126/science.aab0868

Mori, S., Fukui, H., Oishi, M., Sakuma, M., Kawakami, M., Tsukioka, J., Goto, K., Hirai, N., 2018. Biocommunication between Plants and Pollinating Insects through Fluorescence of Pollen and Anthers. J Chem Ecol 44, 591–600. https://doi.org/10.1007/s10886-018-0958-9

Nakazawa, T., Doi, H., 2012. A perspective on match/mismatch of phenology in community contexts. Oikos 121, 489–495. https://doi.org/10.1111/j.1600-0706.2011.20171.x

Nock, C.A., Vogt, R.J., Beisner, B.E., 2016. Functional Traits, in: Encyclopedia of Life Sciences. Wiley, pp. 1–8. https://doi.org/10.1002/9780470015902.a0026282

Nord, E.A., Lynch, J.P., 2009. Plant phenology: a critical controller of soil resource acquisition. Journal of Experimental Botany 60, 1927–1937. https://doi.org/10.1093/jxb/erp018

Pacini, E., Nicolson, S.W., 2007. Introduction, in: Nicolson, S.W., Nepi, M., Pacini, E. (Eds.), Nectaries and Nectar. Springer Netherlands, Dordrecht, pp. 1–18. https://doi.org/10.1007/978-1-4020-5937-7_1

Panchen, Z.A., Primack, R.B., Nordt, B., Ellwood, E.R., Stevens, A.-D., Renner, S.S., Willis, C.G., Fahey, R., Whittemore, A., Du, Y., Davis, C.C., 2014. Leaf out times of temperate woody plants are related to phylogeny, deciduousness, growth habit and wood anatomy. New Phytologist 203, 1208–1219. https://doi.org/10.1111/nph.12892

Pareja-Bonilla, D., Arista, M., Morellato, L.P.C., Ortiz, P.L., 2023. Better soon than never: climate change induces strong phenological reassembly in the flowering of a Mediterranean shrub community. Annals of Botany mcad193. https://doi.org/10.1093/aob/mcad193

Parmesan, C., Yohe, G., 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature 421, 37–42. https://doi.org/10.1038/nature01286

Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., Bret-Harte, M.S., Cornwell, W.K., Craine, J.M., Gurvich, D.E., Urcelay, C., Veneklaas, E.J., Reich, P.B., Poorter, L., Wright, I.J., Ray, P., Enrico, L., Pausas, J.G., Vos, A.C. de, Buchmann, N., Funes, G., Quétier, F., Hodgson, J.G., Thompson, K., Morgan, H.D., Steege, H. ter, Sack, L., Blonder, B., Poschlod, P., Vaieretti, M.V., Conti, G., Staver, A.C., Aquino, S., Cornelissen, J.H.C., 2016. Corrigendum to: New handbook for standardised measurement of plant functional traits worldwide. Aust. J. Bot. 64, 715–716. https://doi.org/10.1071/bt12225_co

Petanidou, T., Kallimanis, A.S., Sgardelis, S.P., Mazaris, A.D., Pantis, J.D., Waser, N.M., 2014. Variable flowering phenology and pollinator use in a community suggest future phenological mismatch. Acta Oecologica 59, 104–111. https://doi.org/10.1016/j.actao.2014.06.001

Phillips, B.B., Shaw, R.F., Holland, M.J., Fry, E.L., Bardgett, R.D., Bullock, J.M., Osborne, J.L., 2018. Drought reduces floral resources for pollinators. Global Change Biology 24, 3226–3235. https://doi.org/10.1111/gcb.14130

Piao, S., Liu, Q., Chen, A., Janssens, I.A., Fu, Y., Dai, J., Liu, L., Lian, X., Shen, M., Zhu, X., 2019. Plant phenology and global climate change: Current progresses and challenges. Global Change Biology 25, 1922–1940. https://doi.org/10.1111/gcb.14619

Post, E., Pedersen, C., Wilmers, C.C., Forchhammer, M.C., 2008. Warming, plant phenology and the spatial dimension of trophic mismatch for large herbivores. Proceedings of the Royal Society B: Biological Sciences 275, 2005–2013. https://doi.org/10.1098/rspb.2008.0463

Primack, R.B., Higuchi, H., Miller-Rushing, A.J., 2009. The impact of climate change on cherry trees and other species in Japan. Biological Conservation, The Conservation and Management of Biodiversity in Japan 142, 1943–1949. https://doi.org/10.1016/j.biocon.2009.03.016

Rafferty, N.E., Ives, A.R., 2011. Effects of experimental shifts in flowering phenology on plant–pollinator interactions. Ecology Letters 14, 69–74. https://doi.org/10.1111/j.1461-0248.2010.01557.x

Rauschkolb, R., Bucher, S.F., Hensen, I., Ahrends, A., Fernández-Pascual, E., Heubach, K., Jakubka, D., Jiménez-Alfaro, B., König, A., Koubek, T., Kehl, A., Khuroo, A.A., Lindstädter, A., Shafee, F., Mašková, T., Platonova, E., Panico, P., Plos, C., Primack, R., Rosche, C., Shah, M.A., Sporbert, M., Stevens, A.-D., Tarquini, F., Tielbörger, K., Träger, S., Vange, V., Weigelt, P., Bonn, A., Freiberg, M., Knickmann, B., Nordt, B., Wirth, C., Römermann, C., 2024. Spatial variability in herbaceous plant phenology is mostly explained by variability in temperature but also by photoperiod and functional traits. Int J Biometeorol. https://doi.org/10.1007/s00484-024-02621-9

Reisch, C., Poschlod, P., 2009. Land use affects flowering time: seasonal and genetic differentiation in the grassland plant Scabiosa columbaria. Evol Ecol 23, 753–764. https://doi.org/10.1007/s10682-008-9270-4

Rering, C.C., Franco, J.G., Yeater, K.M., Mallinger, R.E., 2020. Drought stress alters floral volatiles and reduces floral rewards, pollinator activity, and seed set in a global plant. Ecosphere 11, e03254. https://doi.org/10.1002/ecs2.3254

Roddy, A.B., Martínez-Perez, C., Teixido, A.L., Cornelissen, T.G., Olson, M.E., Oliveira, R.S., Silveira, F.A.O., 2021. Towards the flower economics spectrum. New Phytologist 229, 665–672. https://doi.org/10.1111/nph.16823

Romo-Leon, J.R., van Leeuwen, W.J.D., Castellanos-Villegas, A., 2016. Land Use and Environmental Variability Impacts on the Phenology of Arid Agro-Ecosystems. Environmental Management 57, 283–297. https://doi.org/10.1007/s00267-015-0617-7

Root, T.L., Price, J.T., Hall, K.R., Schneider, S.H., Rosenzweig, C., Pounds, J.A., 2003. Fingerprints of global warming on wild animals and plants. Nature 421, 57–60. https://doi.org/10.1038/nature01333

Rudolf, V.H.W., 2019. The role of seasonal timing and phenological shifts for species coexistence. Ecology Letters 22, 1324–1338. https://doi.org/10.1111/ele.13277

Scaven, V.L., Rafferty, N.E., 2013. Physiological effects of climate warming on flowering plants and insect pollinators and potential consequences for their interactions. Current Zoology 59, 418–426. https://doi.org/10.1093/czoolo/59.3.418

Sporbert, M., Jakubka, D., Bucher, S.F., Hensen, I., Freiberg, M., Heubach, K., König, A., Nordt, B., Plos, C., Blinova, I., Bonn, A., Knickmann, B., Koubek, T., Linstädter, A., Mašková, T., Primack, R.B., Rosche, C., Shah, M.A., Stevens, A.-D., Tielbörger, K., Träger, S., Wirth, C., Römermann, C., 2022. Functional traits influence patterns in vegetative and reproductive plant phenology – a multi-botanical garden study. New Phytologist 235, 2199–2210. https://doi.org/10.1111/nph.18345

Stemkovski, M., Pearse, W.D., Griffin, S.R., Pardee, G.L., Gibbs, J., Griswold, T., Neff, J.L., Oram, R., Rightmyer, M.G., Sheffield, C.S., Wright, K., Inouye, B.D., Inouye, D.W., Irwin, R.E., 2020. Bee phenology is predicted by climatic variation and functional traits. Ecology Letters 23, 1589–1598. https://doi.org/10.1111/ele.13583

Sun, S., Frelich, L.E., 2011. Flowering phenology and height growth pattern are associated with maximum plant height, relative growth rate and stem tissue mass density in herbaceous grassland species. Journal of Ecology 99, 991–1000. https://doi.org/10.1111/j.1365-2745.2011.01830.x

Sun, S., Jin, D., Li, R., 2006. Leaf emergence in relation to leaf traits in temperate woody species in East-Chinese *Quercus fabri* forests. Acta Oecologica 30, 212–222. https://doi.org/10.1016/j.actao.2006.04.001

Tadey, M., 2020. Reshaping phenology: Grazing has stronger effects than climate on flowering and fruiting phenology in desert plants. Perspectives in Plant Ecology, Evolution and Systematics 42, 125501. https://doi.org/10.1016/j.ppees.2019.125501

Taha, E.-K.A., Al-Kahtani, S., Taha, R., 2019. Protein content and amino acids composition of bee-pollens from major floral sources in Al-Ahsa, eastern Saudi Arabia. Saudi Journal of Biological Sciences 26, 232–237. https://doi.org/10.1016/j.sjbs.2017.06.003

Takkis, K., Tscheulin, T., Petanidou, T., 2018. Differential Effects of Climate Warming on the Nectar Secretion of Early- and Late-Flowering Mediterranean Plants. Front. Plant Sci. 9. https://doi.org/10.3389/fpls.2018.00874

Ulrich, J., Bucher, S.F., Eisenhauer, N., Schmidt, A., Türke, M., Gebler, A., Barry, K., Lange, M., Römermann, C., 2020. Invertebrate Decline Leads to Shifts in Plant Species Abundance and Phenology. Front. Plant Sci. 11. https://doi.org/10.3389/fpls.2020.542125

Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., Garnier, E., 2007. Let the concept of trait be functional! Oikos 116, 882–892. https://doi.org/10.1111/j.0030-1299.2007.15559.x

Visakorpi, K., Block, S., Pellissier, L., Levine, J.M., Alexander, J., 2023. Eco-physiological and morphological traits explain alpine plant species’ response to warming. Functional Ecology 37, 287–301. https://doi.org/10.1111/1365-2435.14228

Visser, M.E., Gienapp, P., 2019. Evolutionary and demographic consequences of phenological mismatches. Nat Ecol Evol 3, 879–885. https://doi.org/10.1038/s41559-019-0880-8

Vitasse, Y., 2013. Ontogenic changes rather than difference in temperature cause understory trees to leaf out earlier. New Phytologist 198, 149–155. https://doi.org/10.1111/nph.12130

Vitasse, Y., François, C., Delpierre, N., Dufrêne, E., Kremer, A., Chuine, I., Delzon, S., 2011. Assessing the effects of climate change on the phenology of European temperate trees. Agricultural and Forest Meteorology 151, 969–980. https://doi.org/10.1016/j.agrformet.2011.03.003

Völler, E., Auge, H., Bossdorf, O., Prati, D., 2013. Land use causes genetic differentiation of life-history traits in Bromus hordeaceus. Global Change Biology 19, 892–899. https://doi.org/10.1111/gcb.12087

Wang, L., Han, X., Yin, Q., Wang, G., Xu, J., Chai, Y., Yue, M., 2021. Differences in leaf phenological traits between trees and shrubs are closely related to functional traits in a temperate forest. Acta Oecologica 112, 103760. https://doi.org/10.1016/j.actao.2021.103760

Williams, J.H., Mazer, S.J., 2016. Pollen—Tiny and ephemeral but not forgotten: New ideas on their ecology and evolution. American Journal of Botany 103, 365–374. https://doi.org/10.3732/ajb.1600074

Willmer, P., 2011a. Living with Other Flowers: Competition and Pollination Ecology, in: Willmer, P. (Ed.), Pollination and Floral Ecology. Princeton University Press, p. 0. https://doi.org/10.23943/princeton/9780691128610.003.0022

Willmer, P., 2011b. Why Pollination Is Interesting, in: Willmer, P. (Ed.), Pollination and Floral Ecology. Princeton University Press, p. 0. https://doi.org/10.23943/princeton/9780691128610.003.0001

Willmer, P., 2011c. Floral Design and Function, in: Willmer, P. (Ed.), Pollination and Floral Ecology. Princeton University Press, p. 0. https://doi.org/10.23943/princeton/9780691128610.003.0002

Willmer, P., 2011d. Rewards 1: The Biology of Pollen, in: Willmer, P. (Ed.), Pollination and Floral Ecology. Princeton University Press, p. 0. https://doi.org/10.23943/princeton/9780691128610.003.0007

Willmer, P., 2011e. Rewards 2: The Biology of Nectar, in: Willmer, P. (Ed.), Pollination and Floral Ecology. Princeton University Press, p. 0. https://doi.org/10.23943/princeton/9780691128610.003.0008

Wolf, A.A., Zavaleta, E.S., Selmants, P.C., 2017. Flowering phenology shifts in response to biodiversity loss. Proceedings of the National Academy of Sciences 114, 3463–3468. https://doi.org/10.1073/pnas.1608357114

Wolkovich, E.M., Cleland, E.E., 2011. The phenology of plant invasions: a community ecology perspective. Frontiers in Ecology and the Environment 9, 287–294. https://doi.org/10.1890/100033

Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J.H.C., Diemer, M., Flexas, J., Garnier, E., Groom, P.K., Gulias, J., Hikosaka, K., Lamont, B.B., Lee, T., Lee, W., Lusk, C., Midgley, J.J., Navas, M.-L., Niinemets, Ü., Oleksyn, J., Osada, N., Poorter, H., Poot, P., Prior, L., Pyankov, V.I., Roumet, C., Thomas, S.C., Tjoelker, M.G., Veneklaas, E.J., Villar, R., 2004. The worldwide leaf economics spectrum. Nature 428, 821–827. https://doi.org/10.1038/nature02403

Zhang, B., Hautier, Y., Tan, X., You, C., Cadotte, M.W., Chu, C., Jiang, L., Sui, X., Ren, T., Han, X., Chen, S., 2020. Species responses to changing precipitation depend on trait plasticity rather than trait means and intraspecific variation. Functional Ecology 34, 2622–2633. https://doi.org/10.1111/1365-2435.13675

Zhang, X., Li, B., Peñuelas, J., Sardans, J., Cheng, D., Yu, H., Zhong, Q., 2023. Resource-acquisitive species have greater plasticity in leaf functional traits than resource-conservative species in response to nitrogen addition in subtropical China. Science of The Total Environment 903, 166177. https://doi.org/10.1016/j.scitotenv.2023.166177

Zhang, X., Liu, L., Henebry, G.M., 2019. Impacts of land cover and land use change on long-term trend of land surface phenology: a case study in agricultural ecosystems. Environ. Res. Lett. 14, 044020. https://doi.org/10.1088/1748-9326/ab04d2

Zhou, H., Min, X., Chen, J., Lu, C., Huang, Y., Zhang, Z., Liu, H., 2023. Climate warming interacts with other global change drivers to influence plant phenology: A meta-analysis of experimental studies. Ecology Letters 26, 1370–1381. https://doi.org/10.1111/ele.14259

Chapter II

Interspecific phenological variation in herbaceous species is more strongly reflected in vegetative traits than in floral traits

This chapter has been submitted to *Journal of Ecology* as:

Plos, C., Hornick, T., Dunker, S., Sporbert, M., Jakubka, D., Nordt, B., Lenk, A., Walther, F., Hensen, I., Römermann, C. Interspecific phenological variation in herbaceous species is more strongly reflected in vegetative traits than in floral traits

Abstract

1. Understanding the role of functional traits in constraining interspecific variation of plant phenology can shed light on an organism's ability to adapt to changing environmental conditions. As climate change alters the seasonal timing affecting ecological interactions, knowledge on phenology-trait relationships is crucial for predicting species' responses and potential mismatches between interacting species.

2. While vegetative traits (e.g., plant height, leaf area) are often associated to patterns of phenological variation, floral traits (e.g., floral morphology, flower number, nectar, and pollen traits), which are closely linked to reproductive success, have so received little attention, although they may play a distinct role in shaping phenology.

3. This study aims at understanding the relative influence of floral and vegetative traits on patterns of species-specific phenological variation. As a basis for the inclusion of floral traits in studies on phenology-trait relationships, we further investigated underlying trait correlations and trade-offs between floral and vegetative traits including rarely measured pollen and nectar traits.

4. We monitored the year-round phenology (initial growth, leaf out, flowering, fruiting, senescence) of 68 herbaceous plant species in three German botanical gardens (Halle, Jena, Berlin). In addition to the four vegetative traits, plant height, leaf area, specific leaf area (SLA), and leaf dry matter content (LDMC), 12 floral traits related to flower morphology, flower number, nectar and pollen traits were measured.

5. Analysis of boosted regression trees that accounted for phylogenetic dependence of the species showed that vegetative traits, especially vegetative height, were most important in explaining the patterns in reproductive and vegetative phenology. Taller plants showed initial growth, flowering and fruiting later compared to smaller plants and a higher LDMC was associated to later senescence. Floral traits had additional relative influence on phenological patterns but were of overall minor importance.

6. Synthesis: Our study confirms that vegetative traits offer a robust explanatory framework for phenology, while also emphasizing the value of considering both vegetative and floral traits in understanding these patterns. Our findings offer a basis for exploring the functional relevance of rarely measured floral traits, such as pollen traits, within the plant economic spectrum and in plant–pollinator interaction studies.

Keywords: Botanical garden, flowering, flower traits, fruiting, leaf-out, nectar, PhenObs network, phenology-trait relationships, pollen, senescence

Introduction

Plant phenology – the timing of life cycle events such as leaf emergence, flowering, fruiting and senescence - relates to resource acquisition, reproductive success, and mediates biotic interactions such as herbivory and pollination (Elzinga et al., 2007; Heberling et al., 2019; Kudo and Cooper, 2019; Nord and Lynch, 2009). Global warming shifts plant phenological events like leaf emergence and flowering, though these responses are complex and exhibit strong species-specific variation (Menzel et al., 2020; Root et al., 2003). Understanding interspecific variation in phenological patterns, especially if plants share the same environment, is an important aim of phenological research and may provide insights into the adaptability of plants to changing climatic conditions (Rauschkolb et al., 2024; Sporbert et al., 2022).

Plant species with a shared phylogenetic history show a more synchronized phenology and tend to show similar responses to changing climate due to evolutionary conserved responses to environmental cures (Davies et al., 2013; Davis et al., 2010). Yet, phylogenetic relatedness doesn’t fully explain phenological patterns, suggesting that additional aspects constrain phenological variation (König et al., 2018).

Plant functional traits reflect ecological strategies of plant growth, resource-use efficiency and related trade-offs (Díaz et al., 2016; Westoby et al., 2002). Recent studies have suggested that functional traits such as plant height, leaf traits, leaf nutrient content or seed traits are associated to patterns of interspecific phenological variation (Bucher et al., 2018; Horbach et al., 2023; Liu et al., 2021; Sporbert et al., 2022; Wang et al., 2021) or climate-related phenological shifts in plants (Bucher et al., 2018; König et al., 2018; Plos et al., 2024). Taller plants, for example, are observed to flower later than smaller plants what is attributed to longer developmental times according to plant size (Bolmgren and D. Cowan, 2008; Segrestin et al., 2020; Sporbert et al., 2022; Sun and Frelich, 2011). So far, these studies have mainly linked vegetative traits to the onset of flowering, while floral traits and other phenological stages were largely neglected. One reason for this could be that the measurement of floral traits is very time-consuming and there is not yet a comprehensive protocol for measuring floral traits (E-Vojtkó et al., 2020; Roddy et al., 2021), as is largely available for vegetative traits (Pérez-Harguindeguy et al., 2016). Details on phenology-trait relationships already found and the ecological relevance of the traits investigated can be found in Table II.1.

Floral traits such as flower dimensions, number of flowers, and pollen and nectar characteristics play a key role in plant reproduction and ecosystem functioning, particularly through pollination (Table II.1). Since floral morphology relates to resource allocation and influences development time and flower longevity, it can be linked to differences in the timing and duration of flowering (E-Vojtkó et al., 2022; Roddy et al., 2021). Nectar and pollen traits influence plant-pollinator interactions, reproductive success, and resource allocation, but are rarely included in trait-based studies due to the complex nature of their measurement (but see: Dunker et al., 2021; Filipiak et al., 2022; Fornoff et al., 2017). However, due to their influence on both plant and pollinator fitness, nectar and pollen traits should be included to fully understand phenological patterns and the implications of phenological shifts under climate change. Despite their relevance for pollination and reproduction, floral traits have been largely overlooked in studies of phenology–trait relationships— with only recent work beginning to address this gap (Ahmad et al., 2025; Deilmann et al., 2024; E-Vojtkó et al., 2022). Deilmann et al. (2024) showed that floral traits were strongly associated to interspecific phenological variation. In contrast, Ahmad et al. (2025) found only weak relationships between floral traits and the flowering phenology along elevational gradients. Furthermore, there is a strong focus on flowering phenology while other stages such as leaf out or senescence are rarely considered in studies on phenology-trait relationships (but see (Bucher and Römermann, 2021; Sporbert et al., 2022).

Understanding the potential constraints of vegetative and floral traits on phenological variation requires insights into the coordination of floral traits within the broader plant economic spectrum and the identification of trade-offs with vegetative traits. It has recently been shown that floral and reproductive traits, as well as reproductive phenology, represent distinct dimensions within the plant economic spectrum that are largely independent of leaf economics (E-Vojtkó et al., 2022; Segrestin et al., 2020). These studies suggest that floral traits and phenology uniquely contribute to variation in plant form and function, highlighting their independent ecological role within the wider economic spectrum of plants. Our understanding of phenology-trait relationships is still in its infancy, and especially the role of floral traits in influencing interspecific variation of plant phenology remains largely unexplored. The ecological relevance of the traits investigated in this study and reported links to phenology are summarized in Table II.1.

Table II.1: Investigated floral traits and vegetative traits, their ecological relevance and reported links to phenology.

	Ecological relevance	Link to phenology
Floral traits		
Number of flowers	Resource allocation (trade-off with growth), reproductive success, pollination probability (Arroyo-Correa et al., 2021; E-Vojtkó et al., 2022; Harder and Barrett, 2007; Ohashi and Yahara, 1999)	Flower number positively associated with flowering duration (Schmitt, 1983)
Flower dimensions (size of single flower, size of flower unit, corolla length, petal length)	Flower recognition, pollinator attractiveness (Dafni et al., 1997); investment in reproductive organs (Fabbro and Körner, 2004; Roddy et al., 2021)	Smaller flowers associated with later flowering (Bosch et al., 1997; Shmida and Dukas, 1990)
Nectar characteristics (nectar amount, sucrose concentration, total sucrose mass)	Pollinator attraction and reward, reproductive success (Willmer, 2011a; Zimmerman, 1988); correlations to optical flower signals (Mues, 2020; Parachnowitsch et al., 2019); trade-off with vegetative investment and resistance (Obeso, 2002; Willmer, 2011b)	Nectar amount and phenology not correlated (Bosch et al., 1997)
Pollen characteristics	Overall: Pollinator attraction and reward, reproductive success (Willmer, 2011c)	unknown
Size	- Pollinator specificity and pollinator feeding strategy (Davis, 1997; Hao et al., 2020)	
Shape	- Pollinator specificity (Davis, 1997)	
Fluorescence	- Pollinator attraction and UV protection of pollen (Dunker et al., 2021; Mori et al., 2018; Stanley and Linskens, 1974)	
Surface structure (entropy)	- Resistance against environmental stressors, pollination mechanism and pollinator specificity (Davis, 1997; Edlund et al., 2004; Osborn et al., 1991)	
Vegetative traits		
Plant height	Competitive ability, productivity (Gaudet and Keddy, 1988; Moles et al., 2009)	Taller plants associated with later flowering (Bolmgren and D. Cowan, 2008; Liu et al., 2021; Segrestin et al., 2020) and fruiting (Sporbert et al., 2022)
Leaf area	Competitive ability (Diaz et al., 2004), productivity, light interception, leaf energy and water balance (Díaz et al., 2016)	Large-leafed species associated with later leaf out (Sun et al., 2006) and shorter flowering (Sporbert et al., 2022)
Specific leaf area (SLA)	Productivity, competitive ability, growth rate (Pérez-Harguindeguy et al., 2016; Wright et al., 2004)	Higher SLA associated with later flowering (Sun and Frelich, 2011), stronger shifts in flowering phenology (König et al., 2018; Plos et al., 2024) and earlier senescence (Bucher and Römermann, 2021)
Leaf dry matter content (LDMC)	Resistance to physical hazard, competitive ability, productivity (Pérez-Harguindeguy et al., 2016)	Higher LDMC associated with later leaf senescence (Bucher and Römermann, 2021)

In the present study, we link detailed phenological information on 68 herbaceous species with in-situ measured floral and vegetative plant traits, especially considering rarely studied traits such as floral morphology, pollen and nectar traits. We used a newly developed analytical method based on multispectral imaging flow cytometry for pollen analysis that enables the measurement of morphological pollen traits (Dunker et al., 2022, 2021; Hornick et al., 2022). We first aim to identify correlations and trade-offs between vegetative and floral traits as a basis for understanding how functional trait space may constrain interspecific phenological variation. Second, our main aim is to assess the relative importance of floral traits compared to the more commonly used vegetative traits in explaining interspecific variation in year-round phenology. We expect that floral traits might be of more importance for flowering phenology while vegetative traits might show stronger associations to vegetative phenology such as leaf out or senescence. As closely related species are assumed to show similarities in phenological patterns (Davies et al., 2013) we included phylogenetic information and assessed the importance of traits compared to phylogenetic relatedness for explaining phenological patterns. Third, we tested whether these relationships are consistent across different sites (i.e. three botanical gardens), representing different environmental backgrounds.This study contributes to a better understanding of the relationships between phenology and traits by incorporating rarely measured floral traits.

Materials and Methods

Replication statement

Scale of interest	Scale at which the factor of interest is applied	Number of replicates at the appropriate scale
Species	Species	68 species (5 repetitions per species and garden)

Phenological monitoring

This study was conducted in three different botanical gardens of the PhenObs network (Nordt et al., 2021), as they offer the possibility of studying the phenology, reproductive, and vegetative traits of a large variety of plant species from different habitats and biomes (Primack et al., 2021), while also considering variations in the environment. We monitored the phenology throughout the year (that is, initial growth, leaf unfolding, onset, peak, end and duration of flowering, fruiting, and senescence, Table S II.1) of 68 perennial herbaceous plant species growing in the three botanical gardens of Halle, Jena, and Berlin in Germany (see

Fig. S II.1 for locations, Table S II.2 for climatic characterization, Table S II.3 for the plant species studied) weekly from 2019 to 2021, following the PhenObs Protocol (Nordt et al., 2021). Monitoring was carried out in a 1m² patch per species that was considered a ‘population’, as described in the PhenObs protocol (Nordt et al., 2021). Species selection was based on the PhenObs species list and aimed at maximal coverage across gardens. The species were widely distributed across the three gardens: 45 species (66%) occurred in all three gardens, 10 species (13%) in two gardens, and 13 species (21 %) in one garden. The phylogenetic information for all species was provided by the megatree of the package V.PHYLOMAKER2 (Jin and Qian, 2022; see Figure S II.2 for a phylogenetic tree of all species studied).

Plant functional traits

Functional traits were measured in the same populations in which phenological monitoring was performed (see Table II.3 for an overview of the functional traits measured and their ranges of value). Functional traits were measured once per species and garden on five randomly selected shoots when the respective species was in full flowering. The mean trait value was calculated from the five values measured per species and garden. Four vegetative traits were considered: Per shoot, vegetative and generative height were measured, and two leaves were sampled to measure leaf area (LA), specific leaf area (SLA) and leaf dry matter content (LDMC) strictly following the PhenObs protocol (Nordt et al., 2021). The two sun leaves were randomly collected per shoot and weighed fresh and dried to calculate LDMC. Leaf area (mm²) was determined from scans of fresh leaves (300 dpi resolution) and the R package Leaftraits (M. Bernhardt-Römermann, unpublished) was used to calculate specific leaf area (SLA).

Twelve floral traits were measured on the same shoots from which leaf samples were taken. To assess the number of flowers, individual flowers were counted per shoot/individual. For Asteraceae and Apiaceae, the number of inflorescences (flower heads or umbels) was considered as the number of flowers (applies to 5/68 species). To determine the flower size of a single flower (SF), the diameter of the flower was measured for radial flowers and the length and width of the flower for zygomorphic flowers. From this, the flower size (that is, flower area) was calculated using the circular formula $A = \pi \times d^2/4$ for radial flowers and using the oval formula $A = (\text{length}/2) \times (\text{width}/2) \times \pi$ for zygomorphic flowers assuming an oval shape. To account for both the size of the single flower (SF) and the size of the inflorescence or floral unit (FU), the diameter of the floral unit was also measured. The definition of 'floral unit' followed Fornoff et al. (2017), referring to an '(...) aggregation of flowers that a pollinator can access without flying' and was applied to composite flowers (Asteraceae) or flower umbels (Apiaceae) (5/68 species in total). For the other types of inflorescences, the flower unit corresponded to the size of the individual flower.

To measure nectar traits, nectar samples were taken with 1 µl micro capillaries (minicaps®, Hirschmann®) from five flowers of each of the five sampled shoots/individuals. To avoid nectar consumption by flower visitors prior to sampling, at least five flowers per population were covered with fine mesh bags for at least two hours (Corbet, 2003). Nectar sampling was always conducted in the morning between 8 and 11am. All nectar was collected from each sampled flower. The volume of nectar in the capillary was measured in mm using a ruler and then converted to µl. The sucrose concentration (g/100g) of the nectar samples was measured using a handheld refractometer modified for small volumes (Eclipse, Bellingham & Stanley). The sucrose mass per flower (mg/flower) was calculated using the calibration table of (Kearns and Inouye, 1993). The mean values for nectar amount, sucrose concentration, and sucrose mass were calculated for the five flowers sampled.

To measure pollen traits, flower samples were taken from the same individuals/shoots, placed in paper bags, and frozen at -20°C until further analysis. A sufficient amount of pollen was required for the analyses. Thus, depending on the amount of pollen per flower, a different number of flowers was sampled (range of the number of flowers sampled: min. 1, max. 84, mean 7.3, median 3). Pollen was extracted from the flowers and analyzed using multispectral imaging flow cytometry following the protocols by Dunker et al. (2021) and Walther et al. (under review). This method enables high-throughput assessments of pollen traits. Pollen samples of many species can be analyzed in a short time, and morphological pollen traits related to size, shape, texture, and fluorescence can be easily extracted for thousands of pollen grains per sample (Dunker et al., 2021; Hornick et al., in resubmission; Walther et al., under review). The selection of qualitatively good pollen images for the respective trait extraction followed the protocol of Hornick et al. (in resubmission). Four pollen traits were extracted from the pollen images: 1) pollen size (measured as pollen diameter), 2) pollen shape, measured as the ratio between the height and width of a bounding box surrounding the pollen, referred to as 'elongatedness', 3) pollen fluorescence (green fluorescence intensity, Exc. 488 nm/ Em. 528/65 nm), 4) Pollen surface structure measured as 'entropy' (randomness of intensities in the image). All pollen trait values were averaged per sample.

Table II.2: Measured floral and vegetative traits with the respective units, range of values, and number of species sampled for each trait (n spec). Depending on flower shape and nectar availability, not all targeted traits were measurable for each species, resulting in different species numbers (n spec).

	Unit	Min.	Median	Mean	Max.	n spec.
Floral traits						
Number of flowers	-	0.40	6.00	60.46	1462.00	65
Flower size (floral unit)	cm²	0.22	4.48	17.49	254.51	66
Flower size (single flower)	cm²	0.01	3.24	14.36	254.51	65
Corolla length	cm	0.10	1.25	1.43	8.38	37
Petal length	cm	0.29	1.54	2.26	11.60	53
Nectar amount	µl	0.04	0.63	2.57	21.33	26
Nectar sucrose concentration	g/100g	5.53	43.52	42.45	75.67	26
Nectar total sucrose mass	mg	0.02	0.79	0.90	5.95	26
Pollen size (diameter)	µm	11.46	26.73	29.87	87.23	64
Pollen shape (elongatedness)	ratio	1.02	1.06	1.08	1.51	64
Pollen fluorescence	a.u.	13435	214569	317989	3901065	64
Pollen structure (entropy)	a.u.	0.04	0.12	0.13	0.25	64
Vegetative traits						
Vegetative height	cm	1.44	36.90	48.12	217.00	65
Leaf area	mm²	26.38	2183.59	4782.92	50161.78	67
Specific leaf area (SLA)	mm²/mg	4.87	19.08	20.61	62.06	68
Leaf dry matter content (LDMC)	mg/g	73.78	206.00	207.35	363.64	68

Statistical analysis

All statistical analyzes were performed in R version 4.3.2 (R Core Team, 2023).

We used Pearson's correlations to test whether and to what degree floral and vegetative traits were correlated with each other. All trait variables were ln-transformed prior to analyses. To obtain a general overview of the data, we also tested for correlations between phenological stages using Pearson's correlations. All correlation matrices were calculated using the rcorr function from the Hmisc package (Harell and Dupont, 2024).

Principal component analyzes (PCA) were conducted to identify relationships between a) floral and vegetative traits and b) observed phenological stages. Due to the limited data set on nectar traits (n = 38 vs. n = 117), two PCAs were calculated for functional traits, one with and one without nectar traits. For phenological data, two PCAs were calculated, with (n=92) and without ‘Initial growth’ (n=112), as this stage had the most missing values (41 NAs out of 168 values). The prcomp function was used to compute the PCAs, and the fviz_pca_biplot function from the package factoextra was used to visualize the PCA biplots (Kassambara and Mundt, 2020).

Following the LCVP taxonomy (Leipzig catalogue of vascular plants, Freiberg et al., 2020), we created a phylogenetic tree of the 68 investigated species using the phylo.maker function from the package V.Phylomaker2 (Jin and Qian, 2022). To test for a phylogenetic signal within functional traits and phenological stages, we used Pagel's Lambda statistic (Pagel, 1999) and the phylosig function of the package phytools (Revell, 2024). This was used to quantify the strength of the phylogenetic signal for each functional trait and phenological variable among the 68 investigated species.

To assess the relative importance of floral and vegetative traits for explaining phenological variation, we used boosted regression trees (BRTs) (Elith et al., 2008). This method is well suited for analysing datasets with many predictor variables because it is relatively unaffected by collinearity and efficiently handles missing predictor values by using surrogates to minimize information loss (Bianchini and Morrissey, 2020; Elith et al., 2008). Each phenological stage (Table S II.1) was used as a dependent variable in a separate model (12 overall BRT models). The garden-specific ln-transformed mean values of all functional traits (Table II.2) and 26 phylogenetic eigenvectors (see below) served as explanatory variables. As maintenance by the gardeners (weeding, spacing, irrigation, etc.) and local management regimes can potentially influence plant phenology, we additionally included 'garden' (Halle, Jena, Berlin) as an explanatory variable in our models to investigate whether the relationships between phenology and functional traits are consistent across gardens, as has also been done in Sporbert et al. (2022). We utilized the phylogenetic eigenvector regression method proposed by Diniz-Filho et al. (1998) for our phylogenetic analysis, a technique that has been used in various studies (Bianchini and Morrissey, 2020; Pistón et al., 2019; Rauschkolb et al., 2024; Sporbert et al., 2022). A pairwise distance matrix was calculated from the phylogenetic tree. Subsequently, we conducted a principal coordinate analysis for extracting eigenvectors (i.e. eigenvector loadings on the axes) from this distance matrix. Provided that a sufficient number of eigenvectors are considered, phylogenetic eigenvectors reflect the phylogenetic relationship among species and control for phylogenetic autocorrelation (Bianchini and Morrissey, 2020). Of the 67 phylogenetic eigenvectors, the first 26 eigenvectors represented 90% of the phylogenetic structure in the distance matrix and were included as covariates in the BRT models.

The package gbm (Ridgeway et al., 2024) was used to fit BRT models with a Gaussian error distribution and a fraction of training data (bag fraction) of 0.5, a tree complexity of 1, a learning rate of 0.001, and a tolerance of 0.01. The performance of the models was evaluated using cross-validation. To visualize the relationship between each predictor variable and the corresponding phenological response variable, partial dependency plots were created to isolate the effect of each predictor from the others included in the model. The relative importance of functional traits and garden for each phenological stage was extracted and visualized for the five most important traits. In addition, pie charts were created to assess and compare the relative importance of a) functional traits, b) garden, and c) phylogenetic eigenvectors for the phenological stages.

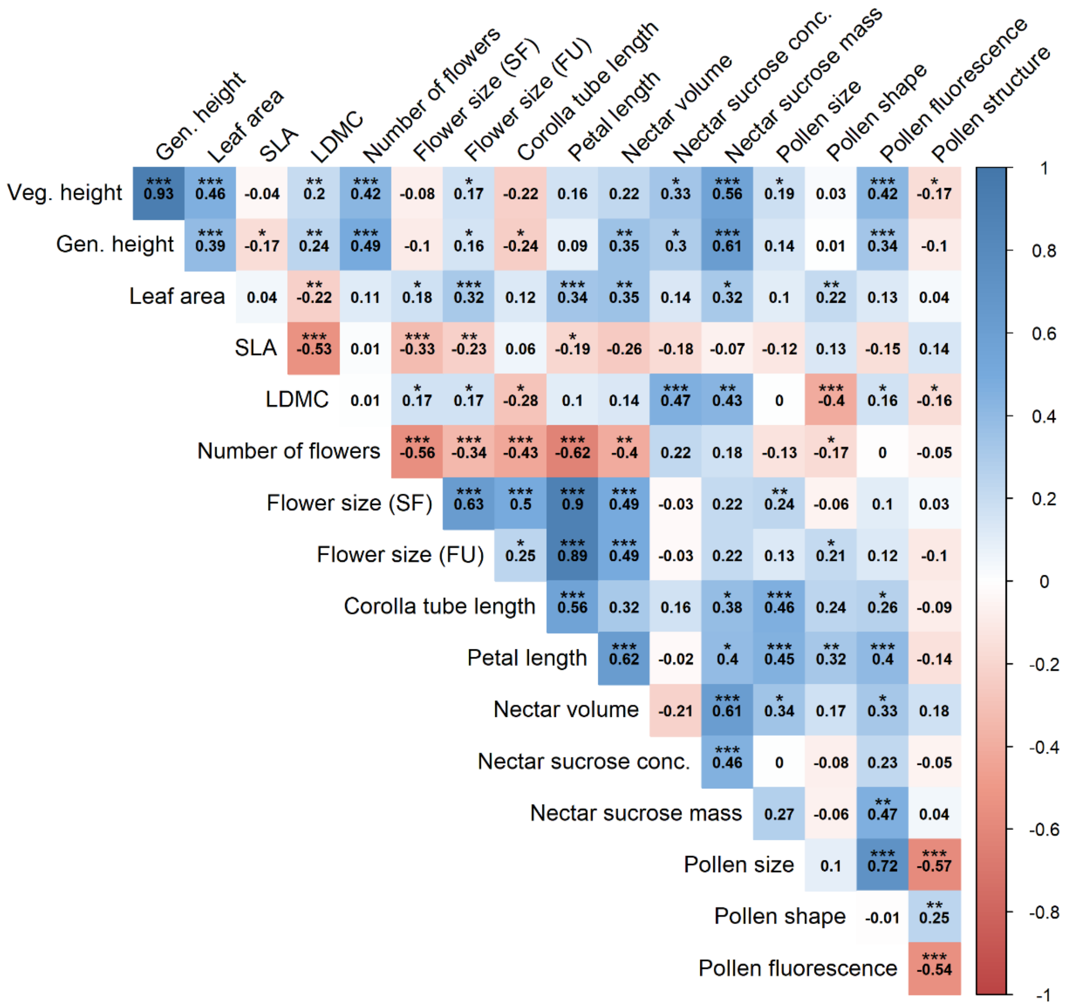
Results

Relationship between floral and vegetative traits and between phenological stages

Vegetative height was positively correlated with the number of flowers, flower size of the floral unit (FU), the concentration and mass of nectar sucrose, and the size and fluorescence of the pollen (Figure II.1). Species with larger leaves had larger flowers (SF and FU, petal length), more nectar and sucrose, and more elongated pollen. Species with high SLA had smaller flowers (SF, FU, petal length). In contrast, plants with a high LDMC had larger flowers (SF, FU), shorter corolla tubes, higher concentrations and mass of nectar sucrose, and rounder pollen. Plants with many flowers were taller (generative and vegetative height), had smaller flowers (SF, FU, tube length, petal length), less nectar per flower (nectar volume), and rounder pollen. Larger flowers had more nectar per flower and larger pollen than smaller flowers. Larger pollen grains showed stronger fluorescence and a less pronounced surface structure (entropy). Furthermore, pollen surface structure was positively correlated with pollen shape (elongatedness) and negatively correlated with pollen fluorescence.

The PCA of the functional traits excluding nectar traits (n=117, 46.5% explained variation, Figure II.2a) revealed that the first axes (25.5%) corresponded to generative and vegetative height, pollen size and the fluorescence of the pollen. The second component (21%) corresponded to flower size (SF), number of flowers, SLA, and LDMC (see Table S II.5 for the trait contributions (loadings) to all 12 PCs). The PCA of the functional trait variables including nectar traits (n=38, 52.2% explained variation, Figure II.2b) revealed a picture very similar to the one described in the previous PCA analysis. Here, in addition to generative and vegetative height, pollen size and pollen fluorescence, also nectar sucrose mass and nectar volume corresponded to the first component, explaining 33.1% of overall variation. The second component (19.1%) corresponded to nectar sucrose concentration, in addition to flower size (SF, FU) and number of flowers (see Table S II.6 for the contribution of traits (loadings) to the

15 PCs). When including nectar traits, leaf traits (leaf area, SLA, LDMC) corresponded to dimensions other than the first two (see also Table S II.6 with loadings to all PCs). The correlation coefficients and PCAs of the phenological stages can be found in the supplements (Figures S II.3, S II.4, Tables S II.7, S II.8). The trait and phenology patterns did not differ between the three botanical gardens (Figure S II.5).



	Gen. height	Leaf area	SLA	LDMC	Number of flowers	Flower size (SF)	Flower size (FU)	Corolla tube length	Petal length	Nectar volume	Nectar sucrose conc.	Nectar sucrose mass	Pollen size	Pollen shape	Pollen fluorescence	Pollen structure
Veg. height	*** 0.93	*** 0.46	-0.04	** 0.2	*** 0.42	-0.08	* 0.17	-0.22	0.16	0.22	* 0.33	*** 0.56	* 0.19	0.03	*** 0.42	* -0.17
Gen. height		*** 0.39	* -0.17	** 0.24	*** 0.49	-0.1	* 0.16	* -0.24	0.09	** 0.35	* 0.3	*** 0.61	0.14	0.01	*** 0.34	-0.1
Leaf area			0.04	** -0.22	0.11	* 0.18	*** 0.32	0.12	*** 0.34	** 0.35	0.14	* 0.32	0.1	** 0.22	0.13	0.04
SLA				*** -0.53	0.01	*** -0.33	** -0.23	0.06	* -0.19	-0.26	-0.18	-0.07	-0.12	0.13	-0.15	0.14
LDMC					0.01	* 0.17	* 0.17	* -0.28	0.1	0.14	*** 0.47	** 0.43	0	*** -0.4	* 0.16	* -0.16
Number of flowers						*** -0.56	*** -0.34	*** -0.43	*** -0.62	** -0.4	0.22	0.18	-0.13	* -0.17	0	-0.05
Flower size (SF)							*** 0.63	*** 0.5	*** 0.9	*** 0.49	-0.03	0.22	** 0.24	-0.06	0.1	0.03
Flower size (FU)								* 0.25	*** 0.89	*** 0.49	-0.03	0.22	0.13	* 0.21	0.12	-0.1
Corolla tube length									*** 0.56	0.32	0.16	* 0.38	*** 0.46	0.24	* 0.26	-0.09
Petal length										*** 0.62	-0.02	* 0.4	*** 0.45	** 0.32	*** 0.4	-0.14
Nectar volume											-0.21	*** 0.61	* 0.34	0.17	* 0.33	0.18
Nectar sucrose conc.												*** 0.46	0	-0.08	0.23	-0.05
Nectar sucrose mass													0.27	-0.06	** 0.47	0.04
Pollen size														0.1	*** 0.72	*** -0.57
Pollen shape															-0.01	** 0.25
Pollen fluorescence																*** -0.54

Figure II.1: Correlation matrix (Pearson correlation) of all pairwise combinations of functional traits, with correlation coefficients r and significance levels (p<0.05 *, p<0.01 **, p<0.001 ***). Positive correlations are highlighted in blue, negative correlations are highlighted in red, and the color gradient indicates correlation strength. Abbreviations: SLA – specific leaf area, LDMC – leaf dry matter content, SF – single flower, FU – flower unit.

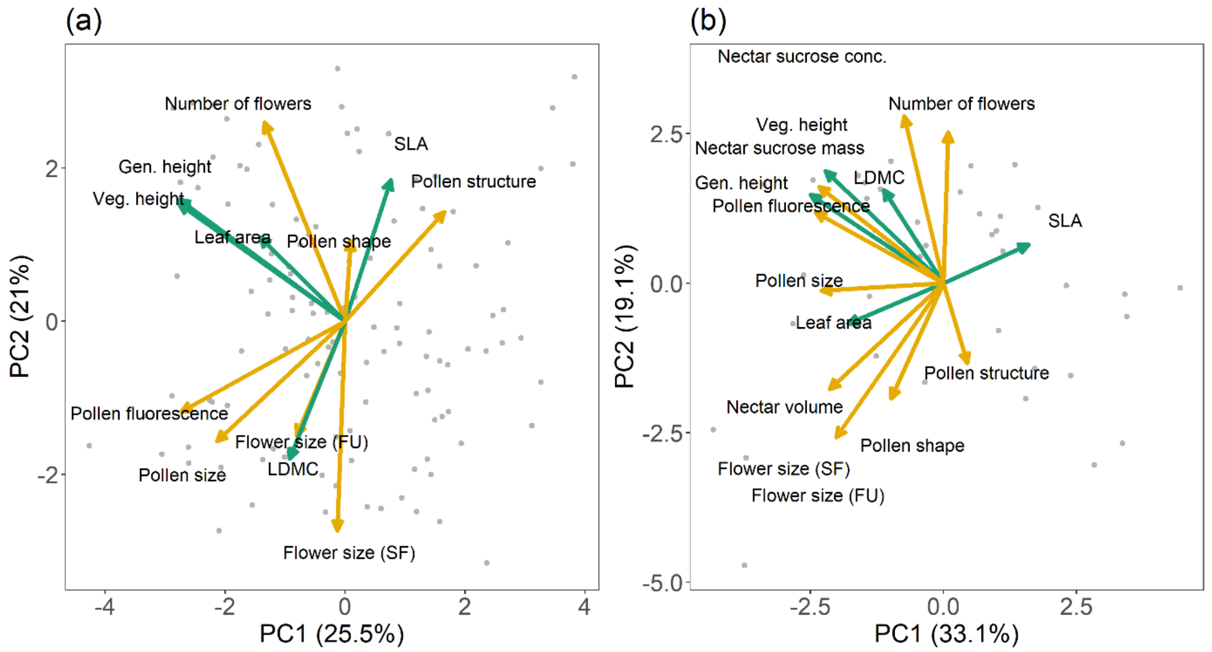


Figure II.2: Principal component analysis of a) functional traits (excluding nectar traits, n=117) and b) functional traits including nectar traits (n=38). The dots represent species for which information on all traits was available. The colors of the vectors indicate floral traits (yellow) and vegetative traits (green).

Relationship between phenology and functional traits, considering the phylogenetic relatedness

The most parsimonious BRT models for the effects of floral and vegetative traits on reproductive phenological stages revealed moderate to good cross-validation (cv = 0.42–0.74; Figures S II.10–S II.16). For the reproductive phenological stages (flowering, fruiting), functional traits were more important than phylogeny in explaining phenological variation (pie charts in Figure II.3a-c, Figure S II.6). The most parsimonious BRT models for vegetative phenological stages revealed poor to moderate cross-validation (cv = 0.15–0.28; Figures S II.8, S II.9). Phylogenetic relatedness had a strong influence on vegetative phenology (initial growth, senescence) and flowering duration, but functional traits were almost equally important for these stages (pie charts in Figure II.3d, f, Figure S II.6). The different locations of the botanical gardens only played a role in the phenological stage of leaf unfolding (relative importancegarden = 10.7%), which was observed earlier in Jena than in Berlin and Halle.

Vegetative traits (plant height, LDMC, leaf area, SLA) were the most important traits in explaining the variation in reproductive and most vegetative phenological stages (mean relative importance = 17.7%), while floral traits were generally less important (mean relative importance = 6.3%) (Figure II.3, Figure S II.6). Vegetative plant height was the most important trait in most stages. Taller species started initial growth later (relative importance = 35.4%), flowered (onset, 49.9%; peak, 52.7%; end, 19.7%) and fruited (onset, 33.9%; end, 37.6%; duration, 38.6%) later and showed later senescence (onset, 10.9%; peak, 5.9%). Species with high SLA flowered earlier (onset, 10.8%; peak, 2.37%). Large-leaved species flowered for a shorter period (11.5%) and fruited for a longer period (10.2%) than small-leaved species. Plants with a high LDMC were related to later flowering (onset, 4.1%; peak, 5.4%; end, 11.8%), later fruiting (onset, 13.9%; end, 13.7%), and later senescence (onset, 12.1%; peak, 22.1%; end, 18.4%).

Floral traits also helped to explain the phenological variation across the phenological stages but played a minor role overall (Figure II.3, Figure S II.6). Species with larger flowers leafed out later (SF, 7.6%; FU, 15.3%) and long corolla tubes were associated with earlier senescence (onset, 5.7%; peak, 10.5%; end, 14.3%). Nectar and pollen traits played a minor role overall in explaining the phenological variation (mean relative importance of nectar traits 3.6%; pollen traits 6.9%). Plants with high nectar sucrose concentrations flowered earlier (5.6%). Pollen shape, measured as the elongatedness of the pollen grains, was associated with earlier leaf unfolding (14.3%), earlier senescence end (21.4%) and shorter flowering (8.7%). Species with stronger fluorescent pollen flowered later (onset, 5.6%).

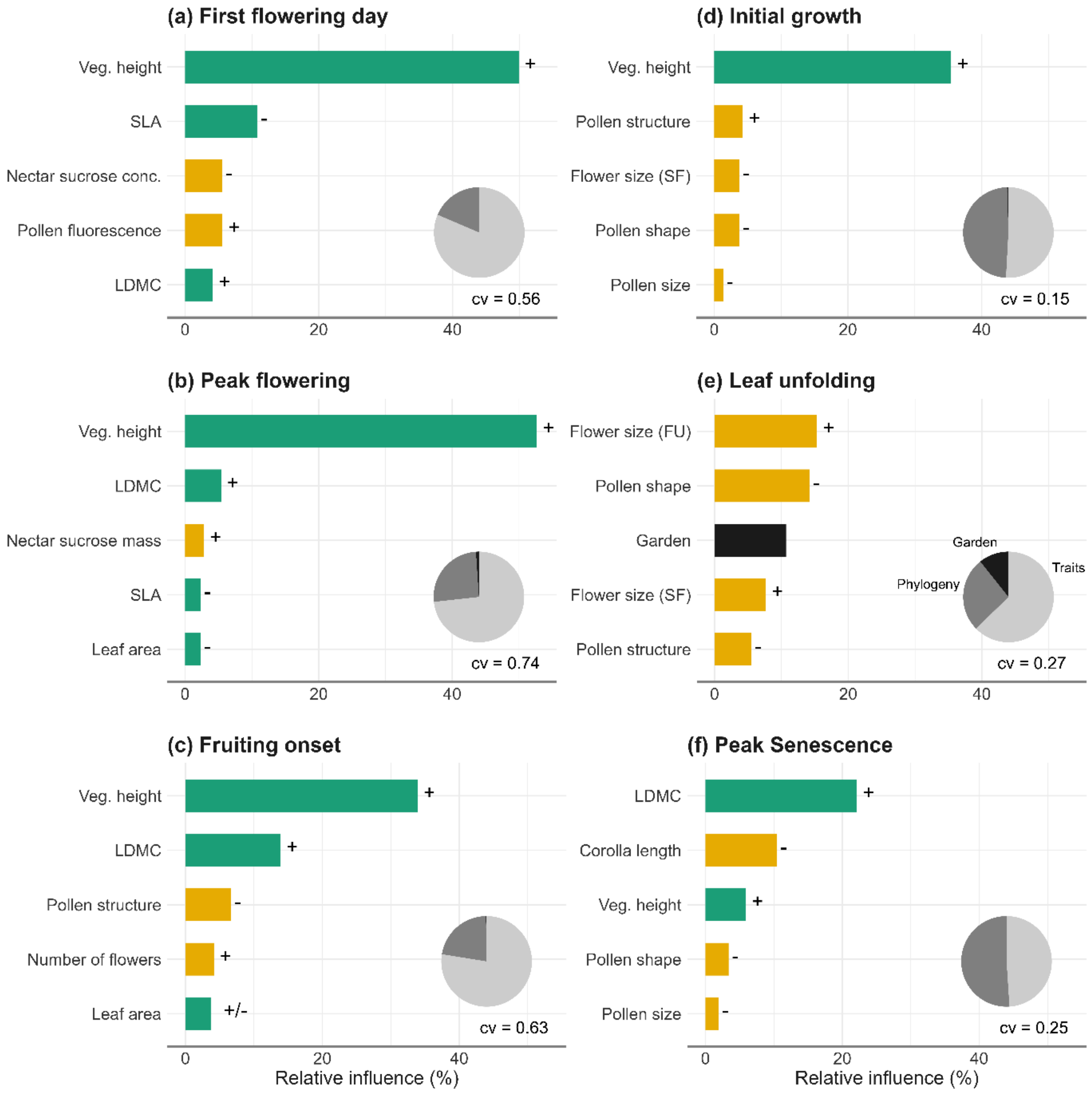


Figure II.3: Relative importance (%) of floral (yellow) and vegetative (green) traits on phenological stages, deduced from boosted regression trees (BRTs) including phylogeny. The direction of the influence of the predictor variable on the phenological stage is represented by '+' positive and '-' negative influence. Pie charts represent the overall contributions of the variables grouped by 'functional traits' (light grey), 'phylogeny' (dark grey) and 'garden' (black). Cross-validation correlation (cv) is given for each phenological stage.

Discussion

Our study showed that vegetative traits were more important than floral traits for explaining interspecific phenological variation, regardless of whether reproductive or vegetative phenology was considered. In particular, plant height and traits related to leaf economics were of importance for phenology. These traits coordinate along the two main dimensions of the global spectrum of plant form and function, reflect plant ecological strategies, and mediate plant growth and survival (Díaz et al., 2016). In contrast, floral traits mediate reproduction and are less involved in growth and survival but require substantial carbon investment (Roddy et al., 2021). Vegetative assimilation tissues such as leaves play a crucial role in providing the energy and carbon required for floral development. This process is only triggered when sufficient energy and metabolites are available. Consequently, traits which define the plant's ability to acquire and maintain resources are central to determining the timing and progression of phenological events. This relationship underscores the functional link between vegetative and reproductive processes and highlights the primary role of vegetative traits in shaping plant phenology.

Correlations among and between floral and vegetative traits

Our findings on trait correlations expand the spectrum of plant form and function, which highlights plant size and leaf economics (SLA, LDMC) as key axes (Díaz et al., 2016), by incorporating rarely studied floral traits. Overall, the significant correlations among vegetative and floral traits were mainly positive. Larger leaves were associated with larger flowers, also found by E-Vojtkó et al. (2022), and taller plants had more flowers, larger pollen and a higher nectar sucrose mass, which could be explained by allometric relationships (E-Vojtkó et al., 2022; Lauri, 2019; Weiner et al., 2009; Willmer, 2011c). In our study, SLA—linked to competitive ability and resource acquisition (Pérez-Harguindeguy et al., 2016; Wright et al., 2004)—was negatively associated with flower size, which influences pollinator attraction (Dafni et al., 1997). Species with high SLA tended to have smaller flowers, suggesting a trade-off between competition for resources (e.g., light and space) and investment in pollinator attraction. Supporting the well-established concept of a number–size trade-off, our findings revealed a strong negative correlation between flower number and size, suggesting that species balance investment between producing many small flowers and fewer large ones (Burd, 1999; E-Vojtkó et al., 2022; Sargent et al., 2007; Worley et al., 2000).

When including nectar traits, a slight change in trait coordination was found, whereby the leaf traits were no longer coordinated along the second but to other dimensions. This is in line with the findings of E-Vojtkó et al. (2022), which indicate that floral traits are an independent dimension within the plant economic spectrum and largely independent of leaf traits. Overall, our results on trait correlations are consistent with E-Vojtkó et al. (2022), who were the first to include floral traits in a comprehensive assessment of plant form and function. However, our study goes beyond this by considering also nectar and pollen traits.

Relative importance of floral and vegetative traits to explain plant phenology

Our results on the relative importance of functional traits, phylogeny, and garden in explaining the year-round phenology of 68 plant species show that functional traits are largely related to phenological patterns across species and are overall more important than phylogenetic relatedness. Our findings confirm the close association between functional traits and phenology presented across studies on the local scale (Deilmann et al., 2024; Liu et al., 2021), global scale (König et al., 2018), along elevational gradients (Bucher et al., 2018) or across botanical gardens (Rauschkolb et al., 2024; Sporbert et al., 2022).

Vegetative traits showed stronger associations with phenological variation than floral traits, with plant height and LDMC—traits linked to competitive ability—most closely reflecting interspecific differences. Plant height, a trait linked to competitive ability and productivity (Gaudet and Keddy, 1988; Moles et al., 2009), emerged as a key trait across multiple phenological stages: taller species started initial growth, flowering, and fruiting later and had longer flowering durations. This may be due to taller plants requiring more time to reach maximum height (Sun and Frelich, 2011), which delays subsequent phenological stages. These findings align with research that highlights the importance of plant height for phenological variation, especially with regard to flowering phenology (Bolmgren and D. Cowan, 2008; Du and Qi, 2010; E-Vojtkó et al., 2022; Huang et al., 2018; Segrestin et al., 2020; Sporbert et al., 2022; Sun and Frelich, 2011). LDMC, negatively correlated with relative growth rate but positively with leaf lifespan and physical resistance (Pérez-Harguindeguy et al., 2016), was associated with later leaf senescence, as also found by (Bucher and Römermann, 2021). Large leaf area, which enhances competitive ability, productivity, and light interception (Diaz et al., 2004; Díaz et al., 2016), was related to shorter flowering periods, indicating a growth-reproduction trade-off (Aragón et al., 2009; Sporbert et al., 2022). Our results highlight that traits associated with the plant economic spectrum, which influence growth and survival (Díaz et al., 2016), are closely associated to year-round phenological patterns.

Overall, floral traits played a secondary role for explaining interspecific phenological variation. This is in line with recent findings along elevational gradients and might reflect an independent selection of floral traits and phenology (Ahmad et al., 2025). Among floral traits, flower size and pollen characteristics were more closely associated with phenological variation than flower number or nectar traits. Species with larger flowers showed later leaf unfolding and earlier senescence, suggesting a trade-off between growth and reproductive investment (Reekie and Avila-Sakar, 2005). Pareja-Bonilla et al. (2025) found that species with larger flowers stronger advanced flowering in response to climate warming compared to species with small flowers, likely due to the high costs of constructing larger flowers. Despite a strong negative correlation between flower size and number, flower quantity played only a limited role in explaining phenological patterns. However, species with many flowers showed a longer flowering period and shorter fruiting, which was also shown by Deilmann et al. (2024).

Of the floral traits investigated, pollen traits are the least studied in relation to both the plant economic spectrum and phenology-trait relationships. Pollen shape, associated with pollinator specificity (Davis, 1997), is known to be partially phylogenetically conserved (Dunker et al., 2021) (see also Table S II.4, Pagel's Lambdapollen shape = 1, p<0.001), and appeared to be more relevant in stages influenced by phylogeny such as initial growth, flowering duration, and senescence, likely reflecting phylogenetic rather than purely phenological patterns. The species with elongated pollen in our study had a short flowering duration and early senescence end and belonged primarily to monocotyledons (except for one species of Apiaceae). These were primarily spring geophytes (Figures S II.6, S II.7), indicating a potential relationship between phenology and belowground characteristics such as storage organs (Ye et al., 2024). Pollen fluorescence, potentially related to UV protection and pollinator attraction (Dunker et al., 2021; Mori et al., 2018; Willmer, 2011c), was associated with later flowering start and end. Late-flowering plants usually flower in summer when solar radiation is more intense, and days are longer, which requires better UV protection for pollen grains carrying the male gamete. Since UV exposure of pollen also relates to flower shape, we recommend considering flower shape in future studies. Historically, pollen traits are mainly studied with regard to pollination or species identification purposes (Dunker et al., 2021) rather than as part of the plant's functional spectrum across species. Our findings provide a foundation for investigating the functional roles of pollen traits in the plant economic spectrum, as well as for plant-pollinator interaction studies.

Nectar traits played a minor role in explaining the phenological patterns. Nectar production represents a considerable resource investment with uncertain benefits for pollination and seed production, suggesting potential trade-offs with other functional traits. However, we found only a trade-off between flower number and nectar volume per flower, with plants producing either many flowers with less nectar or fewer flowers with more nectar, suggesting a balance between these investments. Nectar data was available for only 38% of the species, as small amounts of nectar were often unmeasurable with refractometers, potentially underestimating the role of nectar traits in our study. With new potentially upcoming technologies, plant species with smaller flowers might also be included in these analyses (see, for example: Aronne and Malara, 2019).

The relative importance of phylogenetic relatedness compared to traits differed between phenological stages and was more important for vegetative phenology (initial growth, senescence) and flowering duration than for reproductive phenology (flowering onset, end; fruiting onset, end, duration), emphasizing the relevance of including phylogenetic relatedness in phenological studies (Bolmgren and D. Cowan, 2008; Davies et al., 2013; Rauschkolb et al., 2024; Sporbert et al., 2022). The pattern found could be explained by a clustering between monocotyledonous species (n=10), which in our set of species are mainly spring geophytes that start their growth and senescence early in the year and have a short flowering duration (see Figure S II.7). On the contrary, dicotyledons (n=58) showed a greater variation in vegetative phenology and flowering duration. Thus, our finding could be a consequence of species selection and the pattern should be tested for a larger species set over a larger phylogenetic gradient.

Consistency of phenology-trait relationships across gardens

The functional traits and phenological patterns observed did not differ between the three botanical gardens (Figure S II.5), and we found consistent phenology-trait relationships between the gardens. ‘Garden’ only played a role in the timing of leaf unfolding, with leaf unfolding observed earlier in Jena than in Berlin and Halle. As the climatic conditions in the three gardens were largely comparable (Table S II.2), we assume that garden specific phenological differences may be related to different microsite conditions (microclimate, soil conditions) and different maintenance by the gardeners, e.g., coverage of beds (Sporbert et al., 2022). Our study demonstrates that botanical gardens are suitable locations to study phenology-trait relationships of many species that usually occur in different habitats and would otherwise be much more challenging to investigate. Deilmann et al. (2024) found that while traits were more important than environment in explaining phenological patterns, habitat conditions influenced the specific trait-phenology relationships, suggesting that multispecies analyses from botanical gardens can provide information about natural habitats when habitat conditions are also considered.

Outlook

Future studies should examine whether the traits driving the phenological patterns identified in this and previous studies (Deilmann et al., 2024; Sporbert et al., 2022) are consistent with those influencing phenological responses to climate change (König et al., 2018; Pareja-Bonilla et al., 2025; Plos et al., 2024). Floral traits though barely considered in previous studies (but see Pareja-Bonilla et al., 2025), can reveal distinct relationships with climate-driven phenological changes and should therefore be included in future studies. Understanding phenological and trait changes is vital for assessing impacts on plant and pollinator fitness, as altered timing of resources such as pollen and nectar could lead to mismatches in seasonal availability, morphology, or species recognition (Gérard et al., 2020). Furthermore, future research should focus on elucidating how belowground traits, such as root morphology and nutrient acquisition strategies, influence aboveground phenological patterns, as these traits are likely interconnected through resource acquisition and allocation dynamics.

References

Ahmad, M., Rathee, S., Krishnadas, M., 2025. From low to high elevations, flowers adapt traits and phenology to climate, but phenology-trait relationships weak. Functional Ecology 00, 1–14. https://doi.org/10.1111/1365-2435.14748

Aragón, C.F., Méndez, M., Escudero, A., 2009. Survival costs of reproduction in a short-lived perennial plant: Live hard, die young. American Journal of Botany 96, 904–911. https://doi.org/10.3732/ajb.0800223

Aronne, G., Malara, P., 2019. Fiber-optic refractometer for in vivo sugar concentration measurements of low-nectar-producing flowers. New Phytologist 224, 987–993. https://doi.org/10.1111/nph.16084

Arroyo-Correa, B., Bartomeus, I., Jordano, P., 2021. Individual-based plant–pollinator networks are structured by phenotypic and microsite plant traits. Journal of Ecology 109, 2832–2844. https://doi.org/10.1111/1365-2745.13694

Bianchini, K., Morrissey, C.A., 2020. Species traits predict the aryl hydrocarbon receptor 1 (AHR1) subtypes responsible for dioxin sensitivity in birds. Sci Rep 10, 11706. https://doi.org/10.1038/s41598-020-68497-y

Bolmgren, K., D. Cowan, P., 2008. Time – size tradeoffs: a phylogenetic comparative study of flowering time, plant height and seed mass in a north-temperate flora. Oikos 117, 424–429. https://doi.org/10.1111/j.2007.0030-1299.16142.x

Bosch, J., Retana, J., Cerdá, X., 1997. Flowering phenology, floral traits and pollinator composition in a herbaceous Mediterranean plant community. Oecologia 109, 583–591. https://doi.org/10.1007/s004420050120

Bucher, S.F., König, P., Menzel, A., Migliavacca, M., Ewald, J., Römermann, C., 2018. Traits and climate are associated with first flowering day in herbaceous species along elevational gradients. Ecology and Evolution 8, 1147–1158. https://doi.org/10.1002/ece3.3720

Bucher, S.F., Römermann, C., 2021. The timing of leaf senescence relates to flowering phenology and functional traits in 17 herbaceous species along elevational gradients. Journal of Ecology 109, 1537–1548. https://doi.org/10.1111/1365-2745.13577

Burd, M., 1999. Flower number and floral components in ten angiosperm species: an examination of assumptions about trade-offs in reproductive evolution. Biological Journal of the Linnean Society 68, 579–592. https://doi.org/10.1111/j.1095-8312.1999.tb01189.x

Corbet, S.A., 2003. Nectar sugar content: estimating standing crop and secretion rate in the field. Apidologie 34, 1–10. https://doi.org/10.1051/apido:2002049

Dafni, A., Lehrer, M., Kevan, P.G., 1997. SPATIAL FLOWER PARAMETERS AND INSECT SPATIAL VISION. Biological Reviews 72, 239–282. https://doi.org/10.1017/S0006323196005002

Davies, T.J., Wolkovich, E.M., Kraft, N.J.B., Salamin, N., Allen, J.M., Ault, T.R., Betancourt, J.L., Bolmgren, K., Cleland, E.E., Cook, B.I., Crimmins, T.M., Mazer, S.J., McCabe, G.J., Pau, S., Regetz, J., Schwartz, M.D., Travers, S.E., 2013. Phylogenetic conservatism in plant phenology. Journal of Ecology 101, 1520–1530. https://doi.org/10.1111/1365-2745.12154

Davis, A.R., 1997. Pollen efficiency of insects, in: Shivanna, K., Sawhney, V. (Eds.), Pollen Biotechnology for Crop Production and Improvement. Cambridge University Press, New York, NY, USA.

Deilmann, T.J., Ulrich, J., Römermann, C., 2024. Habitat conditions filter stronger for functional traits than for phenology in herbaceous species. Ecology and Evolution 14, e11505. https://doi.org/10.1002/ece3.11505

Diaz, S., Hodgson, J. g., Thompson, K., Cabido, M., Cornelissen, J. h. c., Jalili, A., Montserrat-Martí, G., Grime, J. p., Zarrinkamar, F., Asri, Y., Band, S. r., Basconcelo, S., Castro-Díez, P., Funes, G., Hamzehee, B., Khoshnevi, M., Pérez-Harguindeguy, N., Pérez-Rontomé, M. c., Shirvany, F. a., Vendramini, F., Yazdani, S., Abbas-Azimi, R., Bogaard, A., Boustani, S., Charles, M., Dehghan, M., de Torres-Espuny, L., Falczuk, V., Guerrero-Campo, J., Hynd, A., Jones, G., Kowsary, E., Kazemi-Saeed, F., Maestro-Martínez, M., Romo-Díez, A., Shaw, S., Siavash, B., Villar-Salvador, P., Zak, M. r., 2004. The plant traits that drive ecosystems: Evidence from three continents. Journal of Vegetation Science 15, 295–304. https://doi.org/10.1111/j.1654-1103.2004.tb02266.x

Díaz, S., Kattge, J., Cornelissen, J.H.C., Wright, I.J., Lavorel, S., Dray, S., Reu, B., Kleyer, M., Wirth, C., Colin Prentice, I., Garnier, E., Bönisch, G., Westoby, M., Poorter, H., Reich, P.B., Moles, A.T., Dickie, J., Gillison, A.N., Zanne, A.E., Chave, J., Joseph Wright, S., Sheremet'ev, S.N., Jactel, H., Baraloto, C., Cerabolini, B., Pierce, S., Shipley, B., Kirkup, D., Casanoves, F., Joswig, J.S., Günther, A., Falczuk, V., Rüger, N., Mahecha, M.D., Gorné, L.D., 2016. The global spectrum of plant form and function. Nature 529, 167–171. https://doi.org/10.1038/nature16489

Diniz-Filho, J.A.F., Sant'Ana, C.E.R. de, Bini, L.M., 1998. An eigenvector method for estimating phylogenetic inertia. Evolution 52, 1247–1262. https://doi.org/10.1111/j.1558-5646.1998.tb02006.x

Du, G., Qi, W., 2010. Trade-offs between flowering time, plant height, and seed size within and across 11 communities of a QingHai-Tibetan flora. Plant Ecol 209, 321–333. https://doi.org/10.1007/s11258-010-9763-4

Dunker, S., Boyd, M., Durka, W., Erler, S., Harpole, W.S., Henning, S., Herzschuh, U., Hornick, T., Knight, T., Lips, S., Mäder, P., Švara, E.M., Mozarowski, S., Rakosy, D., Römermann, C., Schmitt-Jansen, M., Stoof-Leichsenring, K., Stratmann, F., Treudler, R., Virtanen, R., Wendt-Potthoff, K., Wilhelm, C., 2022. The potential of multispectral imaging flow cytometry for environmental monitoring. Cytometry Part A 101, 782–799. https://doi.org/10.1002/cyto.a.24658

Dunker, S., Motivans, E., Rakosy, D., Boho, D., Mäder, P., Hornick, T., Knight, T.M., 2021. Pollen analysis using multispectral imaging flow cytometry and deep learning. New Phytologist 229, 593–606. https://doi.org/10.1111/nph.16882

Edlund, A.F., Swanson, R., Preuss, D., 2004. Pollen and Stigma Structure and Function: The Role of Diversity in Pollination. The Plant Cell 16, S84–S97. https://doi.org/10.1105/tpc.015800

Elith, J., Leathwick, J.R., Hastie, T., 2008. A working guide to boosted regression trees. Journal of Animal Ecology 77, 802–813. https://doi.org/10.1111/j.1365-2656.2008.01390.x

Elzinga, J.A., Atlan, A., Biere, A., Gigord, L., Weis, A.E., Bernasconi, G., 2007. Time after time: flowering phenology and biotic interactions. Trends in Ecology & Evolution 22, 432–439. https://doi.org/10.1016/j.tree.2007.05.006

E-Vojtkó, A., Bello, F., Durka, W., Kühn, I., Götzenberger, L., 2020. The neglected importance of floral traits in trait-based plant community assembly. J Veg Sci 31, 529–539. https://doi.org/10.1111/jvs.12877

E-Vojtkó, A., Junker, R.R., de Bello, F., Götzenberger, L., 2022. Floral and reproductive traits are an independent dimension within the plant economic spectrum of temperate central Europe. New Phytologist 236, 1964–1975. https://doi.org/10.1111/nph.18386

Fabbro, T., Körner, C., 2004. Altitudinal differences in flower traits and reproductive allocation. Flora - Morphology, Distribution, Functional Ecology of Plants 199, 70–81. https://doi.org/10.1078/0367-2530-00128

Filipiak, M., Walczyńska, A., Denisow, B., Petanidou, T., Ziółkowska, E., 2022. Phenology and production of pollen, nectar, and sugar in 1612 plant species from various environments. Ecology e3705. https://doi.org/10.1002/ecy.3705

Fornoff, F., Klein, A.-M., Hartig, F., Benadi, G., Venjakob, C., Schaefer, H.M., Ebeling, A., 2017. Functional flower traits and their diversity drive pollinator visitation. Oikos 126, 1020–1030. https://doi.org/10.1111/oik.03869

Freiberg, M., Winter, M., Gentile, A., Zizka, A., Muellner-Riehl, A.N., Weigelt, A., Wirth, C., 2020. LCVP, The Leipzig catalogue of vascular plants, a new taxonomic reference list for all known vascular plants. Sci Data 7, 416. https://doi.org/10.1038/s41597-020-00702-z

Gaudet, C.L., Keddy, P.A., 1988. A comparative approach to predicting competitive ability from plant traits. Nature 334, 242–243. https://doi.org/10.1038/334242a0

Gérard, M., Vanderplanck, M., Wood, T., Michez, D., 2020. Global warming and plant–pollinator mismatches. Emerging Topics in Life Sciences 4, 77–86. https://doi.org/10.1042/ETLS20190139

Hao, K., Tian, Z.-X., Wang, Z.-C., Huang, S.-Q., 2020. Pollen grain size associated with pollinator feeding strategy. Proceedings of the Royal Society B: Biological Sciences 287, 20201191. https://doi.org/10.1098/rspb.2020.1191

Harder, L.D., Barrett, S.C.H., 2007. Ecology and Evolution of Flowers. Oxford University Press, Incorporated, Oxford, UNITED KINGDOM.

Harell, F.E., Dupont, C., 2024. Hmisc: Harrell Miscellaneous.

Heberling, J.M., McDonough MacKenzie, C., Fridley, J.D., Kalisz, S., Primack, R.B., 2019. Phenological mismatch with trees reduces wildflower carbon budgets. Ecology Letters 22, 616–623. https://doi.org/10.1111/ele.13224

Horbach, S., Rauschkolb, R., Römermann, C., 2023. Flowering and leaf phenology are more variable and stronger associated to functional traits in herbaceous compared to tree species. Flora 300, 152218. https://doi.org/10.1016/j.flora.2023.152218

Hornick, T., Richter, A., Harpole, W.S., Bastl, M., Bohlmann, S., Bonn, A., Bumberger, J., Dietrich, P., Gemeinholzer, B., Grote, R., Heinold, B., Keller, A., Luttkus, M.L., Mäder, P., Motivans Švara, E., Passonneau, S., Punyasena, S.W., Rakosy, D., Richter, R., Sickel, W., Steffan-Dewenter, I., Theodorou, P., Treudler, R., Werchan, B., Werchan, M., Wolke, R., Dunker, S., 2022. An integrative environmental pollen diversity assessment and its importance for the Sustainable Development Goals. PLANTS, PEOPLE, PLANET 4, 110–121. https://doi.org/10.1002/ppp3.10234

Huang, L., Koubek, T., Weiser, M., Herben, T., 2018. Environmental drivers and phylogenetic constraints of growth phenologies across a large set of herbaceous species. Journal of Ecology 106, 1621–1633. https://doi.org/10.1111/1365-2745.12927

Jin, Y., Qian, H., 2022. V.PhyloMaker2: An updated and enlarged R package that can generate very large phylogenies for vascular plants. Plant Diversity 44, 335–339. https://doi.org/10.1016/j.pld.2022.05.005

Karger, D.N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R.W., Zimmermann, N.E., Linder, H.P., Kessler, M., 2018. Data from: Climatologies at high resolution for the earth’s land surface areas. https://doi.org/10.5061/DRYAD.KD1D4

Karger, D.N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R.W., Zimmermann, N.E., Linder, H.P., Kessler, M., 2017. Climatologies at high resolution for the earth’s land surface areas. Sci Data 4, 170122. https://doi.org/10.1038/sdata.2017.122

Kassambara, A., Mundt, F., 2020. factoextra: Extract and Visualize the Results of Multivariate Data Analyses.

Kearns, C.A., Inouye, D.W., 1993. Techniques for pollination biologists. Techniques for pollination biologists.

König, P., Tautenhahn, S., Cornelissen, J.H.C., Kattge, J., Bönisch, G., Römermann, C., 2018. Advances in flowering phenology across the Northern Hemisphere are explained by functional traits. Global Ecology and Biogeography 27, 310–321. https://doi.org/10.1111/geb.12696

Kudo, G., Cooper, E.J., 2019. When spring ephemerals fail to meet pollinators: mechanism of phenological mismatch and its impact on plant reproduction. Proceedings of the Royal Society B: Biological Sciences 286, 20190573. https://doi.org/10.1098/rspb.2019.0573

Lauri, P.-E., 2019. Corner’s rules as a framework for plant morphology, architecture and functioning – issues and steps forward. The New Phytologist 221, 1679–1684.

Liu, Y., Li, G., Wu, X., Niklas, K.J., Yang, Z., Sun, S., 2021. Linkage between species traits and plant phenology in an alpine meadow. Oecologia 195, 409–419. https://doi.org/10.1007/s00442-020-04846-y

Menzel, A., Yuan, Y., Matiu, M., Sparks, T., Scheifinger, H., Gehrig, R., Estrella, N., 2020. Climate change fingerprints in recent European plant phenology. Global Change Biology. https://doi.org/10.1111/gcb.15000

Moles, A.T., Warton, D.I., Warman, L., Swenson, N.G., Laffan, S.W., Zanne, A.E., Pitman, A., Hemmings, F.A., Leishman, M.R., 2009. Global patterns in plant height. Journal of Ecology 97, 923–932. https://doi.org/10.1111/j.1365-2745.2009.01526.x

Mori, S., Fukui, H., Oishi, M., Sakuma, M., Kawakami, M., Tsukioka, J., Goto, K., Hirai, N., 2018. Biocommunication between Plants and Pollinating Insects through Fluorescence of Pollen and Anthers. J Chem Ecol 44, 591–600. https://doi.org/10.1007/s10886-018-0958-9

Mues, A.W., 2020. Functional Integration of Floral Plant Traits: Shape and Symmetry, Optical Signal, Reward and Reproduction in the Angiosperm Flower.

Nord, E.A., Lynch, J.P., 2009. Plant phenology: a critical controller of soil resource acquisition. Journal of Experimental Botany 60, 1927–1937. https://doi.org/10.1093/jxb/erp018

Nordt, B., Hensen, I., Bucher, S.F., Freiberg, M., Primack, R.B., Stevens, A.-D., Bonn, A., Wirth, C., Jakubka, D., Plos, C., Sporbert, M., Römermann, C., 2021. The PhenObs initiative: A standardised protocol for monitoring phenological responses to climate change using herbaceous plant species in botanical gardens. Functional Ecology 35, 821–834. https://doi.org/10.1111/1365-2435.13747

Obeso, J.R., 2002. The costs of reproduction in plants. New Phytologist 155, 321–348. https://doi.org/10.1046/j.1469-8137.2002.00477.x

Ohashi, K., Yahara, T., 1999. How Long to Stay on, and How Often to Visit a Flowering Plant?: A Model for Foraging Strategy When Floral Displays Vary in Size. Oikos 86, 386–392. https://doi.org/10.2307/3546457

Osborn, J.M., Taylor, T.N., Schneider, E.L., 1991. Pollen Morphology and Ultrastructure of the Cabombaceae: Correlations with Pollination Biology. American Journal of Botany 78, 1367–1378. https://doi.org/10.1002/j.1537-2197.1991.tb12603.x

Pagel, M., 1999. Inferring the historical patterns of biological evolution. Nature 401, 877–884. https://doi.org/10.1038/44766

Parachnowitsch, A.L., Manson, J.S., Sletvold, N., 2019. Evolutionary ecology of nectar. Ann Bot 123, 247–261. https://doi.org/10.1093/aob/mcy132

Pareja-Bonilla, D., Ortiz, P.L., Morellato, L.P.C., Arista, M., 2025. Functional traits predict changes in floral phenology under climate change in a highly diverse Mediterranean community. Functional Ecology n/a. https://doi.org/10.1111/1365-2435.70062

Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., Bret-Harte, M.S., Cornwell, W.K., Craine, J.M., Gurvich, D.E., Urcelay, C., Veneklaas, E.J., Reich, P.B., Poorter, L., Wright, I.J., Ray, P., Enrico, L., Pausas, J.G., Vos, A.C. de, Buchmann, N., Funes, G., Quétier, F., Hodgson, J.G., Thompson, K., Morgan, H.D., Steege, H. ter, Sack, L., Blonder, B., Poschlod, P., Vaieretti, M.V., Conti, G., Staver, A.C., Aquino, S., Cornelissen, J.H.C., 2016. Corrigendum to: New handbook for standardised measurement of plant functional traits worldwide. Aust. J. Bot. 64, 715–716. https://doi.org/10.1071/bt12225_co

Pistón, N., Bello, F. de, Dias, A.T.C., Götzenberger, L., Rosado, B.H.P., Mattos, E.A. de, Salguero-Gómez, R., Carmona, C.P., 2019. Multidimensional ecological analyses demonstrate how interactions between functional traits shape fitness and life history strategies. Journal of Ecology 107, 2317–2328. https://doi.org/10.1111/1365-2745.13190

Plos, C., Hensen, I., Korell, L., Auge, H., Römermann, C., 2024. Plant species phenology differs between climate and land-use scenarios and relates to plant functional traits. Ecology and Evolution 14, e11441. https://doi.org/10.1002/ece3.11441

Primack, R.B., Ellwood, E.R., Gallinat, A.S., Miller-Rushing, A.J., 2021. The growing and vital role of botanical gardens in climate change research. New Phytologist 231, 917–932. https://doi.org/10.1111/nph.17410

R Core Team, 2023. R: A Language and Environment for Statistical Computing.

Rauschkolb, R., Bucher, S.F., Hensen, I., Ahrends, A., Fernández-Pascual, E., Heubach, K., Jakubka, D., Jiménez-Alfaro, B., König, A., Koubek, T., Kehl, A., Khuroo, A.A., Lindstädter, A., Shafee, F., Mašková, T., Platonova, E., Panico, P., Plos, C., Primack, R., Rosche, C., Shah, M.A., Sporbert, M., Stevens, A.-D., Tarquini, F., Tielbörger, K., Träger, S., Vange, V., Weigelt, P., Bonn, A., Freiberg, M., Knickmann, B., Nordt, B., Wirth, C., Römermann, C., 2024. Spatial variability in herbaceous plant phenology is mostly explained by variability in temperature but also by photoperiod and functional traits. Int J Biometeorol. https://doi.org/10.1007/s00484-024-02621-9

Reekie, E.G., Avila-Sakar, G., 2005. 7 - The Shape of the Trade-off Function between Reproduction and Growth, in: Reekie, E.G., Bazzaz, F.A. (Eds.), Reproductive Allocation in Plants, Physiological Ecology. Academic Press, Burlington, pp. 189–214. https://doi.org/10.1016/B978-012088386-8/50007-7

Revell, L.J., 2024. phytools 2.0: an updated R ecosystem for phylogenetic comparative methods (and other things). PeerJ 12, e16505. https://doi.org/10.7717/peerj.16505

Ridgeway, G., Edwards, D., Kriegler, B., Schroedl, S., Southworth, H., Greenwell, B., Boehmke, B., Cunningham, J., Developers (https://github.com/gbm-developers), G.B.M., 2024. gbm: Generalized Boosted Regression Models.

Roddy, A.B., Martínez-Perez, C., Teixido, A.L., Cornelissen, T.G., Olson, M.E., Oliveira, R.S., Silveira, F.A.O., 2021. Towards the flower economics spectrum. New Phytologist 229, 665–672. https://doi.org/10.1111/nph.16823

Root, T.L., Price, J.T., Hall, K.R., Schneider, S.H., Rosenzweig, C., Pounds, J.A., 2003. Fingerprints of global warming on wild animals and plants. Nature 421, 57–60. https://doi.org/10.1038/nature01333

Sargent, R.D., Goodwillie, C., Kalisz, S., Ree, R.H., 2007. Phylogenetic evidence for a flower size and number trade-off. American Journal of Botany 94, 2059–2062. https://doi.org/10.3732/ajb.94.12.2059

Schmitt, J., 1983. Individual flowering phenology, plant size, and reproductive success in Linanthus androsaceus, a California annual. Oecologia 59, 135–140. https://doi.org/10.1007/BF00388084

Segrestin, J., Navas, M.-L., Garnier, E., 2020. Reproductive phenology as a dimension of the phenotypic space in 139 plant species from the Mediterranean. New Phytologist 225, 740–753. https://doi.org/10.1111/nph.16165

Shmida, A., Dukas, R., 1990. PROGRESSIVE REDUCTION IN THE MEAN BODY SIZES OF SOLITARY BEES ACTIVE DURING THE FLOWERING SEASON AND ITS CORRELATION WITH THE SIZES OF BEE FLOWERS OF THE MINT FAMILY (LAMIACEAE). Israel Journal of Plant Sciences 39, 133–141. https://doi.org/10.1080/0021213X.1990.10677138

Sporbert, M., Jakubka, D., Bucher, S.F., Hensen, I., Freiberg, M., Heubach, K., König, A., Nordt, B., Plos, C., Blinova, I., Bonn, A., Knickmann, B., Koubek, T., Linstädter, A., Mašková, T., Primack, R.B., Rosche, C., Shah, M.A., Stevens, A.-D., Tielbörger, K., Träger, S., Wirth, C., Römermann, C., 2022. Functional traits influence patterns in vegetative and reproductive plant phenology – a multi-botanical garden study. New Phytologist 235, 2199–2210. https://doi.org/10.1111/nph.18345

Stanley, R.G., Linskens, H.F., 1974. Pollen Pigments, in: Stanley, R.G., Linskens, H.F. (Eds.), Pollen: Biology Biochemistry Management. Springer, Berlin, Heidelberg, pp. 223–246. https://doi.org/10.1007/978-3-642-65905-8_15

Sun, S., Frelich, L.E., 2011. Flowering phenology and height growth pattern are associated with maximum plant height, relative growth rate and stem tissue mass density in herbaceous grassland species. Journal of Ecology 99, 991–1000. https://doi.org/10.1111/j.1365-2745.2011.01830.x

Sun, S., Jin, D., Li, R., 2006. Leaf emergence in relation to leaf traits in temperate woody species in East-Chinese Quercus fabri forests. Acta Oecologica 30, 212–222. https://doi.org/10.1016/j.actao.2006.04.001

Wang, L., Han, X., Yin, Q., Wang, G., Xu, J., Chai, Y., Yue, M., 2021. Differences in leaf phenological traits between trees and shrubs are closely related to functional traits in a temperate forest. Acta Oecologica 112, 103760. https://doi.org/10.1016/j.actao.2021.103760

Weiner, J., Campbell, L.G., Pino, J., Echarte, L., 2009. The allometry of reproduction within plant populations. Journal of Ecology 97, 1220–1233. https://doi.org/10.1111/j.1365-2745.2009.01559.x

Westoby, M., Falster, D.S., Moles, A.T., Vesk, P.A., Wright, I.J., 2002. Plant Ecological Strategies: Some Leading Dimensions of Variation Between Species. Annual Review of Ecology and Systematics 33, 125–159. https://doi.org/10.1146/annurev.ecolsys.33.010802.150452

Willmer, P., 2011a. Rewards 2: The Biology of Nectar, in: Willmer, P. (Ed.), Pollination and Floral Ecology. Princeton University Press, p. 0. https://doi.org/10.23943/princeton/9780691128610.003.0008

Willmer, P., 2011b. Rewards and Costs: The Environmental Economics of Pollination, in: Willmer, P. (Ed.), Pollination and Floral Ecology. Princeton University Press, p. 0. https://doi.org/10.23943/princeton/9780691128610.003.0010

Willmer, P., 2011c. Rewards 1: The Biology of Pollen, in: Willmer, P. (Ed.), Pollination and Floral Ecology. Princeton University Press, p. 0. https://doi.org/10.23943/princeton/9780691128610.003.0007

Worley, A.C., Baker, A.M., Thompson, J.D., Barrett, S.C.H., 2000. Floral Display in Narcissus: Variation in Flower Size and Number at the Species, Population, and Individual Levels. International Journal of Plant Sciences 161, 69–79. https://doi.org/10.1086/314225

Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J.H.C., Diemer, M., Flexas, J., Garnier, E., Groom, P.K., Gulias, J., Hikosaka, K., Lamont, B.B., Lee, T., Lee, W., Lusk, C., Midgley, J.J., Navas, M.-L., Niinemets, Ü., Oleksyn, J., Osada, N., Poorter, H., Poot, P., Prior, L., Pyankov, V.I., Roumet, C., Thomas, S.C., Tjoelker, M.G., Veneklaas, E.J., Villar, R., 2004. The worldwide leaf economics spectrum. Nature 428, 821–827. https://doi.org/10.1038/nature02403

Ye, Z., Mu, Y., Van Duzen, S., Ryser, P., 2024. Root and shoot phenology, architecture, and organ properties: an integrated trait network among 44 herbaceous wetland species. New Phytologist 244, 436–450. https://doi.org/10.1111/nph.19747

Zimmerman, M., 1988. Plant Reproductive Ecology: Patterns and Strategies. Chapter 8: Nectar Production, Flowering Phenology, and Strategies for Pollination. Oxford University Press.

Supplementary Material (S II)

Manuscript title: Interspecific phenological variation in herbaceous species is more strongly reflected in vegetative traits than in floral traits

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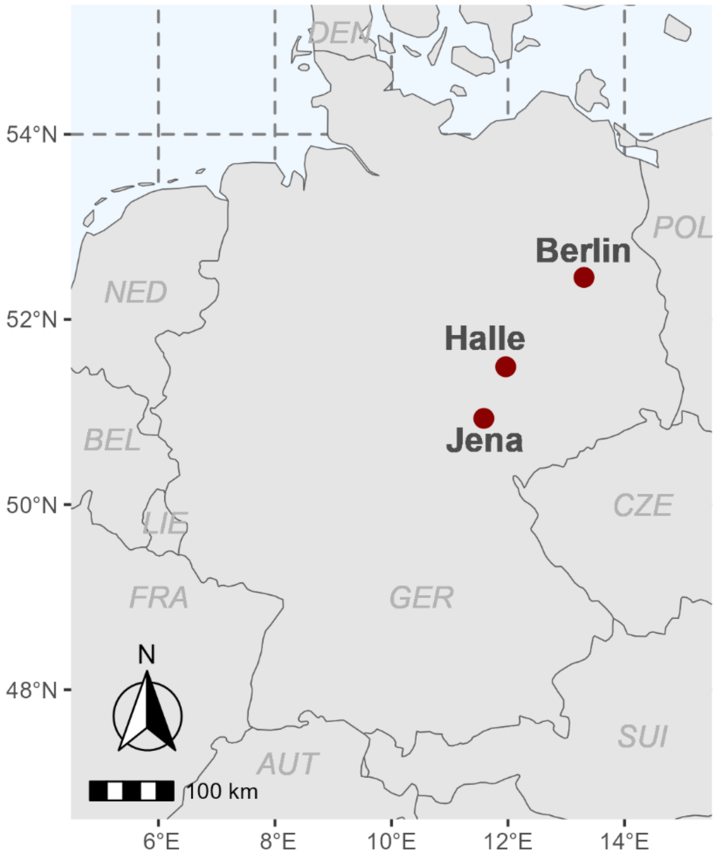


Figure S II.1: Location of the three Botanical Gardens in Germany.

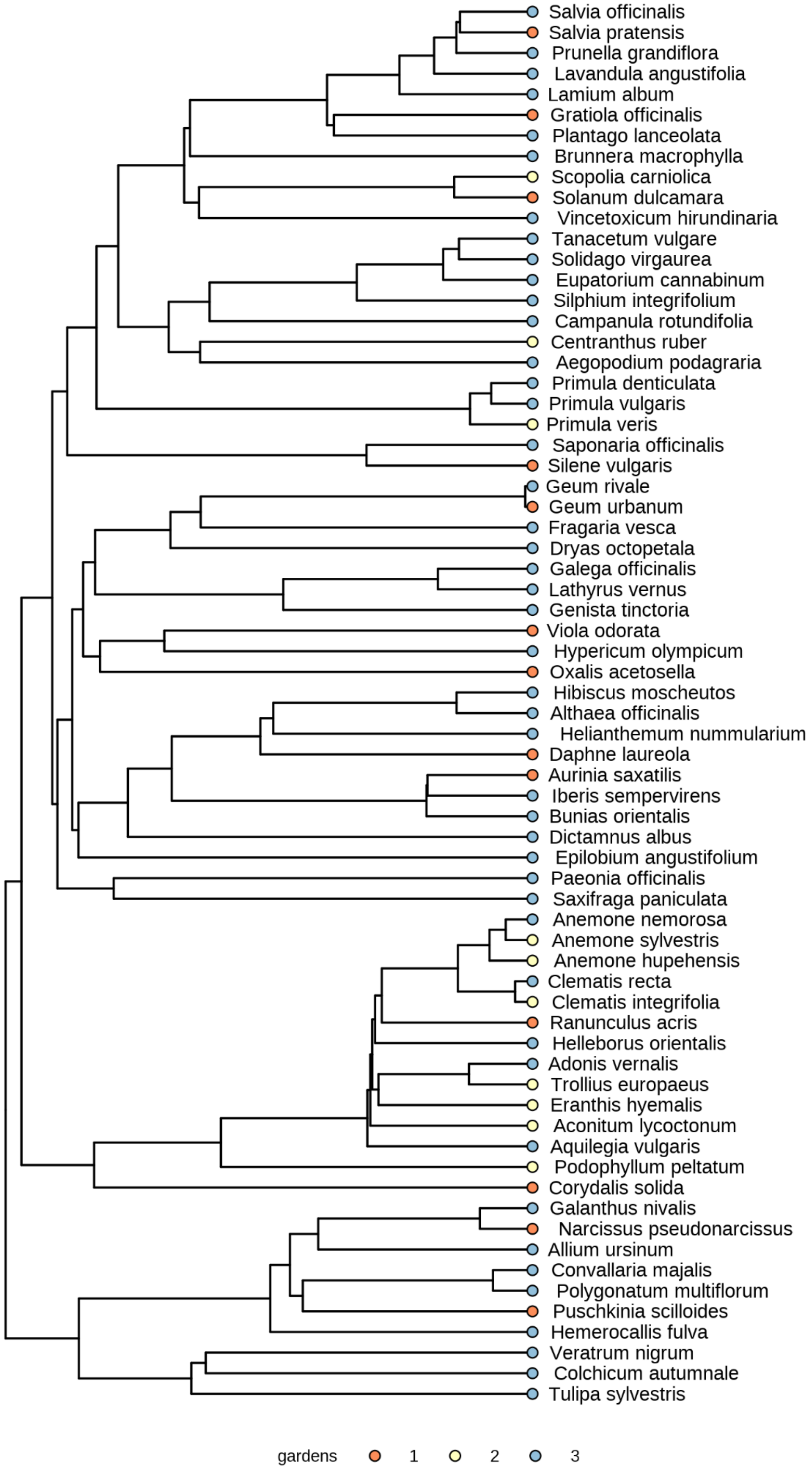


Figure S II.2: Phylogenetic tree of the 68 plant species studied. The number of gardens in which each species was investigated is represented by the colors of the tip labels.

Table S II.1: Investigated phenological stages with the respective units and range of values. A list of all species and their occurrence in the respective gardens can be found in Table S II.2. In case of a missing observation the number of species (n species) may deviate from the total 68 species. (doy = Day of the year)

Phenological stage	Abbrev.	Unit	Min.	Median	Mean	Max.	n species
Initial growth	InitGr	doy	2	56	59.15	358	61
Leaf unfolding	LeafUnf	doy	2	72	72.7	184	66
First flowering day	FFD	doy	2	128	129.7	247	68
Peak of flowering	FlPeak	doy	38	156	152.4	268	66
End of flowering	FlEnd	doy	36	193	199.8	364	68
Flowering duration	FlDur	days	4	48.5	70.09	356	68
Fruiting onset	FrOn	doy	2	184	187.1	338	61
End of fruiting	FrEnd	doy	120	268	251.2	364	60
Fruiting duration	FrDur	days	3	48	65.12	356	60
Senescence onset	SenOn	doy	2	191	193.2	296	68
Peak of senescence	SenPeak	doy	2	293	274.5	358	66
End of senescence	SenEnd	doy	2	324	304.1	364	68

Table S II.2: Bioclimatic variables on long term observations (1979-2013) of the locations of the three Botanical Gardens derived from the CHELSA database (Karger et al., 2018, 2017).

		Halle (Saale)	Jena	Berlin
	Latitude/ Longitude	51.4888/ 11.9611	50.9313/ 11.5852	52.4545/ 13.3050
Bio1	Annual Mean Temperature	9.75	9.45	9.45
Bio5	Max Temperature of Warmest Month	23.65	23.25	23.35
Bio6	Min Temperature of Coldest Month	-1.65	-2.25	-1.95
Bio8	Mean Temperature of Wettest Quarter	18.45	18.15	18.75
Bio9	Mean Temperature of Driest Quarter	1.45	0.95	7.55
Bio10	Mean Temperature of Warmest Quarter	18.95	18.75	18.75
Bio11	Mean Temperature of Coldest Quarter	1.15	0.75	0.65
Bio12	Annual Precipitation	531.9	601.4	603.7
Bio13	Precipitation of Wettest Month	64.7	74.5	62.3
Bio14	Precipitation of Driest Month	28.8	31.5	33.6
Bio16	Precipitation of Wettest Quarter	182.2	209.5	184.6
Bio17	Precipitation of Driest Quarter	90.4	95.0	114.3
Bio18	Precipitation of Warmest Quarter	171.5	206.5	184.6
Bio19	Precipitation of Coldest Quarter	108.9	109.2	152.4

Table S II.3: List of species included in this study and their occurrence across the three botanical gardens.

species	**genus**	**family**	**Halle**	**Berlin**	**Jena**
Allium ursinum	Allium	Amaryllidaceae	x	x	x
Galanthus nivalis	Galanthus	Amaryllidaceae	x	x	x
Narcissus pseudonarcissus	Narcissus	Amaryllidaceae	x		
Aegopodium podagraria	Aegopodium	Apiaceae	x	x	x
Vincetoxicum hirundinaria	Vincetoxicum	Apocynaceae	x	x	x
Eupatorium cannabinum	Eupatorium	Asteraceae	x	x	x
Silphium integrifolium	Silphium	Asteraceae	x	x	x
Solidago virgaurea	Solidago	Asteraceae	x	x	x
Tanacetum vulgare	Tanacetum	Asteraceae	x	x	x
Podophyllum peltatum	Podophyllum	Berberidaceae	x	x	
Brunnera macrophylla	Brunnera	Boraginaceae	x	x	x
Aurinia saxatilis	Aurinia	Brassicaceae	x		
Bunias orientalis	Bunias	Brassicaceae	x	x	x
Iberis sempervirens	Iberis	Brassicaceae	x	x	x
Campanula rotundifolia	Campanula	Campanulaceae	x	x	x
Saponaria officinalis	Saponaria	Caryophyllaceae	x	x	x
Silene vulgaris	Silene	Caryophyllaceae	x		
Helianthemum nummularium	Helianthemum	Cistaceae	x	x	x
Colchicum autumnale	Colchicum	Colchicaceae	x	x	x
Galega officinalis	Galega	Fabaceae	x	x	x
Genista tinctoria	Genista	Fabaceae	x	x	x
Lathyrus vernus	Lathyrus	Fabaceae	x	x	x
Corydalis solida	Corydalis	Fumariaceae	x		
Hemerocallis fulva	Hemerocallis	Hemerocallidaceae	x	x	x
Puschkinia scilloides	Puschkinia	Hyacinthaceae	x		
Hypericum olympicum	Hypericum	Hypericaceae	x	x	x
Lamium album	Lamium	Lamiaceae	x	x	x
Lavandula angustifolia	Lavandula	Lamiaceae	x	x	x
Prunella grandiflora	Prunella	Lamiaceae	x	x	x
Salvia officinalis	Salvia	Lamiaceae	x	x	x
Salvia pratensis	Salvia	Lamiaceae			x
Tulipa sylvestris	Tulipa	Liliaceae	x	x	x
Althaea officinalis	Althaea	Malvaceae	x	x	x
Hibiscus moscheutos	Hibiscus	Malvaceae	x	x	x
Veratrum nigrum	Veratrum	Melanthiaceae	x	x	x
Epilobium angustifolium	Epilobium	Onagraceae	x	x	x
Oxalis acetosella	Oxalis	Oxalidaceae	x		
Paeonia officinalis	Paeonia	Paeoniaceae	x	x	x
Gratiola officinalis	Gratiola	Plantaginaceae	x		
Plantago lanceolata	Plantago	Plantaginaceae	x	x	x
Primula denticulata	Primula	Primulaceae	x	x	x
Primula veris	Primula	Primulaceae	x		x
Primula vulgaris	Primula	Primulaceae	x	x	x

species	**genus**	**family**	**Halle**	**Berlin**	**Jena**
Aconitum lycoctonum	Aconitum	Ranunculaceae	x	x	
Adonis vernalis	Adonis	Ranunculaceae	x	x	x
Anemone hupehensis	Anemone	Ranunculaceae	x	x	
Anemone nemorosa	Anemone	Ranunculaceae	x	x	x
Anemone sylvestris	Anemone	Ranunculaceae	x	x	
Aquilegia vulgaris	Aquilegia	Ranunculaceae	x	x	x
Clematis integrifolia	Clematis	Ranunculaceae	x	x	
Clematis recta	Clematis	Ranunculaceae	x	x	x
Eranthis hyemalis	Eranthis	Ranunculaceae	x		x
Helleborus orientalis	Helleborus	Ranunculaceae	x	x	x
Ranunculus acris	Ranunculus	Ranunculaceae			x
Trollius europaeus	Trollius	Ranunculaceae	x	x	
Dryas octopetala	Dryas	Rosaceae	x	x	x
Fragaria vesca	Fragaria	Rosaceae	x	x	x
Geum rivale	Geum	Rosaceae	x	x	x
Geum urbanum	Geum	Rosaceae			x
Convallaria majalis	Convallaria	Ruscaceae	x	x	x
Polygonatum multiflorum	Polygonatum	Ruscaceae	x	x	x
Dictamnus albus	Dictamnus	Rutaceae	x	x	x
Saxifraga paniculata	Saxifraga	Saxifragaceae	x	x	x
Scopolia carniolica	Scopolia	Solanaceae	x	x	
Solanum dulcamara	Solanum	Solanaceae	x		
Daphne laureola	Daphne	Thymelaeaceae	x		
Centranthus ruber	Centranthus	Valerianaceae	x		x
Viola odorata	Viola	Violaceae	x		

Table S II.4: Pagel's Lambda statistic (Pagel, 1999) was applied to quantify the strength of a phylogenetic signal. It ranges between 0 for traits being phylogenetically unrelated to 1 for traits following trait evolution according to a Brownian motion (BM) model. Traits showing a phylogenetic signal are highlighted in bold print.

Trait	*Pagels Lambda*	*p-value*
Number of flowers	**0.737**	**0.012**
Vegetative height	**0.734**	**0.011**
Generative height	0.458	0.154
Corolla length	0.932	0.288
Petal length	**0.494**	**0.035**
Flower size (SF)	**0.775**	**<0.001**
Flower size (FU)	**0.460**	**0.023**
Leaf area	0.353	0.084
SLA	0.265	0.431
LDMC	**0.697**	**<0.001**
Nectar volume	0.083	0.800
Nectar sucrose conc.	0.00004	1.000
Nectar sucrose mass	0.00004	1.000
Pollen size	0.451	0.124
Pollen shape	**1.003**	**<0.001**
Pollen fluorescence	**0.741**	**0.010**
Pollen structure	0.180	0.293

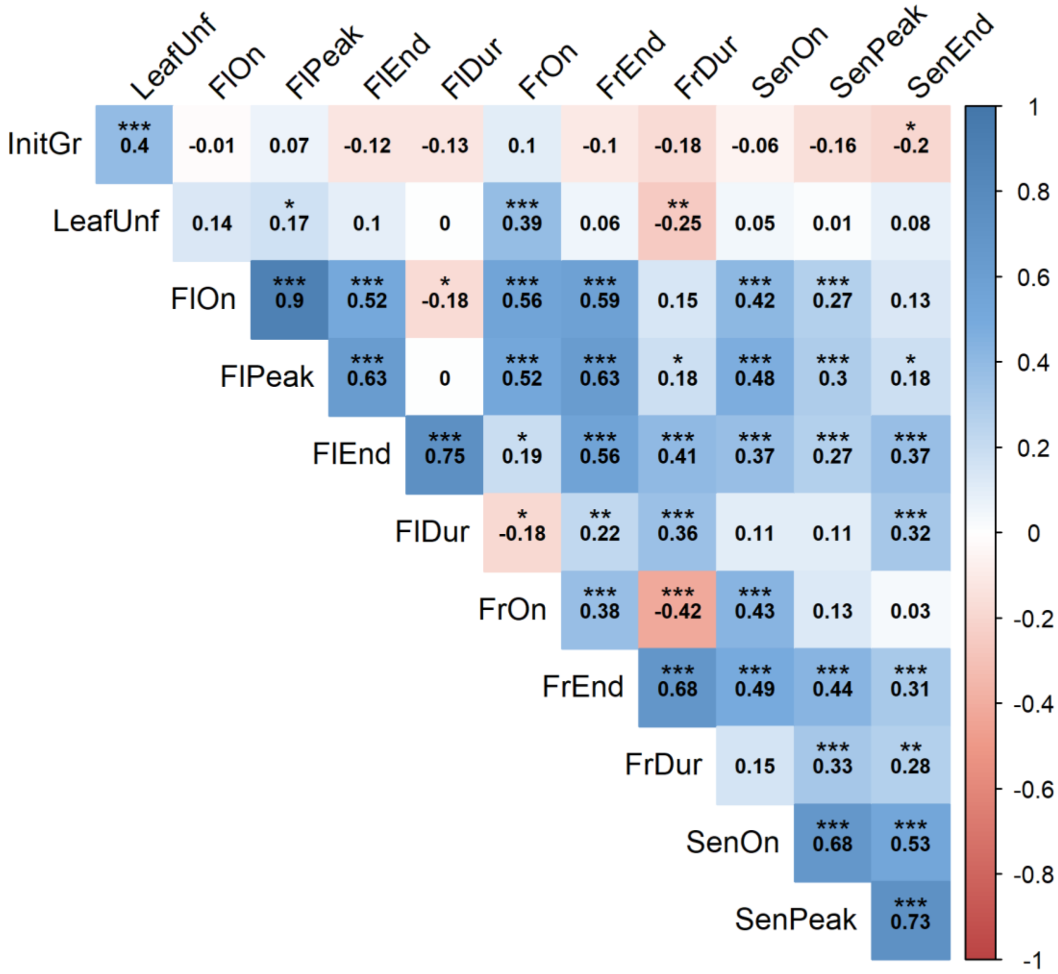
Phenological stage	*Pagels Lambda*	*p-value*
Initial growth	0.519	0.820
Leaf unfolding	0.0001	1.000
First flowering day	0.363	0.108
Peak flowering	0.406	0.065
Last flowering day	**0.378**	**0.013**
Flowering duration	**0.425**	**0.003**
Fruiting onset	**0.995**	**0.028**
Fruiting end	0.191	0.362
Senescence onset	0.050	0.686
Peak senescence	0.171	0.491
Senescence end	0.265	0.213

Table S II.5: Contributions (loadings) of traits (without nectar traits) to the first (Dim.1) to twelfth (Dim.12) PCA axes.

	Dim.1	Dim.2	Dim.3	Dim.4	Dim.5	Dim.6	Dim.7	Dim.8	Dim.9	Dim.10	Dim.11	Dim.12
Number of flowers	5.02	18.61	3.87	4.65	2.85	5.00	6.06	26.38	7.38	6.44	11.27	2.47
Veg. height	21.28	6.49	2.09	1.31	0.07	6.48	4.69	1.50	13.84	0.10	0.52	41.63
Gen. height	21.21	6.98	2.33	3.24	1.42	0.69	3.42	1.43	5.52	0.24	1.30	52.22
Flower size (SF)	0.05	20.73	12.57	0.00	10.66	0.49	16.46	5.28	3.37	3.93	26.48	0.00
Flower size (FU)	1.80	6.16	25.05	0.95	0.01	15.76	25.70	16.76	1.78	0.48	5.33	0.22
Leaf area	5.58	3.33	18.94	1.64	19.17	10.68	4.83	29.90	5.40	0.02	0.12	0.38
SLA	1.60	9.42	1.53	17.30	6.73	46.06	1.63	1.24	2.83	6.15	4.10	1.41
LDMC	2.38	8.94	0.20	28.36	7.65	7.46	2.06	15.44	8.28	14.56	4.64	0.02
Pollen size	12.70	6.82	3.39	14.78	0.07	4.08	4.14	0.44	4.51	28.36	20.09	0.62
Pollen shape	0.03	3.05	9.27	18.78	49.18	2.79	0.48	0.11	0.05	1.99	14.12	0.17
Pollen fluorescence	20.73	3.86	4.64	2.87	0.82	0.52	3.79	0.06	18.83	37.65	6.21	0.02
Pollen structure	7.62	5.62	16.12	6.12	1.36	0.00	26.73	1.45	28.21	0.08	5.83	0.85

Table S II.6: Contributions (loadings) of traits (including nectar traits) to the first (Dim.1) to fifteenth (Dim.15) PCA axes.

	Dim1	Dim2	Dim3	Dim4	Dim5	Dim6	Dim7	Dim8	Dim9	Dim 10	Dim 11	Dim 12	Dim 13	Dim 14	Dim 15
Number of flowers	0.02	12.94	6.00	0.66	26.86	0.00	26.25	2.62	11.19	0.52	3.91	0.04	3.14	5.85	0.00
Veg. height	10.03	7.16	8.81	0.04	0.54	0.49	0.11	8.54	13.17	0.56	16.25	0.09	8.77	25.42	0.00
Gen. height	12.67	4.44	8.73	0.01	0.00	0.41	2.85	5.96	3.43	0.43	0.97	5.28	10.66	44.17	0.00
Flower size (SF)	8.28	13.55	1.62	0.68	5.53	2.46	2.45	10.09	3.27	0.84	1.21	0.00	0.01	0.00	50.00
Flower size (FU)	8.28	13.55	1.62	0.68	5.53	2.47	2.45	10.10	3.27	0.84	1.21	0.00	0.01	0.00	50.00
Leaf area	6.51	0.93	6.71	2.04	17.58	0.30	44.71	0.00	3.52	9.35	0.56	6.46	0.26	1.06	0.00
SLA	5.22	0.84	8.59	21.19	1.01	0.46	0.00	25.00	11.21	11.95	5.03	4.58	4.79	0.13	0.00
LDMC	2.56	4.93	22.32	12.15	1.96	0.73	2.95	1.96	3.40	29.64	0.12	13.63	3.61	0.05	0.00
Nectar volume	9.30	6.42	0.07	0.00	5.00	39.00	0.18	0.25	2.29	0.06	1.64	1.00	24.55	10.26	0.00
Nectar sucrose conc.	1.10	15.86	0.27	8.64	6.53	10.06	12.81	20.22	0.41	5.43	0.05	6.46	8.92	3.23	0.00
Nectar sucrose mass	11.13	5.29	0.02	0.90	5.11	14.82	1.03	14.18	5.23	2.01	0.45	0.18	34.25	5.41	0.00
Pollen size	10.72	0.03	1.36	20.27	0.17	3.79	0.20	0.23	0.16	16.95	19.04	23.45	0.26	3.37	0.00
Pollen shape	1.99	7.59	11.44	0.16	16.88	24.56	3.13	0.43	23.92	1.75	2.71	5.19	0.00	0.23	0.00
Pollen fluorescence	11.78	2.85	0.94	12.57	1.07	0.01	0.02	0.06	0.22	19.39	17.27	33.57	0.24	0.00	0.00
Pollen structure	0.41	3.62	21.50	20.01	6.22	0.45	0.84	0.37	15.31	0.28	29.57	0.06	0.53	0.81	0.00



	LeafUnf	FlOn	FlPeak	FlEnd	FlDur	FrOn	FrEnd	FrDur	SenOn	SenPeak	SenEnd
InitGr	*** 0.4	-0.01	0.07	-0.12	-0.13	0.1	-0.1	-0.18	-0.06	-0.16	* -0.2
LeafUnf		0.14	* 0.17	0.1	0	*** 0.39	0.06	** -0.25	0.05	0.01	0.08
FlOn			*** 0.9	*** 0.52	* -0.18	*** 0.56	*** 0.59	0.15	*** 0.42	*** 0.27	0.13
FlPeak				*** 0.63	0	*** 0.52	*** 0.63	* 0.18	*** 0.48	*** 0.3	* 0.18
FlEnd					*** 0.75	* 0.19	*** 0.56	*** 0.41	*** 0.37	*** 0.27	*** 0.37
FlDur						* -0.18	** 0.22	*** 0.36	0.11	0.11	*** 0.32
FrOn							*** 0.38	*** -0.42	*** 0.43	0.13	0.03
FrEnd								*** 0.68	*** 0.49	*** 0.44	*** 0.31
FrDur									0.15	*** 0.33	** 0.28
SenOn										*** 0.68	*** 0.53
SenPeak											*** 0.73

Figure S II.3: Correlation matrix of phenological stages (Pearson correlations), with correlation coefficients *r* and significance levels (p<0.05 *, p<0.01 **, p<0.001 ***) for all pairwise combinations of phenological stages. Positive correlations are highlighted in blue, negative correlations are highlighted in red and the color gradient indicates correlation strength. Abbreviations: InitGr – Initial growth, LeafUnf – Leaf unfolding, FlOn – Flowering onset (first flowering day), FlPeak –peak of flowering, FlEnd – End of flowering, FlDur – Flowering duration, FrOn – Fruiting onset, FrEnd – Fruiting End of fruiting, FrDur – Fruiting duration, SenOn – Onset of senescence, SenPeak – Peak of senescence.

Phenological stages mostly showed significant positive correlations, e.g. late-flowering species were related to later peak and end of flowering, fruiting and senescence, and shorter flowering durations, while negative and non-significant correlations were also found (see Figure S II.3 for correlation coefficients and significances). The PCA for phenology variables excluding ‘Initial growth’ (n=112) revealed that the first and second principal components accounted for 57.4 % of the total variation in phenology (Figure S II.4a). The first component (35.7%) corresponded to flowering (all stages), end of fruiting and onset of senescence. The second component (21.7%) corresponded to onset and duration of fruiting, flowering duration and leaf unfolding (see Table S II.7 for the contributions (loadings) to all 11 PCs). The PCA for phenology variables including ‘Initial growth’ (n=92, 55.3 % explained variation) was comparable to the PCA excluding ‘Initial growth’ (Figure S II.4b). ‘Initial growth’ additionally corresponded to the second component (see Table S II.8 for the contributions (loadings) to all 12 PCs).

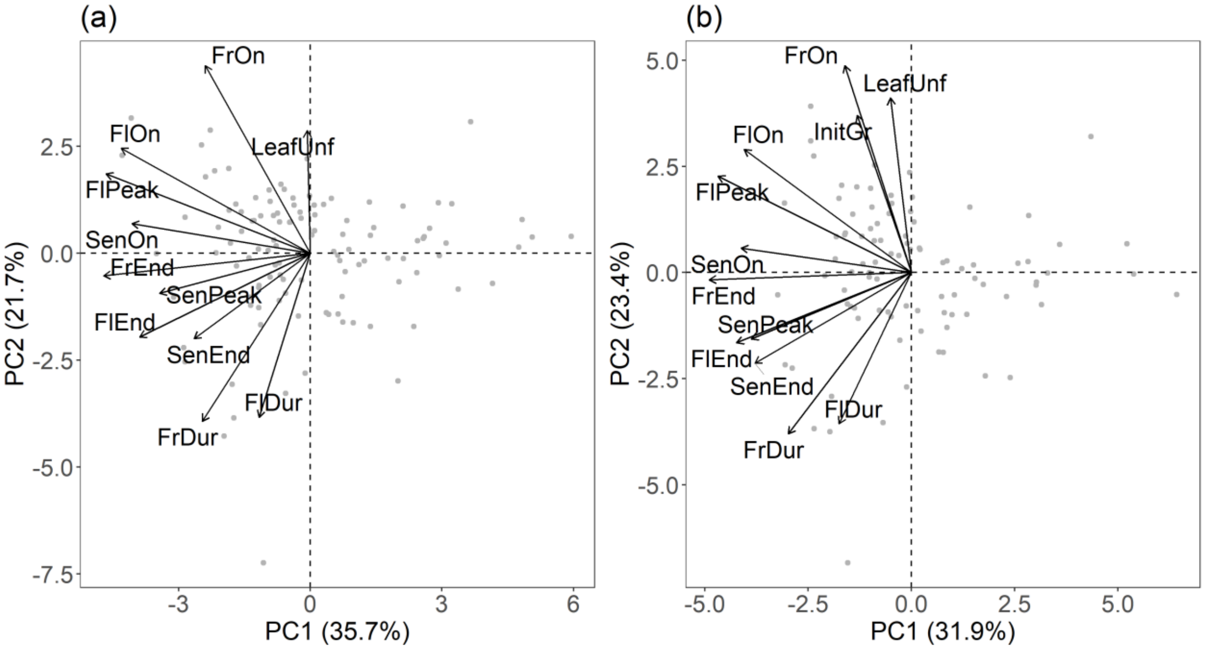


Figure S II.4: Principal component analysis of a) the phenological stages (without InitGr, n=112) and b) the phenological stages including InitGr (n=92). Dots represent species for which information on all stages were available.

Table S II.7: Contributions (loadings) of phenological stages (without Initial growth) to the first (Dim.1) to eleventh (Dim.11) PCA axes.

	Dim.1	Dim.2	Dim.3	Dim.4	Dim.5	Dim.6	Dim.7	Dim.8	Dim.9	Dim.10	Dim.11
LeafUnf	0.00	10.75	3.51	13.78	60.45	1.07	8.91	1.04	0.48	0.00	0.00
FlOn	14.75	7.87	1.21	7.71	1.69	16.00	0.13	0.05	32.03	0.00	18.56
FlPeak	17.18	4.51	3.89	1.73	1.59	10.72	2.34	1.00	57.05	0.00	0.00
FlEnd	12.00	5.00	19.13	5.50	3.66	1.02	0.99	0.79	8.10	0.00	43.81
FlDur	1.08	19.22	15.57	20.08	1.33	2.96	0.68	0.64	0.82	0.00	37.63
FrOn	4.56	25.14	0.54	5.50	0.91	14.34	17.91	5.96	0.08	25.06	0.00
FrEnd	17.59	0.36	0.90	6.95	10.62	16.04	12.46	0.57	0.07	34.43	0.00
FrDur	4.81	20.16	0.09	18.33	14.04	0.54	0.01	1.51	0.00	40.51	0.00
SenOn	13.10	0.62	12.25	2.43	3.90	17.08	12.75	36.68	1.18	0.00	0.00
SenPeak	9.37	1.15	27.13	1.07	0.46	0.00	13.88	46.77	0.17	0.00	0.00
SenEnd	5.57	5.21	15.78	16.92	1.34	20.23	29.94	4.99	0.02	0.00	0.00

Table S II.8: Contributions (loadings) of phenological stages (including Initial growth) to the first (Dim.1) to twelfth (Dim.12) PCA axes.

	Dim.1	Dim.2	Dim.3	Dim.4	Dim.5	Dim.6	Dim.7	Dim.8	Dim.9	Dim.10	Dim.11	Dim.12
InitGr	1.20	13.04	0.17	19.56	16.05	0.95	35.19	13.48	0.03	0.33	0.00	0.00
LeafUnf	0.18	16.09	1.03	17.08	12.53	1.53	29.84	21.04	0.66	0.01	0.00	0.00
FlOn	11.44	8.00	1.66	15.58	1.01	11.87	0.00	0.01	1.87	31.85	0.00	16.72
FlPeak	15.31	4.91	4.89	4.74	1.48	11.06	0.80	0.58	2.68	53.57	0.00	0.00
FlEnd	12.53	2.60	14.96	6.13	10.79	1.42	0.01	0.06	0.00	8.73	0.00	42.77
FlDur	2.14	12.07	9.89	25.79	7.46	0.98	0.01	0.09	0.70	0.35	0.00	40.51
FrOn	1.82	22.58	0.45	0.28	12.25	23.03	4.84	9.39	0.73	0.04	24.60	0.00
FrEnd	16.75	0.03	3.22	3.10	8.72	30.05	2.81	3.42	0.00	0.03	31.86	0.00
FrDur	6.21	13.72	4.18	3.64	26.49	1.19	0.04	0.57	0.40	0.00	43.54	0.00
SenOn	11.89	0.32	17.11	0.22	1.91	9.38	17.35	38.48	3.30	0.04	0.00	0.00
SenPeak	10.49	2.33	23.86	1.10	1.18	3.36	2.36	0.56	52.54	2.22	0.00	0.00
SenEnd	10.04	4.33	18.58	2.79	0.11	5.18	6.73	12.31	37.09	2.85	0.00	0.00

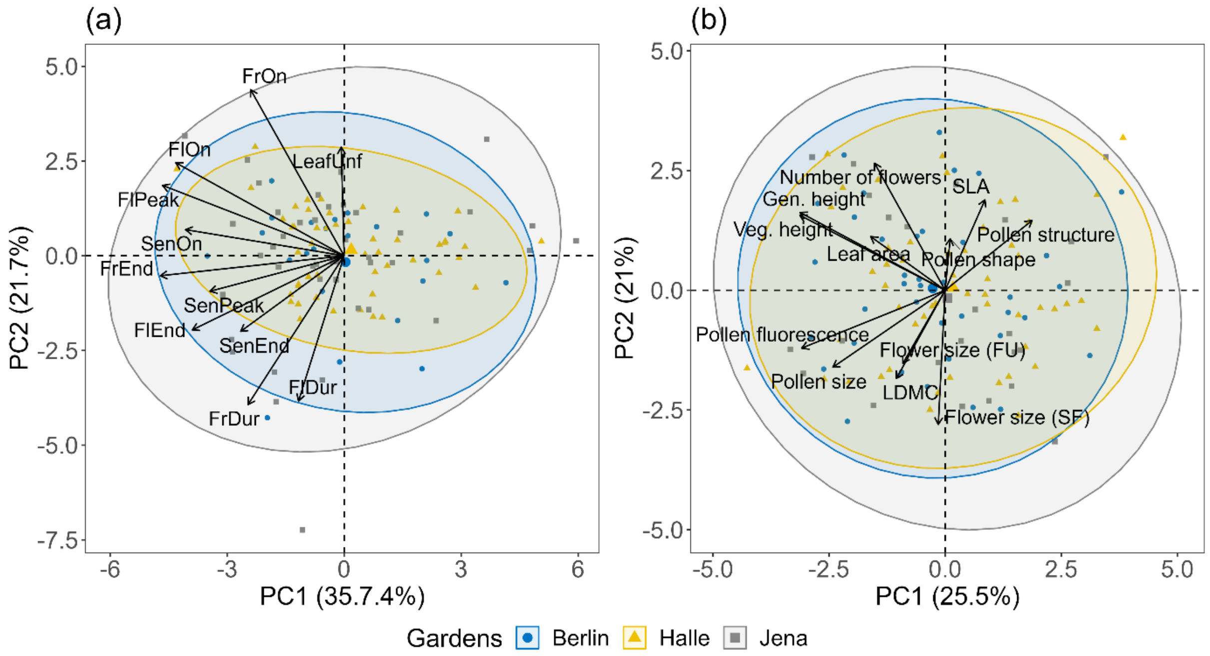


Figure S II.5: Principal component analysis for a) phenological stages (without InitGr) and b) functional traits (without nectar traits) separated across the three gardens (Berlin, Halle, Jena), showing no separation of phenological patterns or functional traits between gardens.

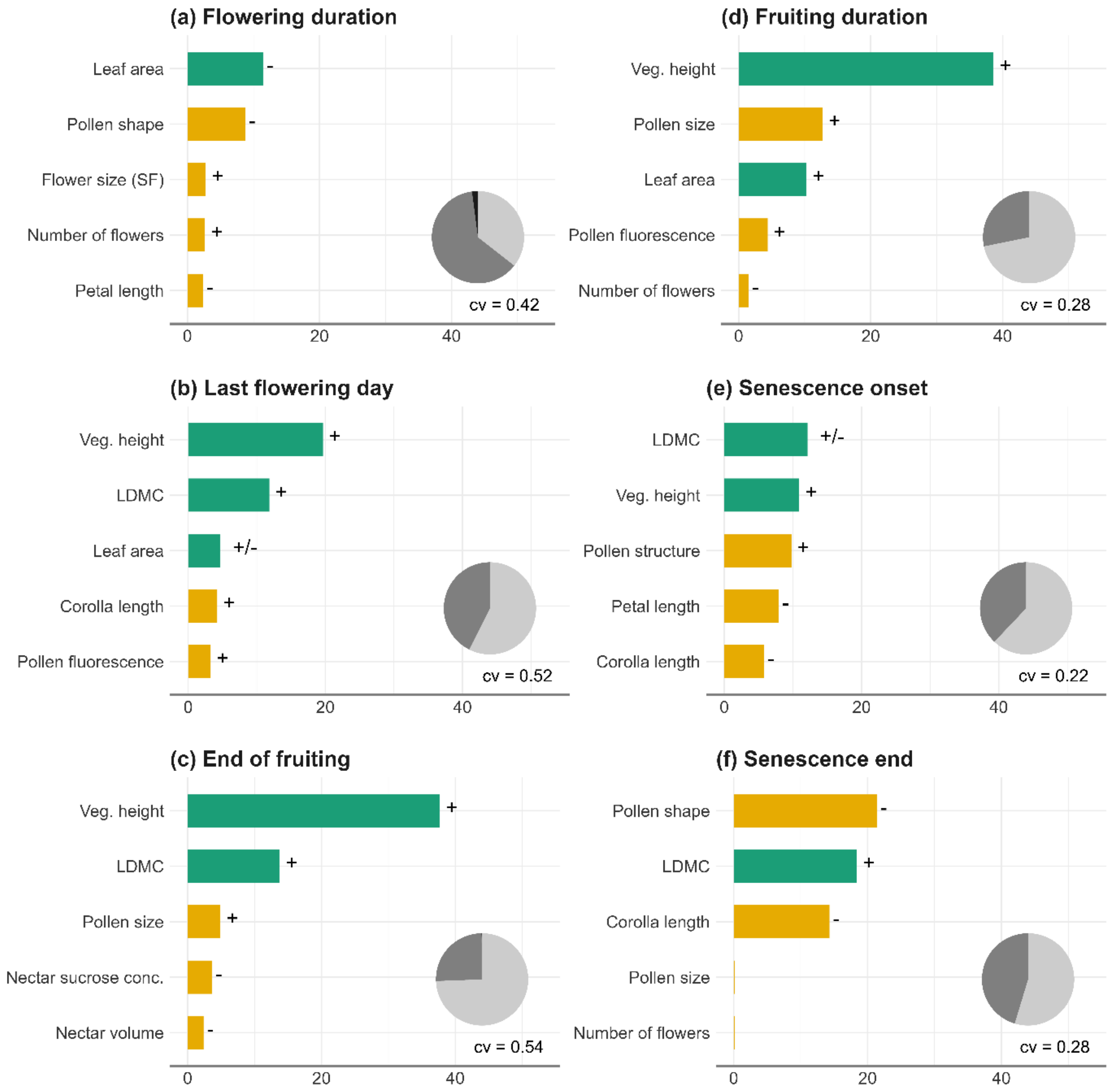


Figure S II.6: Relative importance (%) of floral (yellow) and vegetative (green) functional traits on phenological stages, deduced from boosted regression trees (BRTs) including phylogeny. The direction of the influence of the predictor variable on the phenological stage is represented by ‘+’ positive and ‘-’ negative influence. Pie charts represent the overall contributions of the variables grouped by ‘functional traits’ (lightgrey), ‘phylogeny’ (darkgrey) and ‘garden’ (black). Cross validation correlation (cv) is given for each phenological stage.

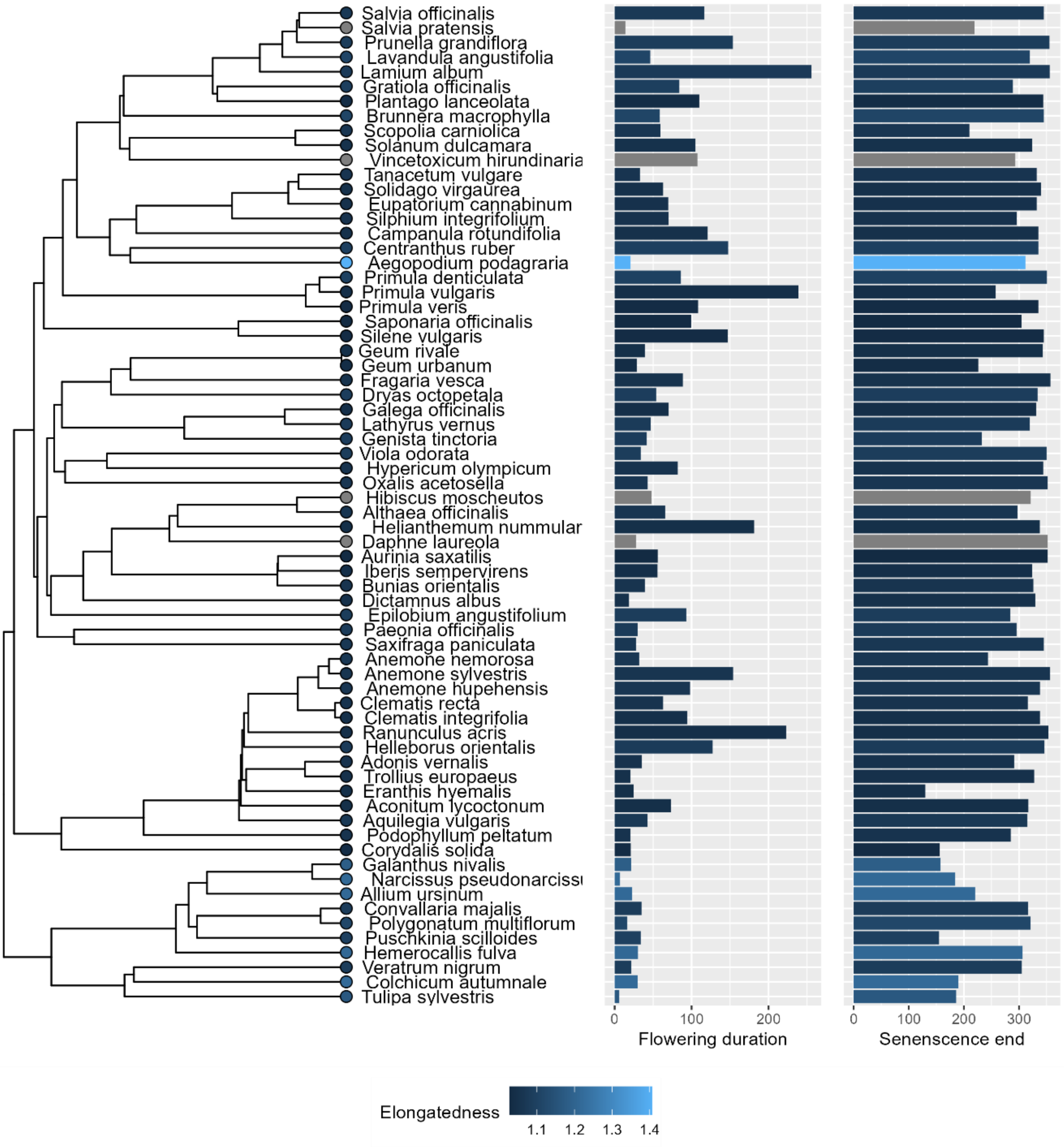


Figure S II.7: Phylogenetic pattern of pollen shape (measured as elongatedness, i.e. ratio between length and width of the pollen grain) together with the flowering duration and senescence end across the phylogenetic gradient. Especially monocotyledonous species at the bottom of the phylogenetic tree were associated with elongated pollen (bright blue) and were at the same time short flowering and early senescing species.

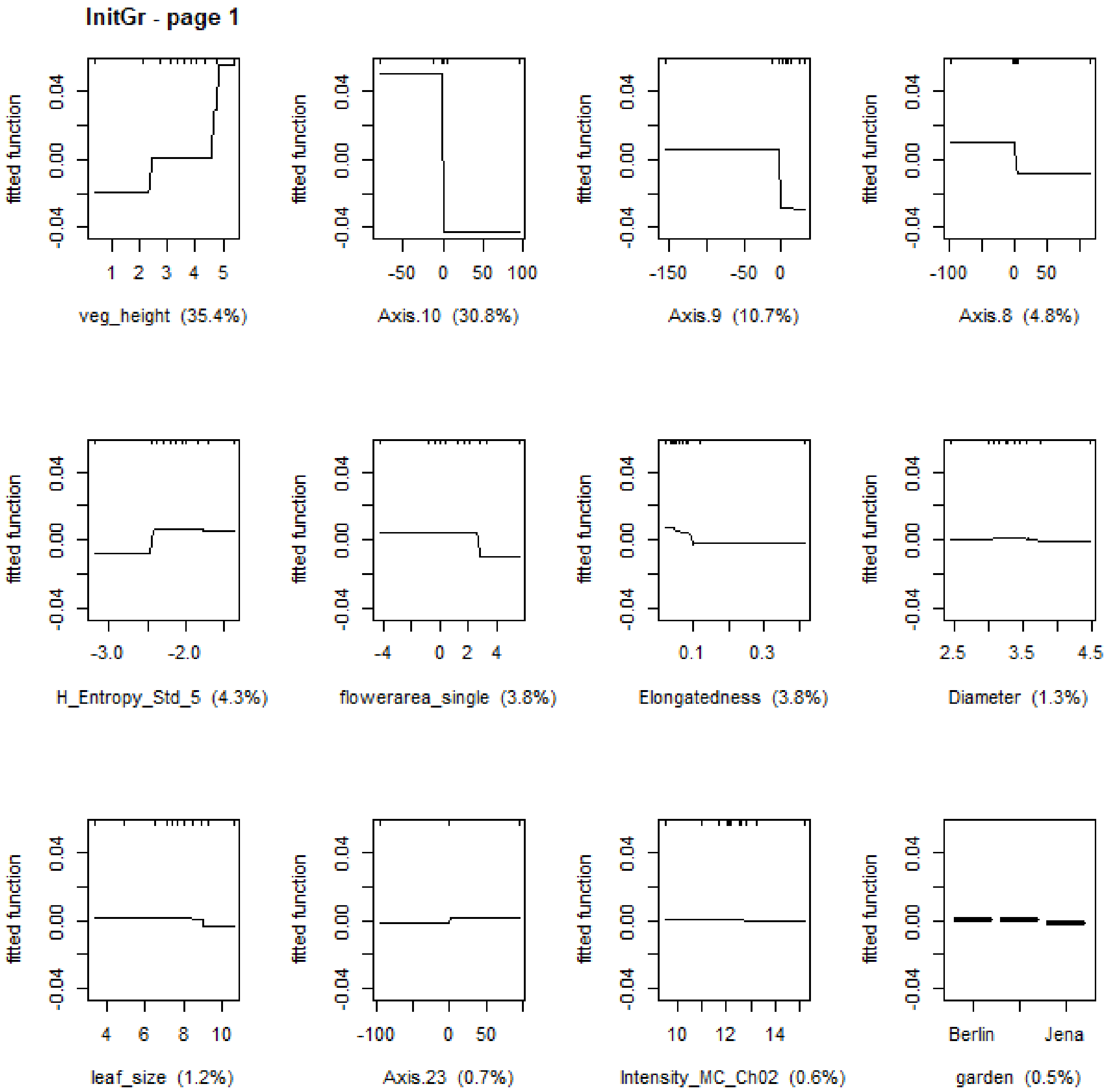


Figure S II.8: Partial dependency plots of boosted regression trees (BRTs) of relationship between ‘**Initial growth**’ (doy) with traits and phylogeny; cross-validation correlation (cv) = 0.15. Relative importance (%) for the variables included in the BRT model. Axis.Nr. refers to phylogenetic Eigenvectors. All trait variables were ln-transformed prior to analyses. Only the first 12 variables from BRT model output are depicted.

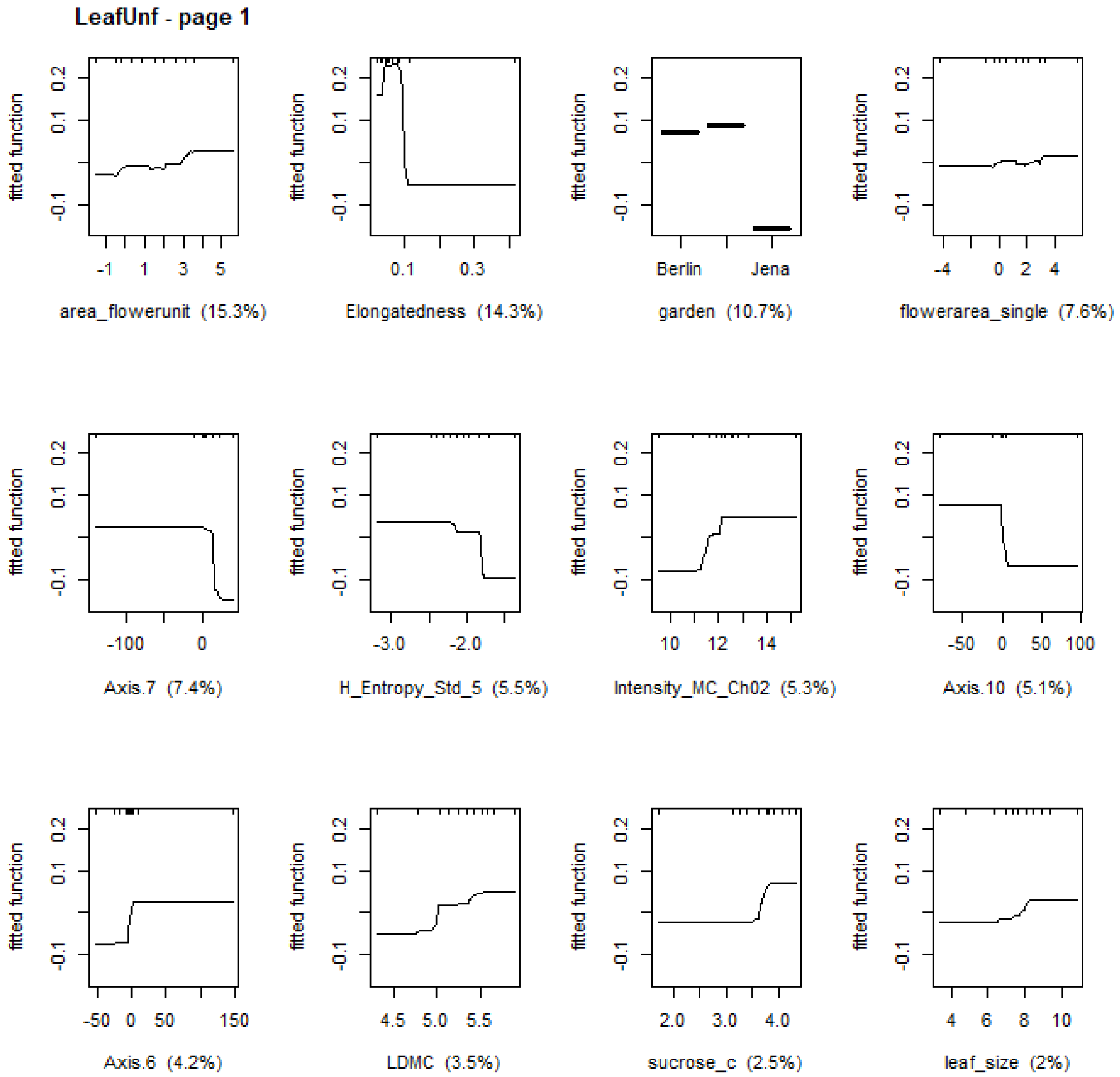


Figure S II.9: Partial dependency plots of boosted regression trees (BRTs) of relationship between '**Leaf unfolding**' (doy) with traits and phylogeny; cross-validation correlation (cv) = 0.27. Relative importance (%) for the variables included in the BRT model. Axis.Nr refers to phylogenetic Eigenvectors. All trait variables were ln-transformed prior to analyses. Only the first 12 variables from BRT model output are depicted.

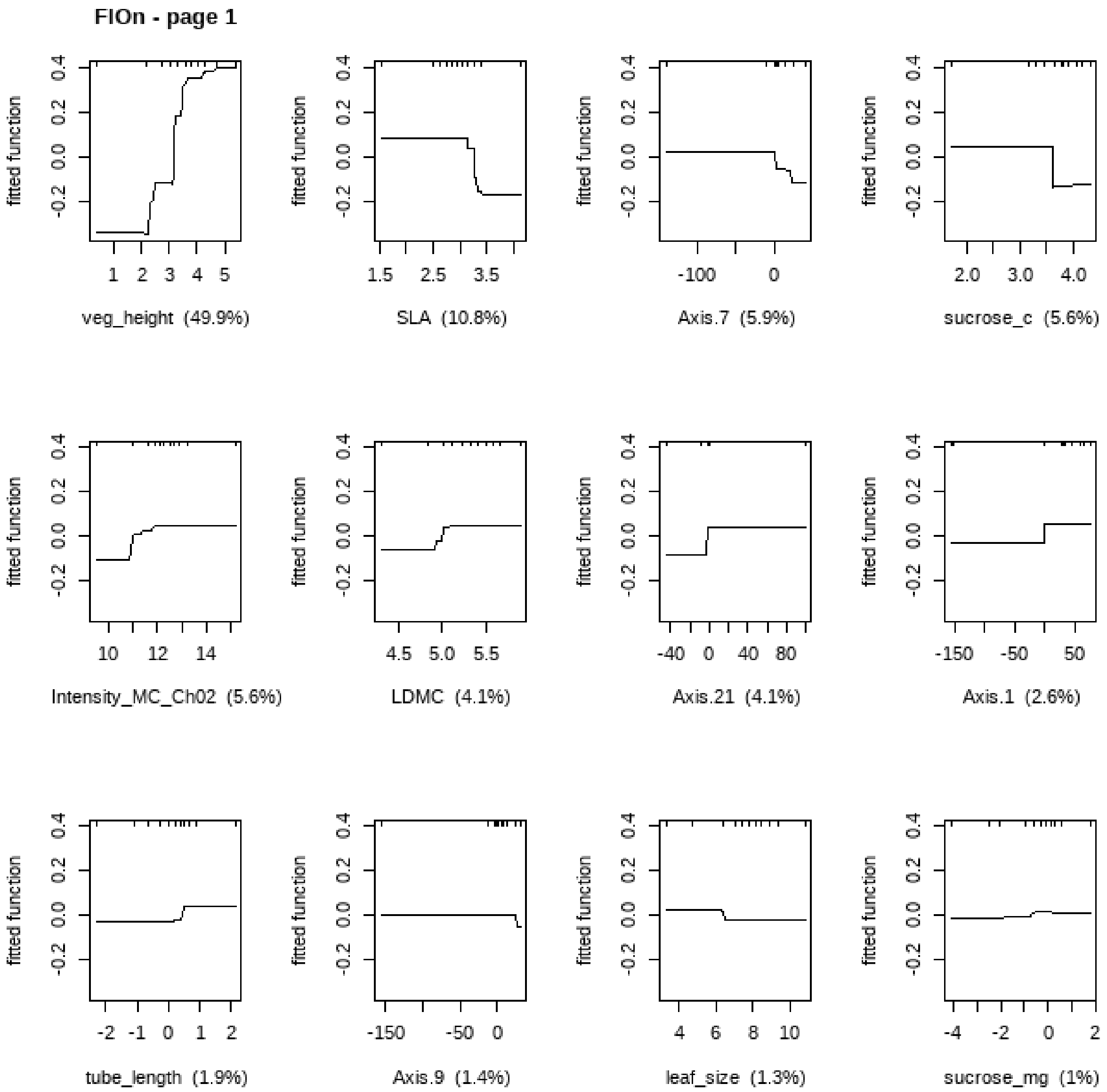


Figure S II.10: Partial dependency plots of boosted regression trees (BRTs) of relationship between ‘**First flowering day**’ (doy) with traits and phylogeny; cross-validation correlation (cv) = 0.56. Relative importance (%) for the variables included in the BRT model. ‘Axis.Nr’ refers to phylogenetic Eigenvectors. All trait variables were ln-transformed prior to analyses. Only the first 12 variables from BRT model output are depicted.

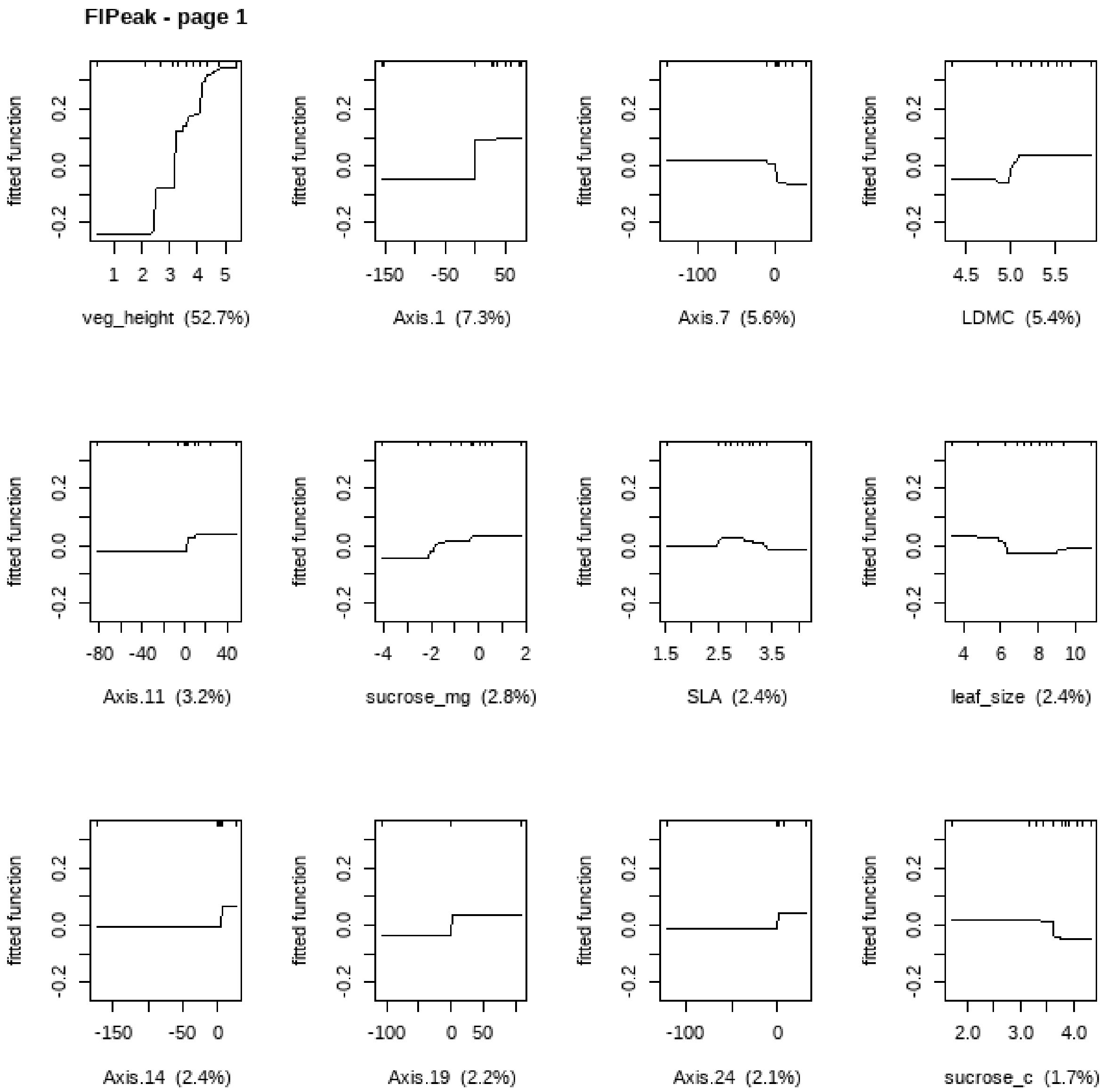


Figure S II.11: Partial dependency plots of boosted regression trees (BRTs) of relationship between '**Peak flowering**' (doy) with traits and phylogeny; cross-validation correlation (cv) = 0.74. Relative importance (%) for the variables included in the BRT model. Axis.Nr refers to phylogenetic Eigenvectors. All trait variables were ln-transformed prior to analyses. Only the first 12 variables from BRT model output are depicted.

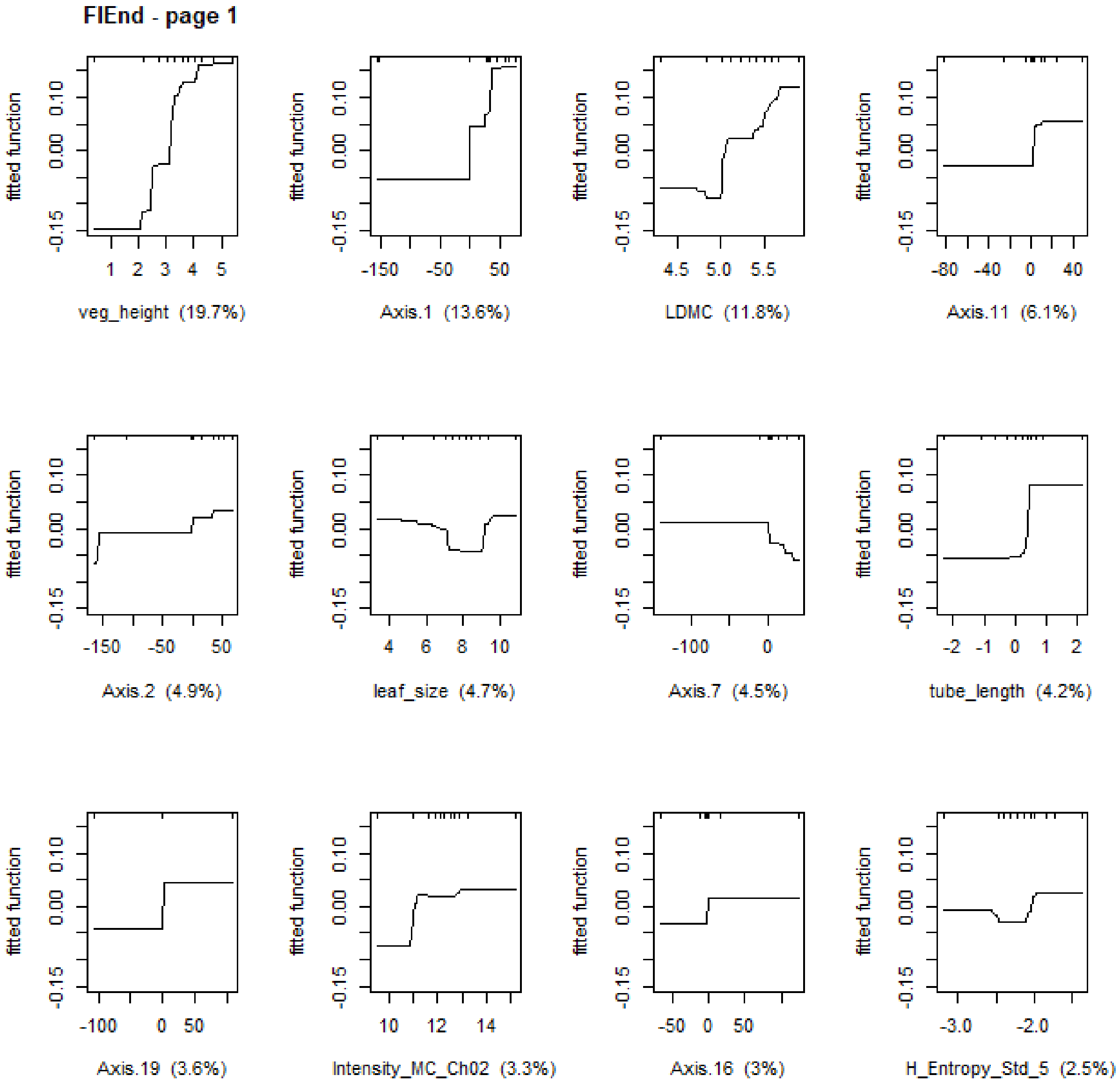


Figure S II.12: Partial dependency plots of boosted regression trees (BRTs) of relationship between ‘**Last flowering day**’ (doy) with traits and phylogeny; cross-validation correlation (cv) = 0.52. Relative importance (%) for the variables included in the BRT model. Axis.Nr refers to phylogenetic Eigenvectors. All trait variables were ln-transformed prior to analyses. Only the first 12 variables from BRT model output are depicted.

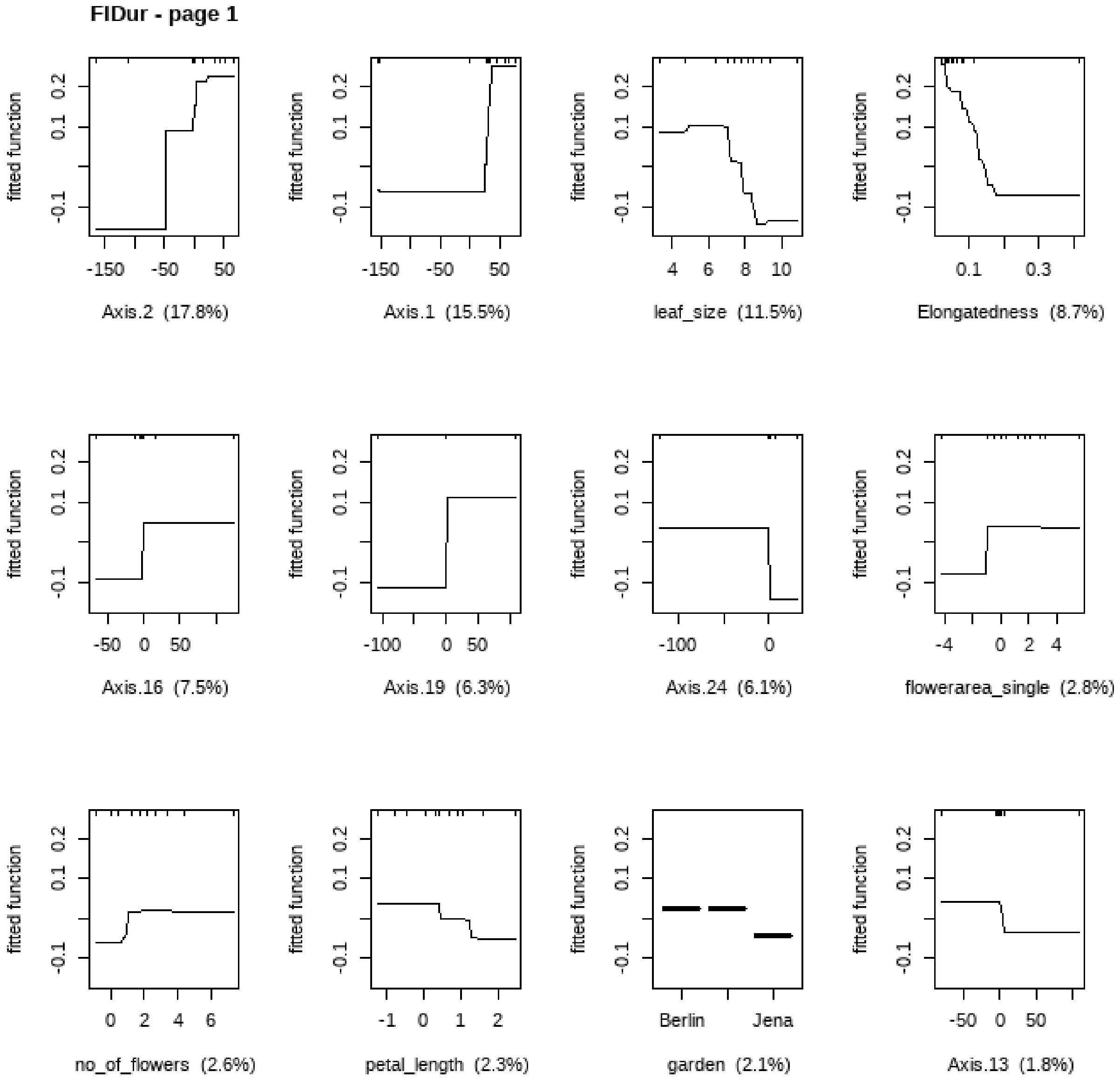


Figure S II.13: Partial dependency plots of boosted regression trees (BRTs) of relationship between '**Flowering duration**' (days) with traits and phylogeny; cross-validation correlation (cv) = 0.42. Relative importance (%) for the variables included in the BRT model. Axis.Nr refers to phylogenetic Eigenvectors. All trait variables were ln-transformed prior to analyses. Only the first 12 variables from BRT model output are depicted.

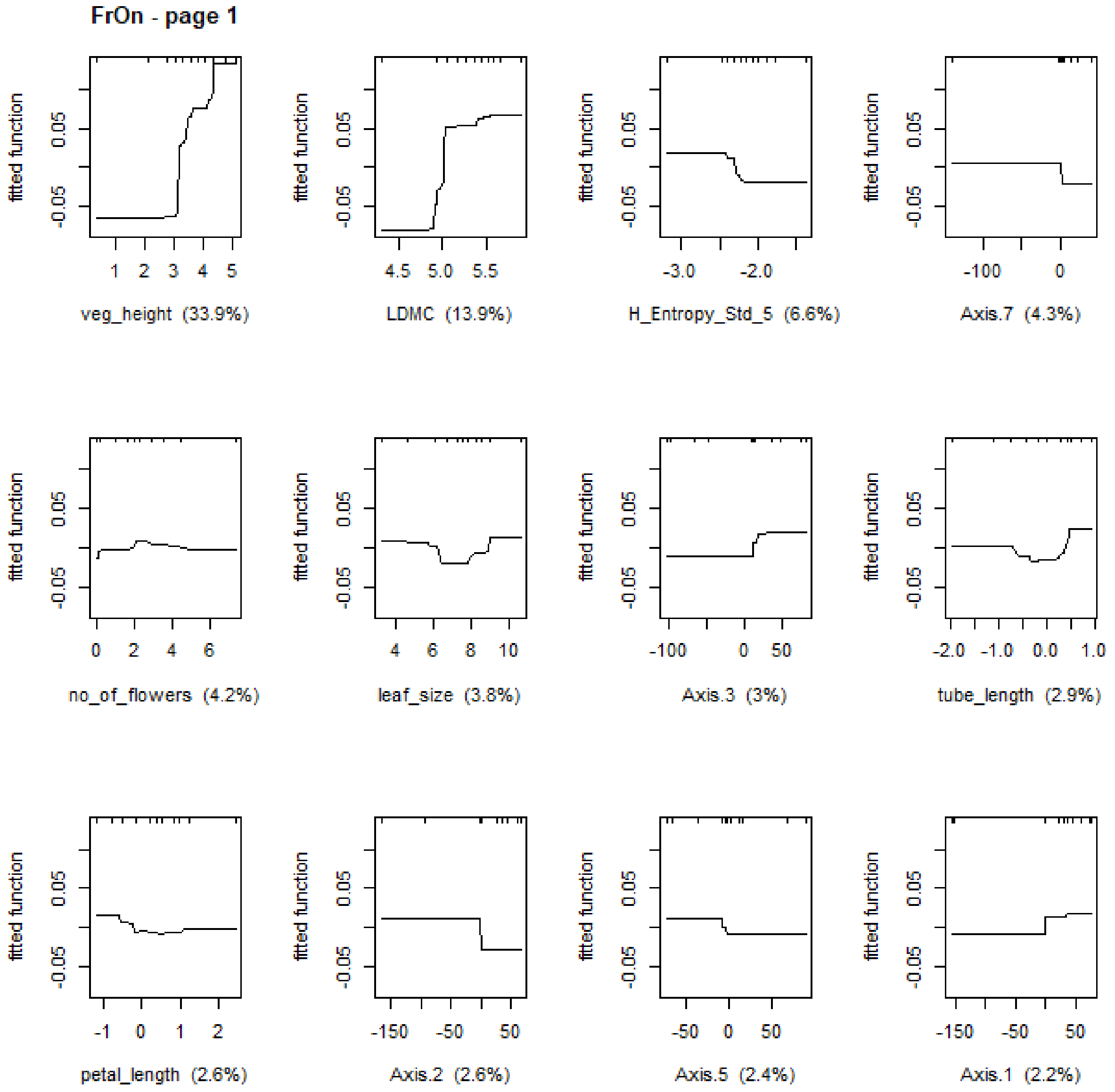


Figure S II.14: Partial dependency plots of boosted regression trees (BRTs) of relationship between '**Fruiting onset**' (doy) with traits and phylogeny; cross-validation correlation (cv) = 0.63. Relative importance (%) for the variables included in the BRT model. Axis.Nr refers to phylogenetic Eigenvectors. All trait variables were ln-transformed prior to analyses. Only the first 12 variables from BRT model output are depicted.

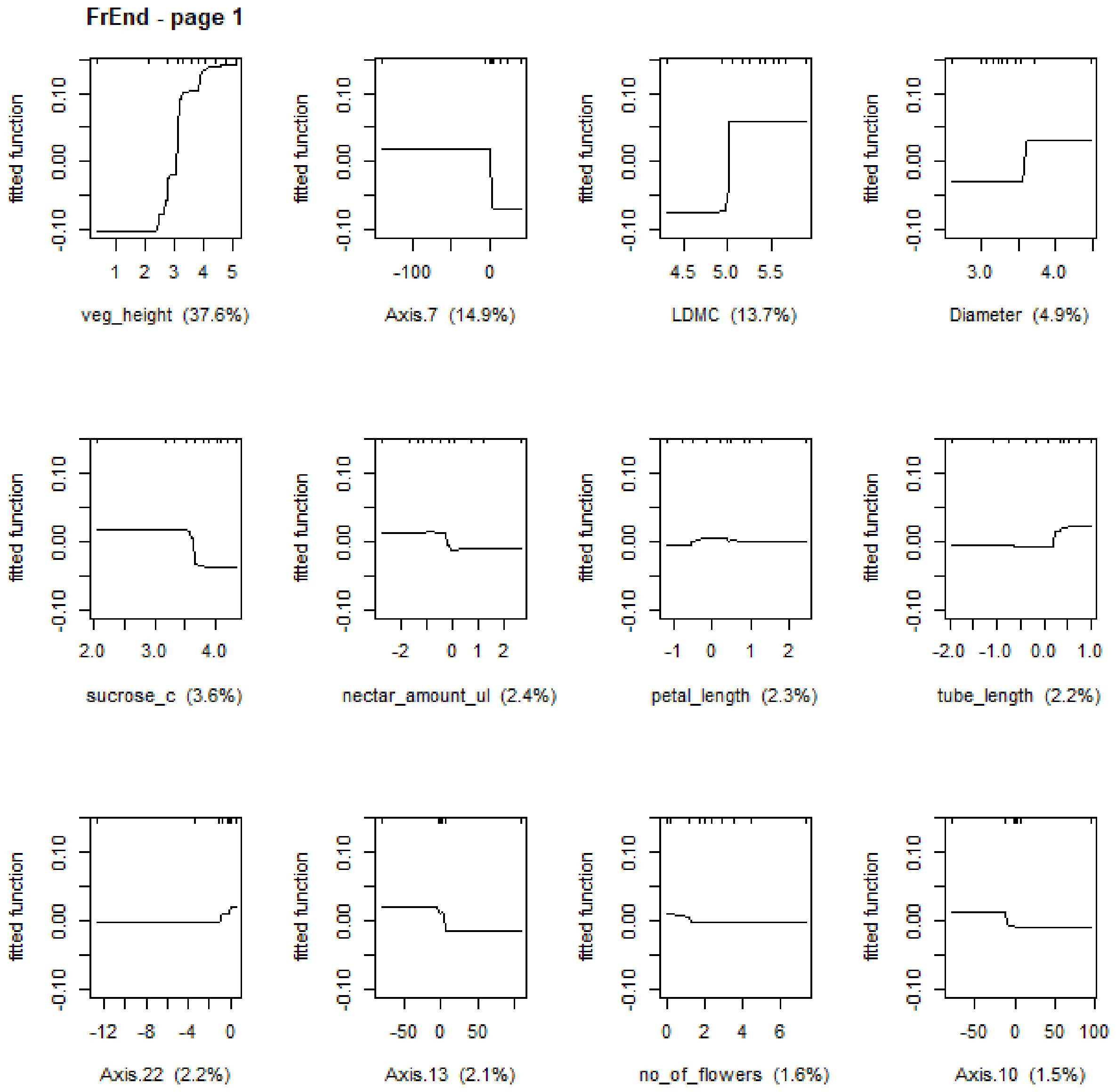


Figure S II.15: Partial dependency plots of boosted regression trees (BRTs) of relationship between '**End of fruiting**' (doy) with traits and phylogeny; cross-validation correlation (cv) = 0.54. Relative importance (%) for the variables included in the BRT model. Axis.Nr refers to phylogenetic Eigenvectors. All trait variables were ln-transformed prior to analyses. Only the first 12 variables from BRT model output are depicted.

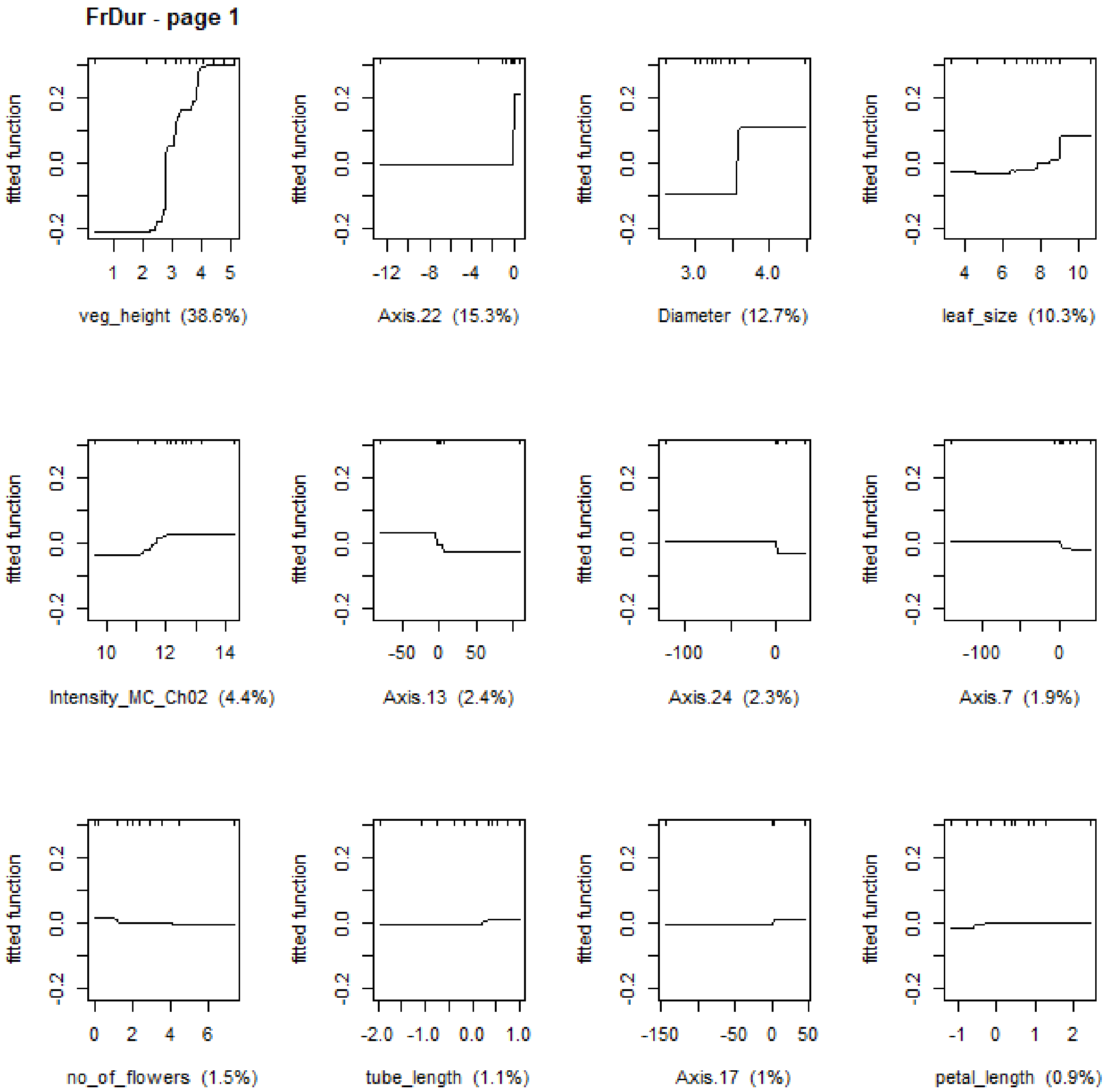


Figure S II.16: Partial dependency plots of boosted regression trees (BRTs) of relationship between ‘**Fruiting duration**’ (days) with traits and phylogeny; cross-validation correlation (cv) = 0.28. Relative importance (%) for the variables included in the BRT model. Axis.Nr refers to phylogenetic Eigenvectors. All trait variables were ln-transformed prior to analyses. Only the first 12 variables from BRT model output are depicted.

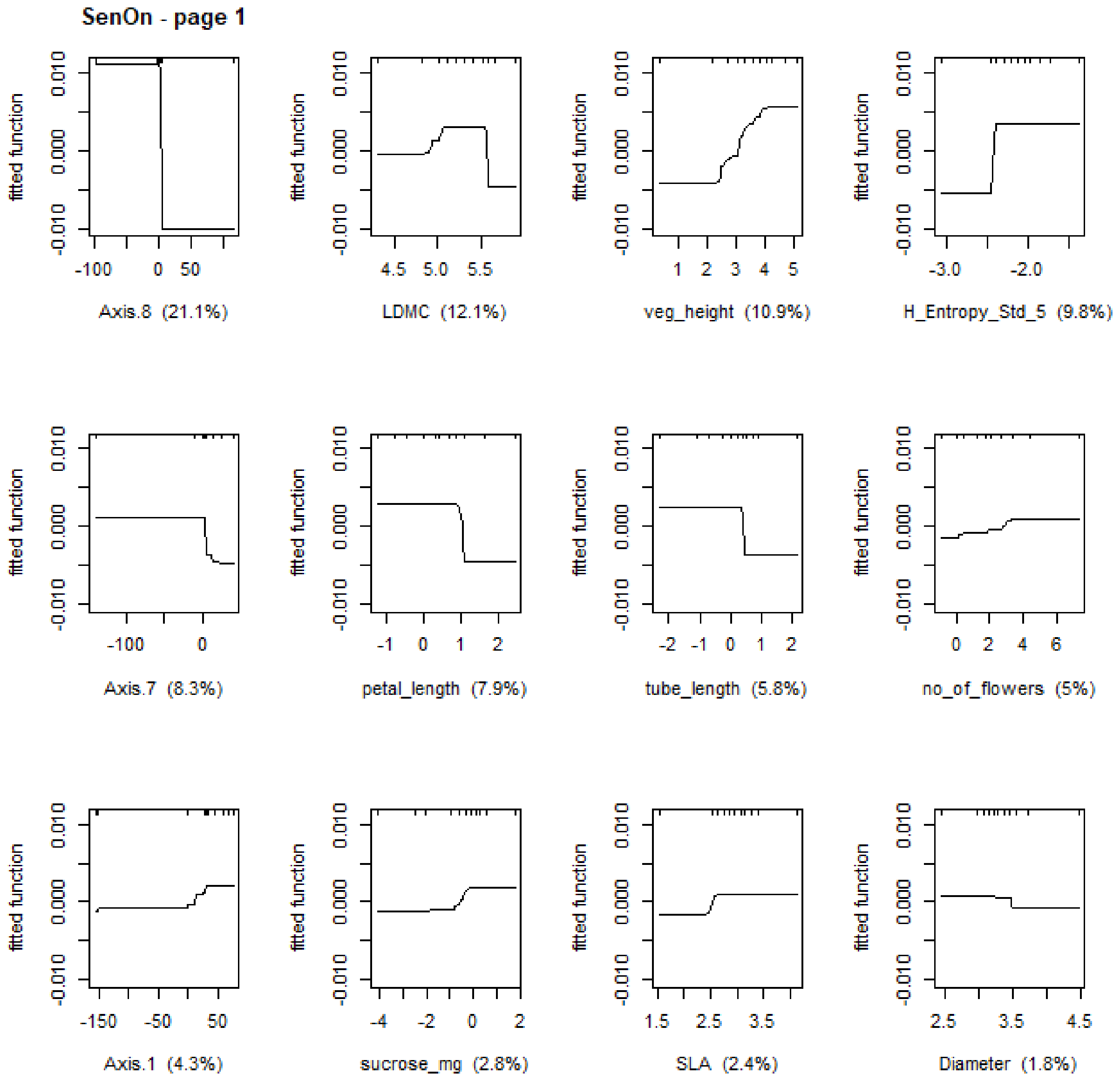


Figure S II.17: Partial dependency plots of boosted regression trees (BRTs) of relationship between '**Senescence onset**' (doy) with traits and phylogeny; cross-validation correlation (cv) = 0.22. Relative importance (%) for the variables included in the BRT model. Axis.Nr refers to phylogenetic Eigenvectors. All trait variables were ln-transformed prior to analyses. Only the first 12 variables from BRT model output are depicted.

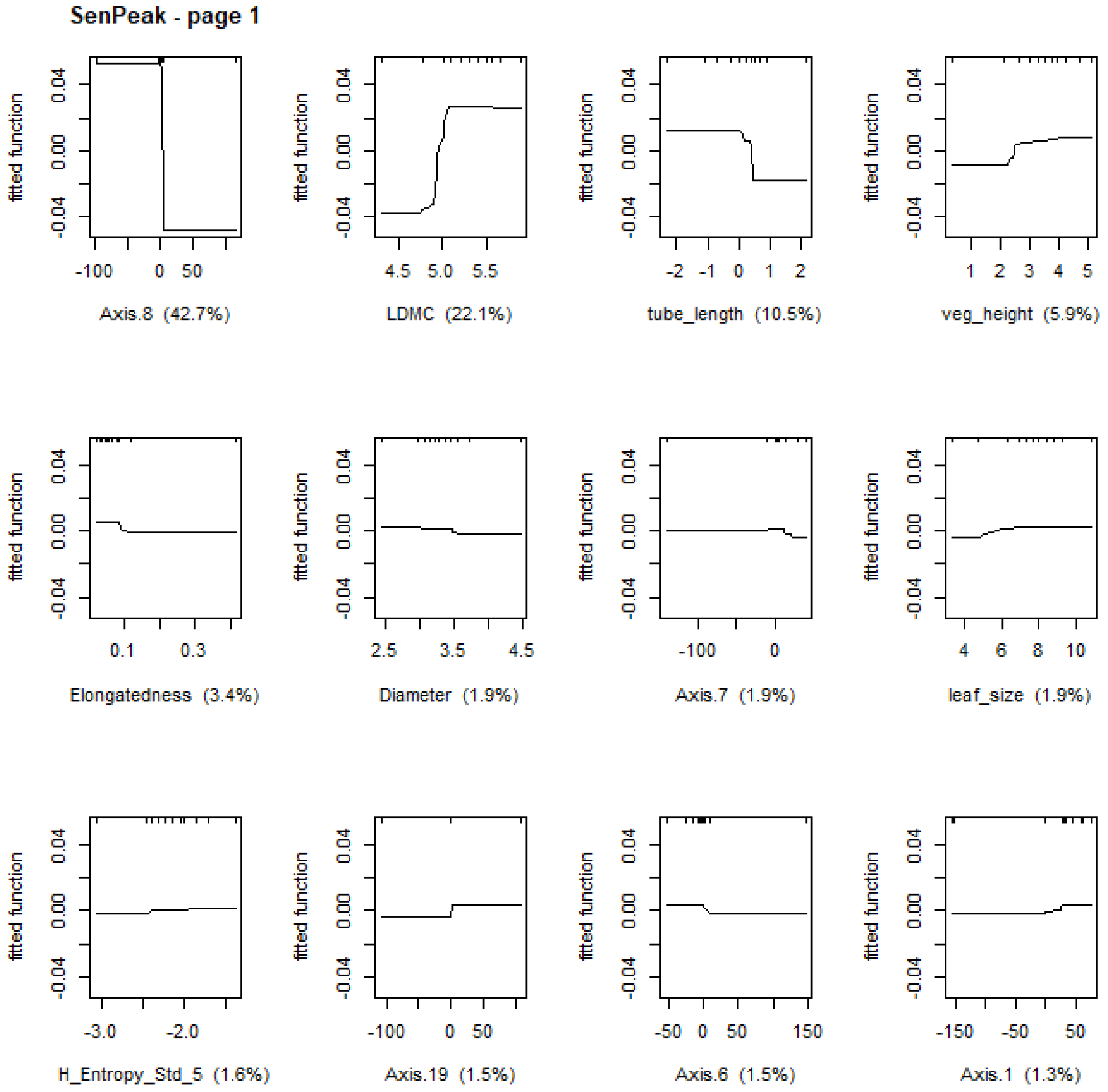


Figure S II.18: Partial dependency plots of boosted regression trees (BRTs) of relationship between ‘**Peak Senescence**’ (doy) with traits and phylogeny; cross-validation correlation (cv) = 0.25. Relative importance (%) for the variables included in the BRT model. Axis.Nr refers to phylogenetic Eigenvectors. All trait variables were ln-transformed prior to analyses. Only the first 12 variables from BRT model output are depicted.

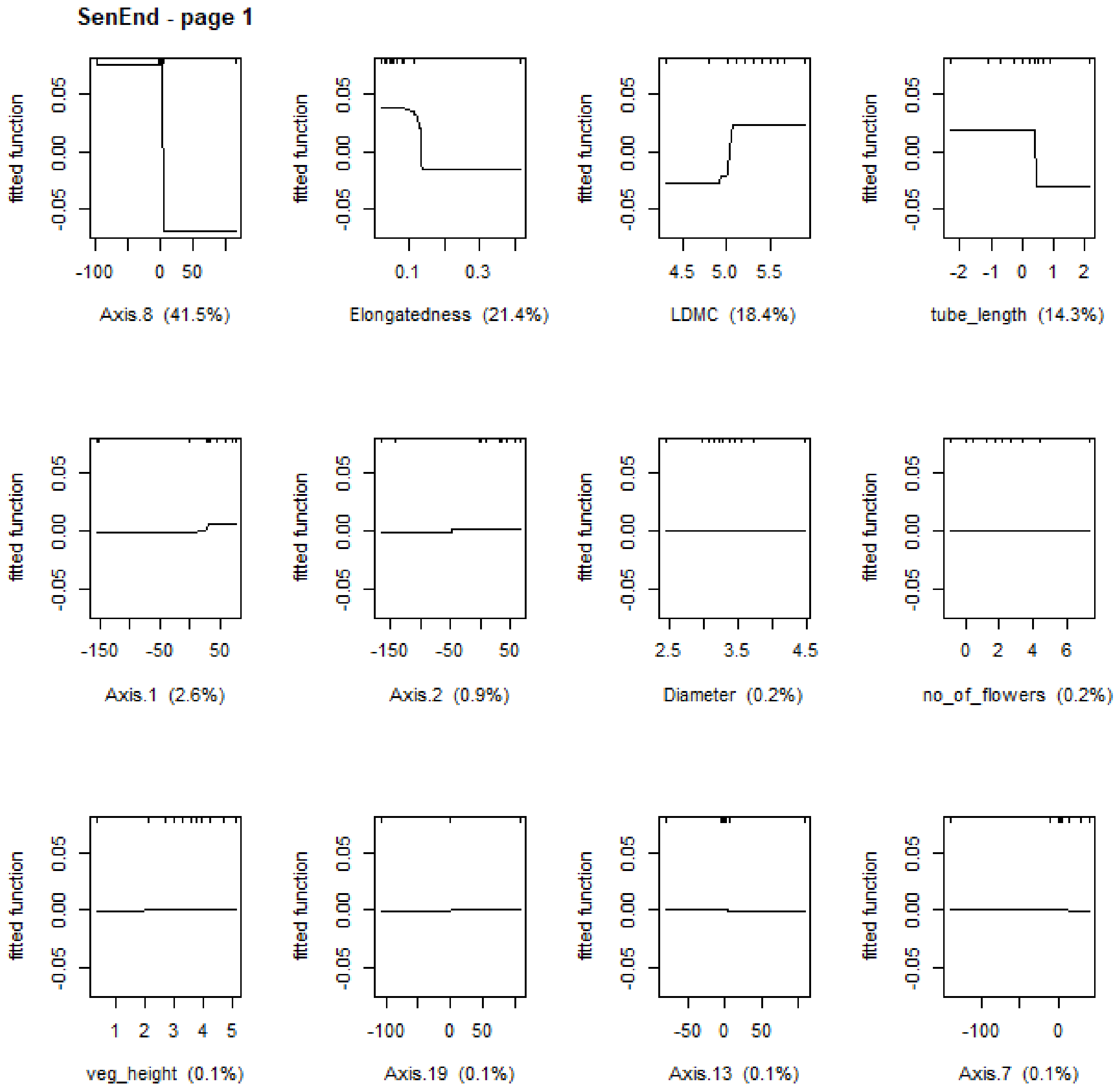


Figure S II.19: Partial dependency plots of boosted regression trees (BRTs) of relationship between '**Senescence end**' (doy) with traits and phylogeny; cross-validation correlation (cv) = 0.28. Relative importance (%) for the variables included in the BRT model. Axis.Nr refers to phylogenetic Eigenvectors. All trait variables were ln-transformed prior to analyses. Only the first 12 variables from BRT model output are depicted.

References Supplementary Material (SII)

Karger, D.N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R.W., Zimmermann, N.E., Linder, H.P., Kessler, M., 2018. Data from: Climatologies at high resolution for the earth's land surface areas. https://doi.org/10.5061/DRYAD.KD1D4 [accessed 9 December 2021].

Karger, D.N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R.W., Zimmermann, N.E., Linder, H.P., Kessler, M., 2017. Climatologies at high resolution for the earth's land surface areas. Sci Data 4, 170122. https://doi.org/10.1038/sdata.2017.122

Pagel, M., 1999. Inferring the historical patterns of biological evolution. Nature 401, 877–884. https://doi.org/10.1038/44766

Chapter III

Plant species phenology differs between climate and land-use scenarios and relates to functional traits

This chapter is published in *Ecology and Evolution* as

Plos, C., Hensen, I., Korell, L., Auge, H., Römermann, C., 2024. Plant species phenology differs between climate and land-use scenarios and relates to plant functional traits. Ecology and Evolution 14, e11441. https://doi.org/10.1002/ece3.11441

Abstract

Phenological shifts due to changing climate are often highly species and context specific. Land-use practices such as mowing or grazing directly affect the phenology of grassland species, but it is unclear if plants are similarly affected by climate change in differently managed grassland systems such as meadows and pastures. Functional traits have high potential to explain phenological shifts and might help to understand species-specific and land-use specific phenological responses to changes in climate. In the large-scale field experiment *Global Change Experimental Facility* (GCEF), we monitored first flowering day, last flowering day, flowering duration and day of peak flowering, of 17 herbaceous grassland species under ambient and future climate conditions, comparing meadows and pastures. Both climate and land use impacted the flowering phenology of plant species in species-specific ways. We did not find evidence for interacting effects of climate and land-use type on plant phenology. However, the data indicate that microclimatic and microsite conditions on meadows and pastures were differently affected by future climate, making differential effects on meadows and pastures likely. Functional traits, including the phenological niche and grassland utilization indicator values, explained species-specific phenological climate responses. Late flowering species and species with a low mowing tolerance advanced their flowering more strongly under future climate. Long flowering species and species following an acquisitive strategy (high specific leaf area, high mowing tolerance and high forage value) advanced their flowering end more strongly and thus more strongly shortened their flowering under future climate. We associated these trait-response relationships primarily with a phenological drought escape during summer. Our results provide novel insights on how climate and land use impact the flowering phenology of grassland species and we highlight the role of functional traits in mediating phenological responses to climate.

Keywords: Climate change; flowering phenology; Global Change Experimental Facility (GCEF); grazing; mowing; species-specific responses

Abbreviations: FFD – first flowering day; FD – flowering duration; ITV - intraspecific trait variation; LFD – last flowering day; Peakfl – day of peak flowering; SLA - specific leaf area

Introduction

Climate-induced shifts in phenology are reported for a broad set of organisms with increasing temperatures mostly leading to advances of phenological events (Cleland et al., 2007; Parmesan, 2007; Root et al., 2003). Plants tend to show earlier spring phenology, often accompanied by a later autumn phenology, resulting in an extended growing season (Ahas et al., 2002; Badeck et al., 2004; Menzel et al., 2006; Menzel and Fabian, 1999). However, the direction and magnitude of phenological shifts is frequently reported to be species-specific (Bock et al., 2014; Bucher et al., 2018; Jentsch et al., 2009; Piao et al., 2019; Root et al., 2003) and context-specific. For example, phenological responses to changes in climate may depend on community composition (Jentsch et al., 2009), habitat type (König et al., 2018), observation site (Bucher et al., 2018) or growth form (Horbach et al., 2023; König et al., 2018). In addition to changes in temperature, changes in precipitation are identified as major drivers of phenological shifts (Jentsch et al., 2009; König et al., 2018; Lesica and Kittelson, 2010). Specifically, drought and heavy rain events can cause phenological shifts of the same magnitude as one decade of gradual warming, shown in a global change experiment (Jentsch et al., 2009).

Shifts in the flowering phenology are of special interest as they can impact biotic interactions like pollination or competition (Forrest and Miller-Rushing, 2010; Gérard et al., 2020; Wolkovich and Cleland, 2011). While shifts in first flowering day are well studied (Bucher et al., 2018; Fitter et al., 1995; König et al., 2018), shifts in other phenological characteristics like last flowering day, flowering duration or peak flowering that strongly affect pollination and reproductive success, are less well studied but recently shown to also shift due to changes in climate (Bock et al., 2014; Bucher and Römermann, 2020; CaraDonna et al., 2014; Jentsch et al., 2009). Species-specific changes in flowering phenology can lead to pollination mismatches when plants shift their flowering times while pollinators do not adapt, or vice versa (Forrest, 2015; Gérard et al., 2020; Hegland et al., 2009; Memmott et al., 2007), potentially affecting plant reproduction and pollinator fitness alike.

Grassland systems are among the most species rich habitats in Central Europe (Wilson et al., 2012) and are maintained by a long tradition of anthropogenic land-use. Although mowing and grazing directly affect phenological dynamics of grassland species, studies on the effect of land-use type on flowering phenology are scarce (but see Reisch and Poschlod, 2011, 2009; Tadey, 2020; Völler et al., 2017, 2013). Plant species have been shown to adapt their flowering timing to typical land-use times (Reisch and Poschlod, 2009; Völler et al., 2013), for example plants growing on meadows flowered earlier compared to pastures (Reisch and Poschlod, 2011, 2009; Van Tienderen and van der Toorn, 1991). Mowing and grazing impose different disturbances to the vegetation and can differently affect plant growth performance (Brys et al., 2004; Herz et al., 2017; Römermann et al., 2009) and microclimate (Briemle et al., 2002; Zhu et al., 2016) on meadows and pastures. Selective grazing and small-scale disturbances, due to trampling, affect the vegetation unevenly and create heterogeneous conditions in terms of light availability, open soil, small scale variation in (soil-)temperature and water balance through changes in soil pore volumes (Borer et al., 2014; Briemle et al., 2002; Lezama and Paruelo, 2016). In contrast, non-selective mowing creates homogeneous conditions regarding light availability and mowing tractors can lead to a more uniform soil compaction (Chyba et al., 2014). Thus, microclimatic and microsite conditions can differ between mown and grazed sites (Zhu et al., 2016, shown for grazing exclusion) and changes in macroclimatic conditions (i.e. climate change) may therefore affect plant communities and their phenology differently on meadows and pastures. Furthermore, the management timing and frequency of extensively used grasslands usually differs between mown and grazed sites (Gilhaus et al., 2017), likely affecting plant phenology in different ways.

As described above, both climate warming and land-use type separately influence the flowering phenology of grassland species. To our knowledge there is no study on interactive effects of both drivers on the flowering phenology of individual plant species (but see Tadey (2020) for effects of grazing and climate). Understanding interactive effects of different global change drivers on plant phenology is crucial to be able to predict phenological responses in natural systems, as combinations of different drivers can lead to diverse to responses (Cleland et al., 2006). Interactive effects of land-use type and climate change on grassland species were already shown regarding the population growth rate of *Bromus erectus* in the context of the same experiment as this study (Global Change Experimental Facility, Lemmer et al., 2021) and regarding the relative growth rate in six grassland species across Germany (Bütof et al., 2012). We would expect that climate change will affect plant phenology differently on meadows and pastures due to potentially different microclimatic and microsite conditions.

Phenological responses to climate or other drivers are oftentimes highly species-specific (Bucher et al., 2018; Fitter and Fitter, 2002; Menzel et al., 2006) and plant functional traits have high potential in explaining species-specific phenological patterns and phenological responses (Bucher et al., 2018; Bucher and Römermann, 2020; Fitter and Fitter, 2002; Horbach et al., 2023; König et al., 2018; Sporbert et al., 2022; Sun and Frelich, 2011). For example, specific leaf area, which is related to productivity, competitive ability and growth performance (Pérez-Harguindeguy et al., 2016; Wright et al., 2004) was shown to explain shifts in first flowering day (Bucher et al., 2018; König et al., 2018). Plant height that is linked to competitive ability and productivity (Gaudet and Keddy, 1988; Moles et al., 2009) is among the most important traits explaining variations in the flowering phenology of herbaceous plants in a botanical garden study (Sporbert et al., 2022) and is positively related to flowering start (Bolmgren and D. Cowan, 2008; Liu et al., 2021; Segrestin et al., 2020; Sun and Frelich, 2011). Furthermore, the phenological niche relates to the magnitude of phenological climate responses: Earlier flowering plants are repeatedly shown to advance their flowering time more strongly under changing climate conditions (Fitter and Fitter, 2002; Lesica and Kittelson, 2010;

Menzel et al., 2006; Miller-Rushing and Primack, 2008) though contrasting patterns are found as well (Bucher et al., 2018). Long flowering species change their flowering duration more strongly compared to short flowering species, shown along an elevational gradient (Bucher and Römermann, 2020). Plant traits like plant height, growth and life form or growth rate relate to the plants tolerance to mowing, grazing or trampling and can be summarized with grassland utilization indicator values (Briemle et al., 2002). We propose that plants that are more tolerant towards mowing, grazing or trampling might be less affected by the land management compared to more sensitive plants, which could in turn also affect the responses to future climate conditions. We use this set of commonly available functional traits to understand species-specific phenological responses to future climate and under different land uses.

Here we use an experimental approach to understand the interacting effects of climate and land-use type on plant phenology and its associations to plant traits. We monitor the flowering phenology of characteristic grassland species under ambient and future climate conditions growing in the two different land-use types: extensively managed species-rich meadows and pastures in the Global Change Experimental Facility in Germany (Schädler et al., 2019). In contrast to purely observational studies, this experiment allows us to unequivocally identify causal effects of manipulated climate and land use on plant phenology under the same set of background abiotic and biotic conditions.

More specifically, we ask the following questions:

1. How does the flowering phenology of different grassland species respond to a) future climate and b) different land-use types (i.e. mowing or grazing) and c) what is the interacting effect of climate and land-use on the flowering phenology?

2. Can functional traits explain species-specific and land-use specific responses in phenology to changes in climate?

Materials and Methods

The Global Change Experimental Facility (GCEF)

Data were sampled in 2020 in the “Global Change Experimental Facility” (GCEF), a large-scale field experiment to investigate the consequences of climate and land-use change on ecosystem processes, located in Bad Lauchstädt in central Germany (51°22060 N, 11°50060 E, 118 m a.s.l.). The mean annual temperature of the study site is 9.7 °C , the mean annual precipitation is 525 mm and the soil is a nutrient-rich haplic chernozem (Schädler et al., 2019). The experiment is set up using a split-plot design combining a climate treatment (ambient and future climate, abbreviated amb; fut) at the main-plot level and different land-use types at the sub-plot level. The experiment was established in 2014. For detailed information on the experimental setup see Schädler et al. (2019) and for a schematic overview of the setup see Appendix S2 in Schädler et al. (2019). The future climate treatment was established according to projections of regional climate change models for 2070-2100, which corresponds with a realistic manipulation of future climate (Korell et al., 2020). This applies in particular to the precipitation manipulation: the spring and autumn precipitation is increased by ~10% using sprinkler systems and the summer precipitation is reduced by ~20% (see also Appendix S III.1, Figure S III.1) using movable roof systems. As temperature is passively manipulated by closing these roofs at night, the mean daily increase in temperature by ~0.55°C is less than projected (~2°C), but still leads to an increase in the number of growing degree days (GDD) by ~5.2% (Schädler et al., 2019). Minimum temperatures increased more strongly under the climate treatment (by ~1°C) than mean temperatures did (for more details see Schädler et al., 2019). According to the application of a whole scenario of future climate, effects of altered precipitation patterns and altered temperature cannot be disentangled.

All observations were done on the two land-use types extensively used meadows (abbreviated EM) and extensively used pastures (abbreviated EP). In the study year 2020, mowing was conducted once in the beginning of June (calendar week 24). Grazing occurred twice per year, in late May (calendar week 20 or 21) and late June (calendar week 26 or 27), as a high-intensity, short-time grazing with a group of ~20 sheep that remain on the pasture plots for 24h. Because of the low overall productivity due to the extreme drought conditions during the years before (2018/19) there was a lower overall management intensity. Before 2018, management intensity was higher (usually three times grazing, two times mowing). Treatment plots (i.e. ambient meadows (EM amb), future meadows (EM fut), ambient pastures (EP amb), future pastures (EP fut)) are replicated five times leading to overall 20 experimental plots in this study. Each treatment plot has a size of 16 m x 24 m. In the center of each treatment plot a 3 m x 3 m permanent plot (hereafter referred to as “plot”) was established for the phenological observations. For more detailed information on the experimental setup and manipulation in the GCEF see Schädler et al. (2019).

Phenological monitoring

The flowering phenology (i.e. the presence of flowers (y/n)) and the flowering intensity (0-100%) of each of the co-occurring plant species in the plot were monitored once per week following the PhenObs protocol (Nordt et al., 2021). Per species, all individuals growing inside the plot were observed as a “population”. The phenological observations were conducted between 01 April 2020 and 04 December 2020. From the data, we extracted the day of the year (doy) for the phenological stages first flowering day (FFD), last flowering day (LFD), day of maximum flowering intensity resp. peak flowering (PeakFl) as well as the flowering duration (FD) (i.e. the number of days between FFD and LFD).

Species selection

Plant species that occurred and flowered in at least three out of five plots of each treatment combination (ambient meadow, future meadow, ambient pasture, future pasture) were selected from the monitoring data (see above "*Phenological monitoring*") and used for further analysis. Thus, 17 out of 95 species that occurred at the study site were selected (Table III.1), from which four species were grasses, two legumes and 11 herbs.

Five of the 17 selected species (i.e. *Capsella bursa-pastoris, Senecio vulgaris, Stellaria media, Taraxacum officinalis, Veronica persica*) already started flowering in some of the plots when the phenological monitoring was started and were thus excluded from the analysis of FFD and FD.

Functional trait data

To analyze whether functional traits can explain species-specific and land-use specific responses in phenology to changes in climate, trait data on various traits previously shown to be relevant to phenological patterns was compiled. Specific leaf area (SLA) and vegetative plant height were extracted from the TRY database (Kattge et al., 2020) and the mean value for SLA and plant height were calculated per species (Table III.1). Grassland utilization indicator values (hereafter referred to as "grassland indicator values") for mowing, grazing, trampling tolerance, and forage value are individual, morphological-ecophysiological traits that were developed by experts (Briemle et al., 2002). They range between 1 and 9 and characterize plants according to their realized ecological niche regarding mowing, grazing and trampling tolerance and evaluate the forage value for livestock (Briemle et al., 2002). More precisely, an indicator value of 1 represents species that do not tolerate mowing, grazing or trampling respectively, while a value of 9 represents a very high tolerance to the respective disturbance. They were developed and validated on decade-long experience in grassland habitats taking life and growth form and plant height into account summarizing a suite of relevant traits (Briemle et al., 2002). Grassland indicator values from Briemle et al. (2002) were extracted from the BiolFlor database (Klotz et al., 2002) for all species for which information was available (n= 15, Table III.1). For *Scabiosa ochroleuca* L.*,* values of the closely related species *Scabiosa columbaria* L., that occurs in the same habitat, were used and for *Festuca rupicola* Heuff.*,* values of the closely related species *Festuca ovina* L. s. str. that forms a species aggregate to which *F. rupicola* belongs, were taken.

To classify the phenological niche of the species as a species trait (i.e., early- and late-flowering and short- and long-flowering species), per species the mean first flowering day (FFD) and mean flowering duration (FD) were extracted from the control plots (ambient meadows and ambient pastures) and considered as additional functional traits. As a result, a trait table with a mean value per trait and species was used for further analysis (see Table III.1).

Statistical analysis

All statistical analyses were performed in R Version 4.2.1 (R Core Team, 2022).

Main and interactive effects of climate and land-use on plant phenology

To test for the effect of a) climate (ambient vs. future), b) land-use type (meadow vs. pasture), c) species and d) their interactions on phenology, generalized linear mixed effect models using the function *glmer* (family 'Poisson') from the package *lme4* (Bates et al., 2015, p. 4) were performed. As our phenological data were integer, never negative, had a left-skewed distribution, and can be considered count data (number of days), we chose the family Poisson for the models. Each model was tested for overdispersion using the function *dispersion_glmer* from the package *blmeco* (Korner-Nievergelt et al., 2015). Overdispersion was only detected for the model for flowering duration (FD), for which then the model was refitted using negative binomial distribution (function *glmmTMB*, package *glmmTMB*; Brooks et al., 2017). The day of the year (doy) for the phenological stages first flowering day (FFD), last flowering day (LFD), the day of peak flowering (PeakFl) and the flowering duration (FD, measured in number of days) served as response variables. As the GCEF is set up as a split-plot design, main plot (i.e. experimental unit, n=10, Schädler et al. 2019) nested in climate treatment (ambient or future) was used as random effect (1|mainplot:climate). The 17 species were present within land-use sub-plots rather than randomly assigned to separate experimental units, thus we considered them as the sub-sub-plot level. In order to avoid pseudo-replication at the sub-plot level (i.e. land use), we therefore included the interaction between land use and main plot nested in climate treatment as a second random effect (1|landuse:mainplot:climate). The models were simplified by stepwise removing non-significant interaction terms in accordance with the AIC until the most parsimonious model was found. Estimated marginal means were calculated from the simplified models using the *emmeans* function from the package *emmeans* (Lenth, 2022) to identify significant differences between the treatment combinations for each plant species.

Table III.1: Overview of plant species that occurred and flowered in all treatments together with mean trait values derived from a) the observed phenological data (timing and length of phenological niche), b) the TRY database (plant height, SLA) (Kattge et al., 2020) and c) BiolFlor (mowing, grazing and trampling tolerance and forage value) (Klotz et al., 2002).

species	family	timing of pheno-logical niche	length of pheno-logical niche	plant height	SLA	mowing tolerance	grazing tolerance	trampling tolerance	forage value
Achillea millefolium L.	Asteraceae	154	134	35	16.8	NA	NA	NA	NA
Bromus erectus Huds.	Poaceae	149	6	70	16.1	5	4	4	6
Capsella bursa-pastoris (L.) Medik.	Brassicaceae	101	25	33	40.8	3	7	6	2
Dactylis glomerata L.	Poaceae	153	6	72	24.8	8	4	6	8
Dianthus carthusianorum L.	Caryophyllaceae	145	167	44	17.7	3	4	4	3
Festuca rupicola Heuff.	Poaceae	146	13	29	24.1	6	4	4	4
Galium album Mill.	Rubiaceae	158	117	60	23.2	7	3	3	4
Galium verum L.	Rubiaceae	191	84	45	17.7	5	4	4	4
Medicago falcata L.	Fabaceae	188	48	51	20.5	5	2	2	7
Poa pratensis agg.	Poaceae	140	9	47	20.2	8	8	8	6
Scabiosa ochroleuca L.	Dipsacaceae	193	115	41	11.6	5	3	4	4
Senecio vulgaris L.	Asteraceae	98	24	33	27.6	3	5	3	2
Stellaria media (L.) Vill.	Caryophyllaceae	94	20	32	42.2	7	4	4	3
Taraxacum sect. Ruderalia Kirschner et. al.	Asteraceae	96	28	28	32.8	8	7	7	7
Trifolium dubium Sibth.	Fabaceae	138	19	25	29.4	7	4	4	7
Veronica arvensis L.	Scrophulariaceae	109	13	17	27.7	7	4	4	2
Veronica persica Poir.	Scrophulariaceae	97	20	21	35.0	NA	NA	NA	NA

Abbreviations and units: Timing of phenological niche (first flowering day as day of the year - doy), length of phenological niche (flowering duration in days), plant height (vegetative height in cm), SLA (specific leaf area in mm²/mg), mowing, grazing, trampling tolerance and forage value are given in classes from 1-9 (from low to high tolerance or forage value)(Briemle et al., 2002). Nomenclature follows (Jäger, 2016).

Explaining phenological shifts by functional traits

To quantify the climate effects on each phenological parameter (i.e. FFD, LFD, FD, Peakfl) for each land-use type in a standardized way, log response ratios (LRR) were calculated for each species following Hedges et al. (1999). The LRR is calculated as the natural logarithm (ln) of the response ratio (RR), that is characterized as the quotient of the mean of the treatment group $\overline{x}_T$ (future climate) and the mean of the control group $\overline{x}_C$ (ambient climate):

$$1. \qquad LRR = \ln(\overline{x}_T / \overline{x}_C) = \ln(\overline{x}_{future} / \overline{x}_{ambient})$$

To test whether shifts in phenological stages (i.e., climate responses represented by LRRs) can be explained by plant functional traits (Table III.1) and depend on the land-use type, we performed linear models. As the indicator values for trampling and grazing tolerance were strongly correlated ($r = 0.86$, $p < 0.001$, Appendix S III.1, Figure S III.2) and as on short-term intensively grazed pastures, grazing tolerance is equivalent to mowing tolerance combined with trampling tolerance, only trampling tolerance was considered for the models. The plant functional traits mean FFD, mean FD, SLA, plant height, mowing and trampling tolerance and forage value, all alone and in interaction with land-use type, served as explanatory variables (full model). The LRR of each phenological stage (i.e. LRR_{FFD}, LRR_{LFD}, LRR_{FD}, LRR_{PeakFl}) served as response variable, respectively. To identify the most parsimonious model identifying relevant traits for the four studied response variables we used the *dredge* function from the *MuMIn* package that selects the best model according to the Akaike Information Criterion (AIC) (Bartoń, 2023). The respective model selection tables are presented in Appendix S III.2, Tables S III.1 - S III.4.

Results

Main and interactive effects of climate and land use on plant phenology

Both climate and land use had significant effects on flowering phenology in a species-specific way (Table III.2). We did not find evidence for interactive effects of climate and land use on the flowering phenology, meaning that climate effects were independent of land-use type (Table III.2). Figure III.1 gives an overview of the flowering times (i.e. start, peak and end of flowering) per treatment (ambient meadow, future meadow, ambient pasture, future pasture) along with the timing of land-use activities (mowing or grazing) exemplary for five species showing phenological responses to climate and land use. The same figures for all remaining species can be found in Appendix S III.1, Figure S III.3.

Regarding first flowering day, the fixed effects explained 76% of the variation ($R^2_{marginal} = 0.76$). Land use and climate both affected first flowering day in a species-specific manner (significant species*climate and species*land-use interactions, Table III.2), however there was no interaction between climate and land-use. Figure III.2 shows an overview of the species-wise estimated marginal means of FFD with the 95% confidence intervals, resulting from the generalized linear mixed model. For example, the first flowering day of *Achillea millefolium* occurred significantly later in pastures than in meadows, while climate treatment had no effect (land-use effect). In *Dianthus carthusianorum,* flowering started later in pastures than in meadows (land-use effect) and tended to start earlier under future climate in both land-use types (climate trend). In contrast, *Galium verum* flowered earlier in pastures than in meadows and tended to advance flowering under future climate. *S. ochroleuca* started flowering significantly later in pastures than in meadows and significantly advanced flowering under future climate in both land-use types (climate and land-use effect). *Galium album* and *Veronica arvensis* showed trends for delayed flowering under future climate, while *Medicago falcata* and *Trifolium dubium* showed trends for advanced flowering under future climate, although these trends were not significant. FFD of the other species did not significantly differ between land-use and climate treatments.

Table III.2: Results of the simplified generalized linear mixed effect models testing for the effect of climate, land-use, species and their interactions on the flowering phenology i.e. first flowering day (FFD), last flowering day (LFD), flowering duration (FD), day of peak flowering (Peak flowering). Significant p-values are highlighted in bold. Missing information refers to interaction terms that were excluded due to model simplification.

	FFD			**LFD**			**FD**			**Peak flowering**		
	$R^2_{marg.} = 0.76$ $R^2_{cond.} = 0.76$			$R^2_{marg.} = 0.95$ $R^2_{cond.} = 0.96$			$R^2_{marg.} = 0.82$ $R^2_{cond.} = 0.83$			$R^2_{marg.} = 0.92$ $R^2_{cond.} = 0.92$		
predictors	***Chi²***	***df***	***p-value***	***Chi²***	***df***	***p-value***	***Chi²***	***df***	***p-value***	***Chi²***	***df***	***p-value***
intercept	23401.7	1	**< 0.001**	39722.2	1	**< 0.001**	1152.6	1	**< 0.001**	39420.2	1	**< 0.001**
climate	0.01	1	0.91	23.37	1	**< 0.001**	0.18	1	0.67	0.41	1	0.52
land-use	20.19	1	**< 0.001**	0.08	1	0.78.	1.55	1	0.21	23.47	1	**< 0.001**
species	307.8	11	**< 0.001**	3116.1	16	**< 0.001**	957.4	11	**< 0.001**	2118.8	16	**< 0.001**
climate * land-use	-	-	-	-	-	-				-	-	-
climate * species	32.7	11	**< 0.001**	66.27	16	**< 0.001**				-	-	-
land-use* species	54.5	11	**< 0.001**	38.41	16	**< 0.01**				57.3	16	**< 0.001**
climate * land-use * species	-	-	-	-	-	-				-	-	-

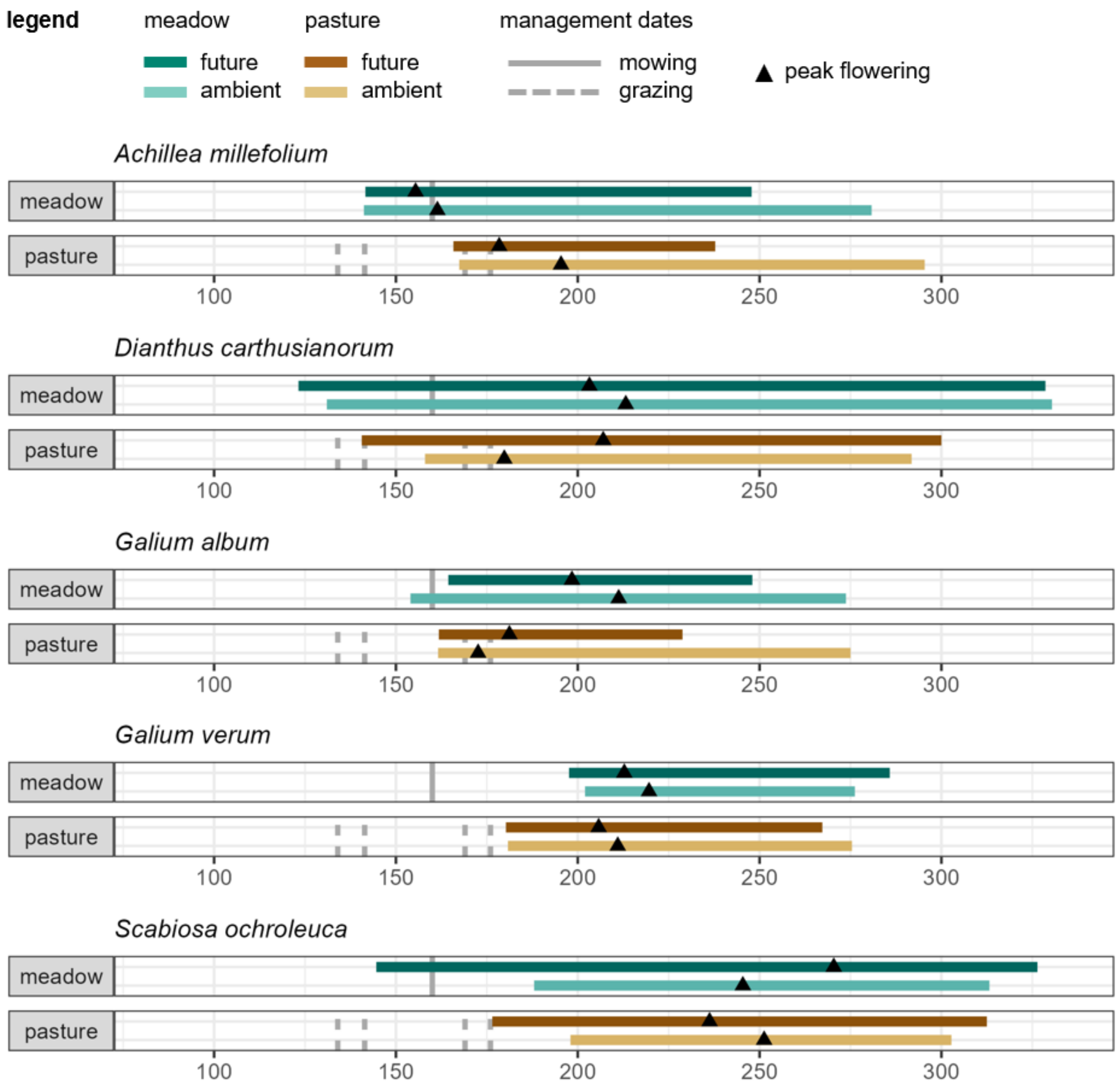


Figure III.1: Flowering times and timing of land management (mowing or grazing) across all treatments for five exemplary species. Strips summarize the mean FFD, LFD and day of peak flowering per treatment, the x-axis shows day of the year (doy). The same figure on the remaining 12 species investigated can be found in Appendix SIII.1, Figure S III.3.

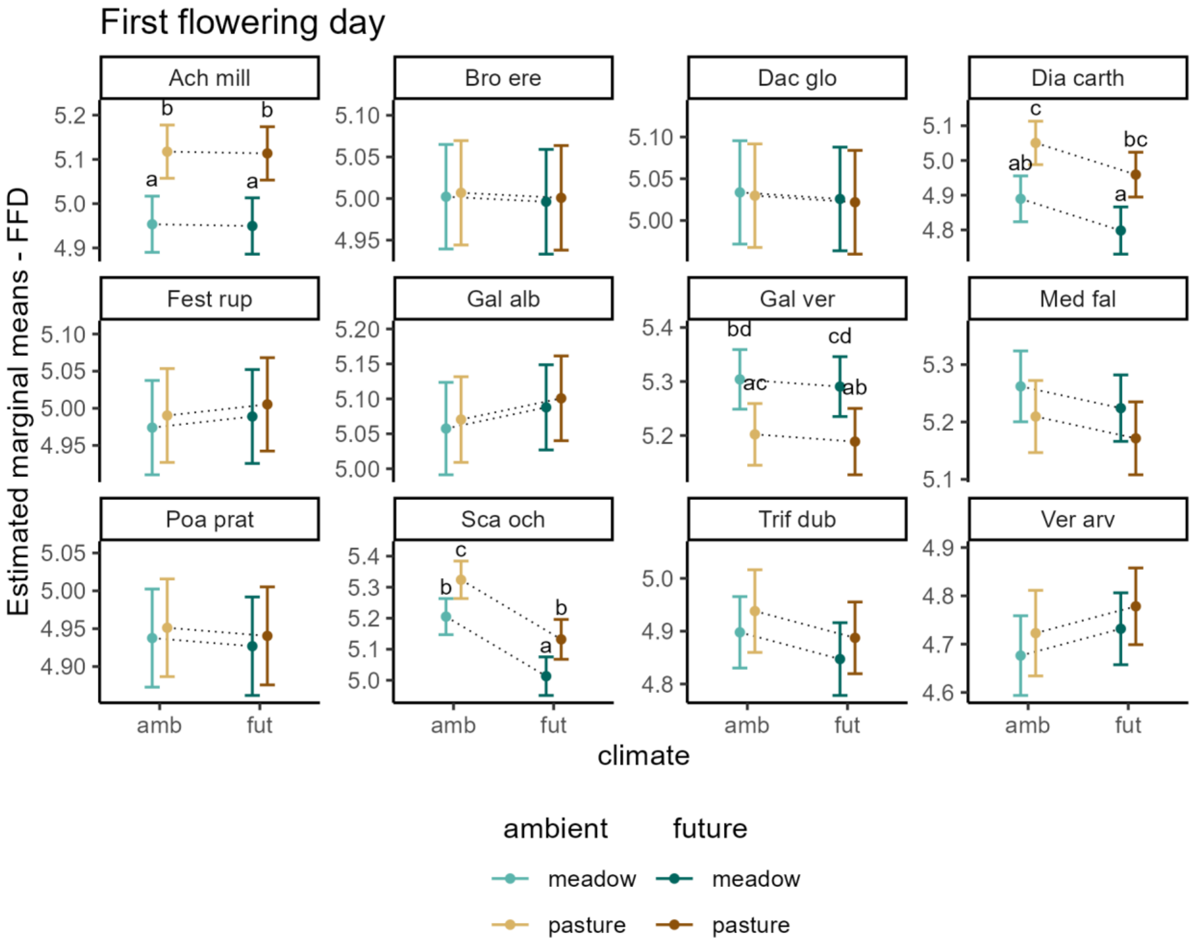


Figure III.2: Effects of climate and land use on first flowering day. Shown are estimated marginal means of FFD with the 95% confidence intervals, resulting from the generalized linear mixed model. Results compare FFD between ambient and future climate on meadows and pastures for each species. Letters indicate significant differences between treatments. If no letters are shown, no significant difference between treatment groups was found. Dotted lines are only shown for better interpretation of interacting effects of climate and land use.

For last flowering day, the model explained 95% of the variation ($R^2_{marginal} = 0.95$). Similar to first flowering day, species responded species-specifically to climate and land use (Table III.2), and climate effects were again independent of land-use type. The following species responses are presented in Figure III.3: We found significant treatment effects in four species. *A. millefolium* and *G. album* ended flowering significantly earlier under future climate regardless of land-use type (climate effect). LFD of *D. carthusianorum* and *M. falcata* occurred significantly earlier on pastures (land-use effect). Furthermore, under future climate LFD of *M. falcata* tended to advance while for *D. carthusianorum* LFD tended to delay (climate trends). LFD of the other species did not significantly differ between land-use and climate treatments.

For flowering duration, the model explained 82% of the variation ($R^2_{marginal}$ = 0.82). The investigated species differed in their flowering duration (species effect), but no significant effect of climate or land use was detected for the flowering duration (Table III.2). See Appendix SIII.1, Figure S III.4 for individual trends.

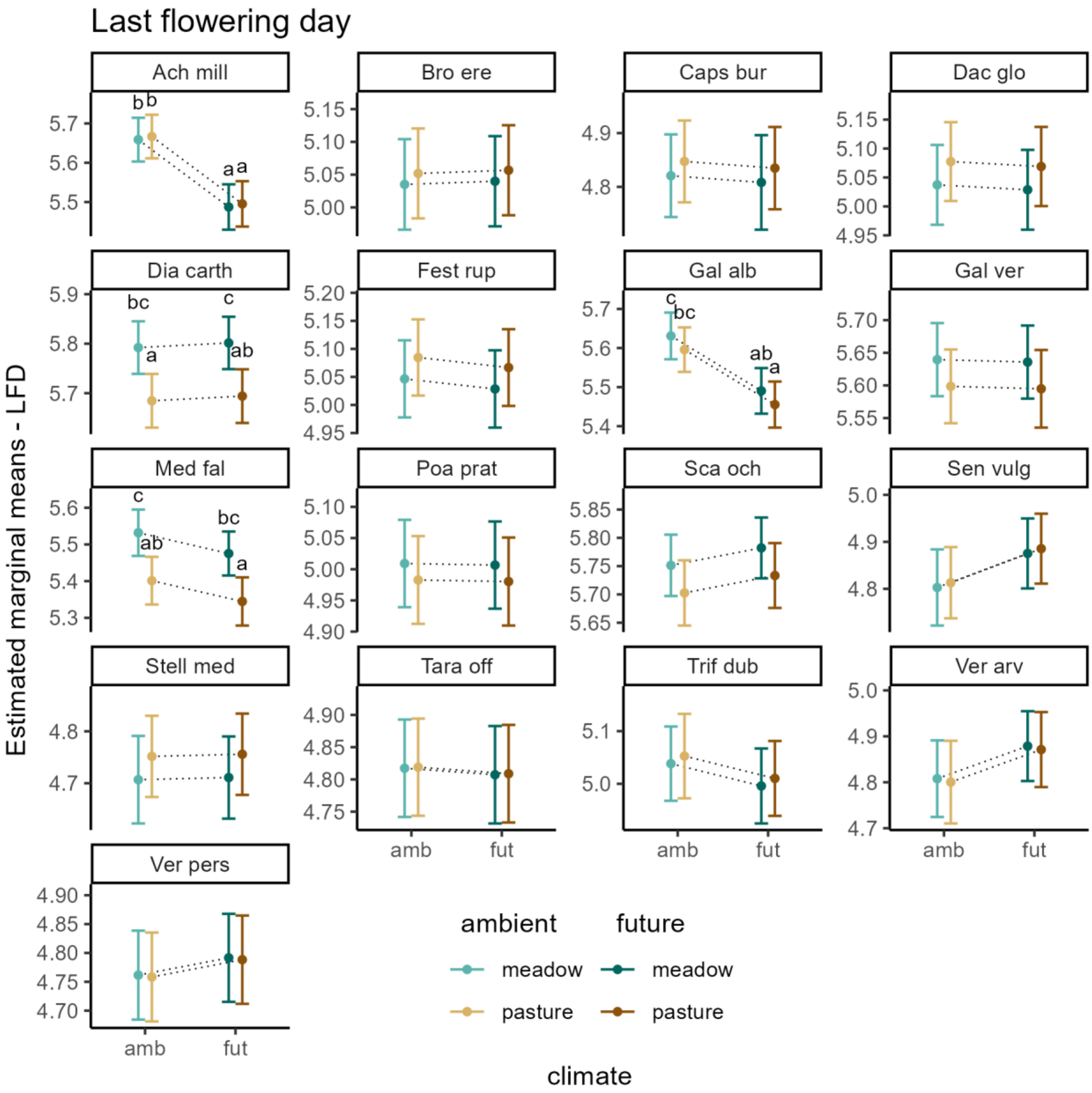


Figure III.3: Effects of climate and land use on last flowering day. Shown are estimated marginal means of LFD with the 95% confidence intervals, revealed from the generalized linear mixed model. Results compare LFD between ambient and future climate on meadows and pastures for each species. Letters indicate significant differences between treatments. If no letters are shown, no significant difference between treatment groups was found. Dotted lines are only shown for better interpretation of interactive effects of climate and land use.

For the day of peak flowering, the model explained 92% of the variation ($R^2_{maginal} = 0.92$). Land use affected the day of peak flowering in a species-specific manner (Table III.2, Appendix SIII.1, Figure S III.5), while climate didn't have a significant effect. We found significant land-use effects in two species. Peak flowering of *A. millefolium* occurred significantly later in pastures than in meadows regardless of climate (Appendix S III.1, Figure S III.5). In contrast, peak flowering of *G. album* occurred significantly earlier in pastures than in meadows (Appendix S III.1, Figure S III.5). Most other species showed similar trends either advancing or delaying peak flowering in pastures compared to meadows (Appendix S III.1, Figure S III.5).

Explaining phenological shifts by functional traits

Functional traits explained species-specific phenological responses to changes in climate (LRR) (Figure III.4, Table III.3).
The best model describing changes in FFD contained the phenological niche (mean FFD) and the mowing tolerance (Table III.3). The model selection table that displays all models with a delta AIC < 2 is shown in Appendix S III.2, Table S III.1. The model on shifts in FFD explained 42% of the variation ($R^2_{multiple} = 0.42$, $F_{2,27} = 9.81$, $p < 0.001$). The phenological niche (represented by the mean FFD under ambient climate) was negatively related to changes in FFD under future climate (Table III.3). Late flowering species showed stronger advances in their first flowering day under future climate (Figure III.4, Appendix S III.1, Figure S III.6). Mowing tolerance was positively related to the FFD response (Figure III.4, Appendix SIII.1, Figure S III.6). Species with a low mowing tolerance more strongly advanced FFD under future climate compared to species with high mowing tolerance, which tended to show no response (Appendix SIII.1, Figure S III.6).

The best model describing changes in LFD contained the phenological niche (mean FFD), the length of the phenological niche (mean FD), SLA and forage value (Table III.3). The model selection table that displays all models with delta AIC < 2 is shown in Appendix S III.2, Table S III.2. The model on shifts in LFD explained 36 % of the variation ($R^2_{multiple} = 0.36$, $F_{4,25} = 3.56$, $p < 0.05$, S2, Table III.3). Long flowering species, species with a high SLA and high forage value advanced their LFD more strongly under future climate (Figure III.4, Appendix S III.1, Figure S III.7). Late flowering species tended to advance LFD more strongly under future climate, even though this effect was non-significant ($p = 0.11$, Figure III.4, Appendix S III.1, Figure S III.7).

The best model describing changes in FD contained the length of the phenological niche (mean FD), SLA and mowing tolerance (Table III.3). The model selection table that displays all models with delta AIC < 2 is shown in Appendix S III.2, Table S III.3. The model on shifts in FD explained 32 % of the variation ($R^2_{multiple} = 0.32$, $F_{3,23} = 4.12$, $p < 0.05$; Table III.3). Shifts in the flowering duration (LRR_{FD}) related to future climate were explained by SLA and mowing tolerance (Figure III.4). Under future climate species with a high SLA and a high mowing tolerance shortened their flowering duration more strongly compared to species with low SLA and low mowing tolerance (Appendix S III.1, Figure S III.8). Furthermore, long flowering species tended to shorten their FD more strongly under future climate when compared to short flowering species, even though this effect was non-significant (p = 0.06, Figure III.4, Appendix SIII.1, Figure S III.8).

Table III.3: Model results for the most parsimonious models explaining phenological shifts in first flowering day (FFD shift), last flowering day (LFD shift) and flowering duration (FD shift) to future climate by functional traits and grassland indicator values. None of the investigated traits related to shifts in peak flowering.

	FFD shift				**LFD shift**				**FD shift**			
	$R^2_{multiple} = 0.42$ $R^2_{adjusted} = 0.38$				$R^2_{multiple} = 0.36$ $R^2_{adjusted} = 0.26$				$R^2_{multiple} = 0.32$ $R^2_{adjusted} = 0.24$			
	$F_{2,27} = 9.81$; $p < 0.001$				$F_{4,25} = 3.558$; $p = 0.019$				$F_{3,23} = 4.12$; $p = 0.016$			
Predictor	***Estimate***	***SE***	***p-value***		***Estimate***	***SE***	***p-value***		***Estimate***	***SE***	***p-value***	
intercept	-0.013	0.011	0.251		-0.004	0.009	0.641		-0.022	0.048	0.653	
FFD	-0.039	0.011	0.001	**	-0.030	0.018	0.107					
FD					-0.027	0.013	0.044	*	-0.115	0.060	0.066	.
SLA					-0.045	0.017	0.016	*	-0.142	0.055	0.017	*
mowing tolerance	0.028	0.011	0.017	*					-0.138	0.054	0.016	*
forage value					-0.028	0.012	0.030	*				

Abbreviations: FFD – timing of phenological niche measured as first flowering day, FD – length of phenological niche measured as flowering duration in days, SLA – specific leaf area, SE – standard error.

The best model describing changes in peak flowering contained none of the variables, i.e. none of the considered traits related to shifts in peak flowering. Thus, no further results can be reported. The model selection table that displays all models with delta AIC < 2 is shown in Appendix S III.2, Table S III.4.

The functional traits ‘plant height’ and ‘trampling tolerance’ did not relate to shifts in any of the tested phenological parameters. However, there is some indication that plant height might play a role for responses in LFD (compare model selection table in Appendix S III.2, Table S III.2) and that trampling tolerance might play a role for responses in FFD (model selection table in Appendix S III.2, Table S III.1).

Further, we did not find evidence for interactive effects between traits and land-use type, meaning that the investigated traits were not of different importance for phenological shifts on meadows and pastures.

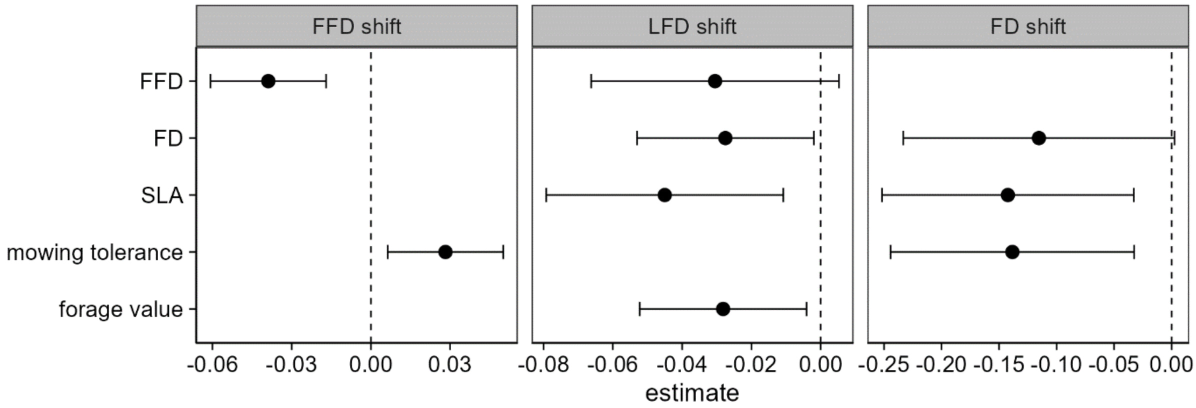


Figure III.4: Effect of functional traits on the response to climate (LRR) of first flowering day (FFD shift), last flowering day (LFD shift) and flowering duration (FD shift). Estimates of the final linear models with 95% confidence intervals are shown. Abbreviations of response variables: FFD = phenological niche measured as flowering start; FD = length of phenological niche measured as flowering duration, SLA = specific leaf area.

Discussion

Our results clearly show that the flowering phenology of the 17 studied grassland species responded to both changes in climate and different land-use types in species-specific ways. Especially FFD and LFD were species-specifically affected by climate and land use. Plant functional traits and grassland indicator values explained these species-specific climate responses. Furthermore, different sets of traits explained shifts in the different phenological stages.

Conducting our study at the Global Change Experimental Facility enabled us to unequivocally identify the causal effects of manipulated climate and land use on plant phenology under the same abiotic and biotic background conditions. However, large experiments as this have the disadvantage of a smaller sample size (n=5, i.e. five replicates per treatment) and the high variability of the data may mask subtle effects of climate or land use, thereby decreasing the likelihood to detect small but true effects (i.e. decreasing the statistical power). Therefore, in the following we also present and discuss marginal effects and trends.

Effects of land use and climate on plant phenology

Land-use type significantly influenced the flowering phenology in a species-specific way. Most of the species growing on meadows flowered earlier than those growing on pastures, which is a frequently reported pattern (Reisch and Poschlod, 2011, 2009; Van Tienderen and van der Toorn, 1991), but we also found opposing patterns in single species. Phenological studies on the effects of land-use type are scarce and usually link their findings to genetic differentiation and evolutionary processes that act on a larger temporal scale (Reisch and Poschlod, 2009; Völler et al., 2017, 2013). However, rapid responses of the flowering time to land use or other drivers such as climate have also been shown (Bucharova et al., 2024; Franks et al., 2007; Rauschkolb et al., 2022; Zopfi, 1993). Due to the comparably short duration of the experiment (six years by the time of our study), we think that genetic differentiation or evolutionary processes have not yet played a prominent role in our study system, at least not for the perennial species strongly dominating our dataset. We assume, that the effects of the land-use type alone are on the one hand attributed to the timing of the land management that differed between pastures and meadows (first grazing occurred three to four weeks before mowing). On the other hand, the heterogeneity of microsite conditions in meadows and pastures may also give rise to land-use-specific phenological patterns. For example, LFD of *D. carthusianorum* occurred significantly earlier on pastures than on meadows but long after the land management events. We observed higher proportions of open soil (Appendix S III.1, Figure S III.9) and increased maximum temperatures on pastures (Appendix S III.1, Figure S III.11), especially during summer, which probably led to generally more stressful growing conditions on pastures. Different land-use types may furthermore alter biotic interactions like competition or herbivory that might further influence phenological patterns (Busch et al., 2018; Freeman et al., 2003; Gossner et al., 2014; Tadey, 2020; Völler et al., 2017). Overall, results from this study indicate that land-use effects on the flowering phenology of grassland species are due to a combination of timing, frequency, altered microsite conditions and biotic interactions on meadows and pastures (Tälle et al., 2016).

Climate significantly influenced the flowering phenology in a species-specific way. Advances in FFD are frequently reported in response to climate alterations (Fitter and Fitter, 2002; Lesica and Kittelson, 2010; Menzel et al., 2006; Miller-Rushing and Primack, 2008). In our study, advances in FFD might be mostly related to increased spring precipitation (Dorji et al., 2020) and increased minimum temperatures (Appendix S III.1, Figure S III.11) under future climate conditions that might enhance plant growth and thus phenology. Advances in LFD, on the other hand, might be mainly explained by the reduced precipitation in the future climate plots during the summer months (June-Sept, Appendix S III.1, Figure S III.1, S III.12) that coincide with the main flowering time of many species (Figure III.1, Appendix S III.1, Figure S III.3). Drought stress can lead to a trade-off between reproduction and survival so that plants might shift their priorities to survival, ending flowering earlier (Galen, 2000; Lauder et al., 2019). However, due to the application of a whole scenario of future climate, effects of altered precipitation patterns and altered temperature cannot be disentangled.

An important aim of this study was to test whether climate and land use interactively affect the flowering phenology of grassland species. We did not find statistical evidence for interacting effects of climate and land use for the flowering phenology of the investigated grassland species, i.e. phenological responses to climate did not differ between land-use types. However, monitoring of the microclimate and -site conditions indicated that the climate treatment differently affected microclimate and -site conditions on meadows and pastures (Appendix S III.1, Figures S III.9 - S III.12). We observed that under future climate pastures were warmer (Appendix S III.1, Figure S III.11) and drier (especially in deeper soil layers, Appendix S III.1, Figure S III.12) and showed larger proportions of open soil in summer (Appendix S III.1, Figure S III.9) compared to meadows that in contrast had slightly higher litter cover under future climate (Appendix S III.1, Figure S III.10). Furthermore, competition may play a greater role on meadows than on pastures because of the higher stand density that mediates climate change effects differently (Bütof et al., 2012; Tälle et al., 2016). Thus, we conclude that growing conditions on meadows and pastures were modified by the future climate in different ways, making interactive effects of climate and land use on phenology or other variables like survival or productivity likely. However, the lack of those interactions in our study, could be related to the fact that microclimatic differences were not strong enough to influence phenology in a detectable way, as well as high variability of the data.

The species-specific responses in our study and across other studies show that the drivers of flowering phenology are complex and might, depending on the context, be driven by various factors such as temperature, soil moisture, accumulated heat or biotic interactions (Bock et al., 2014; Pau et al., 2011). We encourage further studies investigating each of these effects separately to contribute to a better understanding on species-specific responses to land use and climate.

Explaining phenological shifts by functional traits

Functional traits explained species-specific phenological shifts in response to climate as has also been shown in previous studies (Bucher et al., 2018; Bucher and Römermann, 2020; König et al., 2018), but trait-response relationships did not differ between land-use types.

Plant species with an early phenological niche (early flowering) have been frequently reported to advance their phenology more strongly in response to changing climate compared to late flowering species (e.g. Fitter and Fitter, 2002; Lesica and Kittelson, 2010; Menzel et al., 2006; Miller-Rushing and Primack, 2008; Rauschkolb et al. 2024). In contrast, in our study we found that late flowering species showed the strongest advances in FFD and LFD, also reported by Bucher et al. (2018) for FFD. Phenological advances can relate to the escape from drought conditions (Franks et al., 2007) and drought can lead to phenological advances of the same magnitude as one decade of gradual warming (Jentsch et al., 2009). Moreover, drought stress can lead to a trade-off between reproduction and survival, leading plants to prioritize survival and consequently end flowering earlier (Galen, 2000; Lauder et al., 2019). As in our experimental setup summer precipitation was drastically reduced under future climate conditions (Appendix S III.1, Figure S III.1), species with a later phenological niche (i.e. flowering in summer) may therefore be more affected by drought and subsequently advanced flowering start and end. However, in our study we might have missed a few very early flowering species, as we started the phenological monitoring in the beginning of April. We thus recommend, when working in comparable grassland systems, to start phenological monitoring earlier, if possible.

Long flowering species (length of phenological niche) ended their flowering earlier and thus shortened their flowering under future climate. In contrast to short flowering species, they face a higher probability that the timing of land management coincides with the flowering period, damaging vegetative and reproductive parts of the plant. Bucher and Römermann (2020) found similar patterns along an elevational gradient, where land use did not play a prominent role. Furthermore, long flowering species are more likely to flower during high summer, when drought conditions are most pronounced under future climate and are thus more likely to end flowering earlier.

Species with a high SLA ended flowering earlier under future climate consequently shortening their flowering durations more strongly. Plants with a high SLA have thinner and less resistant leaves and might thus face more damage by mowing or grazing and are also less resistant to drought (Díaz et al., 2016; Reich et al., 1997; Wright et al., 2004). Species with a high SLA follow an acquisitive strategy (Díaz et al., 2016) that may allow a more plastic response to climate, but also a stronger need to escape drought conditions (Blumenthal et al., 2020; Griffin-Nolan et al., 2019; Visakorpi et al., 2023; Zhang et al., 2020). König et al. (2018) also found stronger phenological shifts with increasing SLA on a global scale while Bucher et al. (2018) found an opposing relationship on the local scale along an elevational gradient. Interestingly, species with a high mowing tolerance less strongly advanced their flowering but shortened their flowering duration more strongly under future climate. Mowing tolerance is closely related to regeneration capacity, growth rate and the ability to store sufficient assimilates prior to mowing (Briemle et al., 2002). Thus, mowing tolerance is, just like SLA, ecologically related to the growth strategy (conservative vs. acquisitive) but no correlation between SLA and mowing tolerance was found in our dataset (Appendix S III.1, Figure S III.2). Additionally, a high forage value was related to stronger advances of LFD under future climate. As the forage value for livestock strongly relates to the plants protein and mineral content as well as the growth rate (Briemle et al., 2002), a high forage value can also be associated with an acquisitive strategy.

Trampling tolerance that is related to plant height, growth and life form (Briemle et al., 2002) as well as the trait plant height did not play a role in mediating phenological climate responses in our study. Although plant height did not relate to phenological shifts in our models (but see Appendix S III.1, Table S III.2), we suggest that it should still be considered in future studies as it was frequently shown to be of great importance in explaining phenological patterns and shifts (Huang et al., 2018; König et al., 2018; Sporbert et al., 2022; Zhu et al., 2016).

To summarize, our results indicate that late flowering species stronger advanced flowering start and end, which is likely related to drought escape and survival over reproduction. Further, our results show that long flowering species and species with an acquisitive strategy (high SLA, mowing tolerance and forage value), which are more susceptible to stressful conditions like summer drought (Díaz et al., 2016) were more strongly affected by future climate, advancing flowering end and consequently shortening flowering duration. Drought related decreases in flowering durations were observed before (Llorens and Peñuelas, 2005; Steyn et al., 1996), but contrasting responses were found as well (Jentsch et al., 2009; Llorens and Peñuelas, 2005). In contrast, early and short flowering species are less likely to be affected by land management and summer droughts and species following a more conservative strategy have a higher drought resistance accompanied by a lower phenotypic plasticity (Blumenthal et al., 2020; Griffin-Nolan et al., 2019; Visakorpi et al., 2023; Zhang et al., 2023). Thus, these species did not show strong responses. Another reason for species not responding to climate and/or land-use treatments may relate to the comparably short duration of the experiment (six years), that makes genetic differentiation or evolutionary processes rather unlikely in our study system (not impossible though: Bucharova et al., 2024; Franks et al., 2007; Rauschkolb et al., 2022; Zopfi, 1993). Non-responding species could also be rather controlled by photoperiod than by climate (Flynn and Wolkovich, 2018; Meng et al., 2021) or characterized by a generally lower trait plasticity (Zhang et al., 2020), but further investigations would be necessary to test this.

Overall, traits related to growth rate and competitive ability, but also the phenological niche (FFD, FD) were important traits mediating climate driven phenological responses. In our study system, namely semi-natural and extensively managed grasslands, traits like forage value and mowing tolerance seem promising to explain differing climate responses among species and potentially land-use types and can complement ‘classical’ functional traits.

We did not find evidence that traits differently affected phenological climate responses on meadows compared to pastures. This was not expected, as depending on the land-use type different traits were expected to be advantageous to cope with the different disturbances and microsite conditions on meadows and pastures as outlined above (Zhu et al., 2016). As we used mean values from the TRY database for plant height and SLA, we did not capture the intraspecific trait variability (ITV) that we might expect for the different land-use types and climate treatments. Thus, our study may underestimate the effect of those traits (Zhang et al., 2020). However, we were not able to measure traits *in-situ* due to constrained sampling possibilities owing to multiple side experiments running on the plots. We would recommend measuring the respective traits *in-situ* if possible and to add also relevant physiological traits (Bucher et al., 2018; Visakorpi et al., 2023) to account for the role of ITV.

Conclusion

This study contributes to the understanding on how climate change and land use impact temperate grassland systems and how functional traits can mediate those impacts. Both global change drivers, climate and land use, affected the flowering phenology in a species-specific way, but we didn’t find evidence for interacting effects of climate and land use on phenology. Still, we found that microsite conditions on meadows and pastures were differently affected by future climate, making divergent effects on plant phenology (but also plant vitality, e.g. survival or productivity) likely and should be further explored. Particularly, we recommend further research focusing on microclimatic and microsite effects on phenology and phenology-trait relationships including a larger species set and maybe more importantly, considering that also traits strongly respond to variations in the environment, suggesting the need to measure traits *in-situ*. We further conclude that functional traits and grassland indicator values offer a promising approach to understanding phenological responses to climate, with grassland indicator values being particularly useful when focusing on different grassland management practices.

The observed phenological shifts under future compared to ambient climate and the related traits mirror a phenological escape from drought which is particularly relevant in summer. Thus, late flowering, long flowering and acquisitive species were particularly affected and shifted and shortened their flowering while species with the opposite traits did not. Thus, our findings suggest that under future climate the community of simultaneously flowering plant species will be changed especially during summer. This may therefore lead to a shortage of available pollinator resources (pollen and nectar) during summer, affecting pollinator fitness and pollination alike. To better be able to understand potential implications for pollinators within this experiment, the flowering intensity, flower cover as well as nectar and pollen characteristics should be considered in future studies.

References

Ahas, R., Aasa, A., Menzel, A., Fedotova, V.G., Scheifinger, H., 2002. Changes in European spring phenology. International Journal of Climatology 22, 1727–1738. https://doi.org/10.1002/joc.818

Badeck, F.-W., Bondeau, A., Böttcher, K., Doktor, D., Lucht, W., Schaber, J., Sitch, S., 2004. Responses of Spring Phenology to Climate Change. The New Phytologist 162, 295–309.

Bartoń, K. (2023) 'MuMIn: Multi-Model Inference'. Available at: https://cran.r-project.org/web/packages/MuMIn/index.html (Accessed: 12 April 2024).

Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software 67. https://doi.org/10.18637/jss.v067.i01

Blumenthal, D.M., Mueller, K.E., Kray, J.A., Ocheltree, T.W., Augustine, D.J., Wilcox, K.R., 2020. Traits link drought resistance with herbivore defence and plant economics in semi-arid grasslands: The central roles of phenology and leaf dry matter content. Journal of Ecology 108, 2336–2351. https://doi.org/10.1111/1365-2745.13454

Bock, A., Sparks, T.H., Estrella, N., Jee, N., Casebow, A., Schunk, C., Leuchner, M., Menzel, A., 2014. Changes in first flowering dates and flowering duration of 232 plant species on the island of Guernsey. Global Change Biology 20, 3508–3519. https://doi.org/10.1111/gcb.12579

Bolmgren, K., D. Cowan, P., 2008. Time – size tradeoffs: a phylogenetic comparative study of flowering time, plant height and seed mass in a north-temperate flora. Oikos 117, 424–429. https://doi.org/10.1111/j.2007.0030-1299.16142.x

Borer, E.T., Seabloom, E.W., Gruner, D.S., Harpole, W.S., Hillebrand, H., Lind, E.M., Adler, P.B., Alberti, J., Anderson, T.M., Bakker, J.D., Biederman, L., Blumenthal, D., Brown, C.S., Brudvig, L.A., Buckley, Y.M., Cadotte, M., Chu, C., Cleland, E.E., Crawley, M.J., Daleo, P., Damschen, E.I., Davies, K.F., DeCrappeo, N.M., Du, G., Firn, J., Hautier, Y., Heckman, R.W., Hector, A., HilleRisLambers, J., Iribarne, O., Klein, J.A., Knops, J.M.H., La Pierre, K.J., Leakey, A.D.B., Li, W., MacDougall, A.S., McCulley, R.L., Melbourne, B.A., Mitchell, C.E., Moore, J.L., Mortensen, B., O'Halloran, L.R., Orrock, J.L., Pascual, J., Prober, S.M., Pyke, D.A., Risch, A.C., Schuetz, M., Smith, M.D., Stevens, C.J., Sullivan, L.L., Williams, R.J., Wragg, P.D., Wright, J.P., Yang, L.H., 2014. Herbivores and nutrients control grassland plant diversity via light limitation. Nature 508, 517–520. https://doi.org/10.1038/nature13144

Briemle, G., Nitsche, S., Nitsche, L., 2002. Nutzungswertzahlen für Gefäßpflanzen des Grünlandes. Schriftenreihe für Vegetationskunde, Bundesamt für Naturschutz, Bonn 38, 203–225.

Brooks, M.E. et al. (2017) ‘glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling’, The R Journal, 9(2), pp. 378–400.

Brys, R., Jacquemyn, H., Endels, P., Blust, G.D., Hermy, M., 2004. The effects of grassland management on plant performance and demography in the perennial herb Primula veris. Journal of Applied Ecology 41, 1080–1091. https://doi.org/10.1111/j.0021-8901.2004.00981.x

Bucharova, A. et al. (2024) ‘Rapid evolution of flower phenology and clonality in restored populations of multiple grassland species’, Journal of Applied Ecology, 61(4), pp. 836–846. Available at: https://doi.org/10.1111/1365-2664.14600.

Bucher, S.F., König, P., Menzel, A., Migliavacca, M., Ewald, J., Römermann, C., 2018. Traits and climate are associated with first flowering day in herbaceous species along elevational gradients. Ecology and Evolution 8, 1147–1158. https://doi.org/10.1002/ece3.3720

Bucher, S.F., Römermann, C., 2020. Flowering patterns change along elevational gradients and relate to life-history strategies in 29 herbaceous species. Alp Botany 130, 41–58. https://doi.org/10.1007/s00035-020-00231-w

Busch, V., Klaus, V.H., Penone, C., Schäfer, D., Boch, S., Prati, D., Müller, J., Socher, S.A., Niinemets, Ü., Peñuelas, J., Hölzel, N., Fischer, M., Kleinebecker, T., 2018. Nutrient stoichiometry and land use rather than species richness determine plant functional diversity. Ecology and Evolution 8, 601–616. https://doi.org/10.1002/ece3.3609

Bütof, A., von Riedmatten, L.R., Dormann, C.F., Scherer-Lorenzen, M., Welk, E., Bruelheide, H., 2012. The responses of grassland plants to experimentally simulated climate change depend on land use and region. Global Change Biology 18, 127–137. https://doi.org/10.1111/j.1365-2486.2011.02539.x

CaraDonna, P.J., Iler, A.M., Inouye, D.W., 2014. Shifts in flowering phenology reshape a subalpine plant community. Proceedings of the National Academy of Sciences 111, 4916–4921. https://doi.org/10.1073/pnas.1323073111

Chyba, J., Kroulík, M., Krištof, K., Misiewicz, P.A., Chaney, K., 2014. Influence of soil compaction by farm machinery and livestock on water infiltration rate on grassland. Agronomy Research 12, 59–64.

Cleland, E.E., Chiariello, N.R., Loarie, S.R., Mooney, H.A., Field, C.B., 2006. Diverse responses of phenology to global changes in a grassland ecosystem. Proceedings of the National Academy of Sciences 103, 13740–13744. https://doi.org/10.1073/pnas.0600815103

Cleland, E.E., Chuine, I., Menzel, A., Mooney, H.A., Schwartz, M.D., 2007. Shifting plant phenology in response to global change. Trends in Ecology & Evolution 22, 357–365. https://doi.org/10.1016/j.tree.2007.04.003

Díaz, S., Kattge, J., Cornelissen, J.H.C., Wright, I.J., Lavorel, S., Dray, S., Reu, B., Kleyer, M., Wirth, C., Colin Prentice, I., Garnier, E., Bönisch, G., Westoby, M., Poorter, H., Reich, P.B., Moles, A.T., Dickie, J., Gillison, A.N., Zanne, A.E., Chave, J., Joseph Wright, S., Sheremet’ev, S.N., Jactel, H., Baraloto, C., Cerabolini, B., Pierce, S., Shipley, B., Kirkup, D., Casanoves, F., Joswig, J.S., Günther, A., Falczuk, V., Rüger, N., Mahecha, M.D., Gorné, L.D., 2016. The global spectrum of plant form and function. Nature 529, 167–171. https://doi.org/10.1038/nature16489

Dorji, T., Hopping, K.A., Meng, F., Wang, S., Jiang, L., Klein, J.A., 2020. Impacts of climate change on flowering phenology and production in alpine plants: The importance of end of flowering. Agriculture, Ecosystems & Environment 291, 106795. https://doi.org/10.1016/j.agee.2019.106795

Fitter, A.H., Fitter, R.S.R., 2002. Rapid Changes in Flowering Time in British Plants. Science 296, 1689–1691. https://doi.org/10.1126/science.1071617

Fitter, A.H., Fitter, R.S.R., Harris, I.T.B., Williamson, M.H., 1995. Relationships Between First Flowering Date and Temperature in the Flora of a Locality in Central England. Functional Ecology 9, 55–60. https://doi.org/10.2307/2390090

Flynn, D.F.B. and Wolkovich, E.M. (2018) 'Temperature and photoperiod drive spring phenology across all species in a temperate forest community', New Phytologist, 219(4), pp. 1353–1362. Available at: https://doi.org/10.1111/nph.15232.

Forrest, J., Miller-Rushing, A.J., 2010. Toward a synthetic understanding of the role of phenology in ecology and evolution. Philosophical Transactions of the Royal Society B: Biological Sciences 365, 3101–3112. https://doi.org/10.1098/rstb.2010.0145

Forrest, J.R.K., 2015. Plant–pollinator interactions and phenological change: what can we learn about climate impacts from experiments and observations? Oikos 124, 4–13. https://doi.org/10.1111/oik.01386

Franks, S.J., Sim, S., Weis, A.E., 2007. Rapid evolution of flowering time by an annual plant in response to a climate fluctuation. Proceedings of the National Academy of Sciences 104, 1278–1282. https://doi.org/10.1073/pnas.0608379104

Freeman, R.S., Brody, A.K., Neefus, C.D., 2003. Flowering phenology and compensation for herbivory in Ipomopsis aggregata. Oecologia 136, 394–401. https://doi.org/10.1007/s00442-003-1276-6

Galen, C., 2000. High and Dry: Drought Stress, Sex-Allocation Trade-offs, and Selection on Flower Size in the Alpine Wildflower Polemonium viscosum (Polemoniaceae). The American Naturalist 156, 72–83. https://doi.org/10.1086/303373

Gaudet, C.L., Keddy, P.A., 1988. A comparative approach to predicting competitive ability from plant traits. Nature 334, 242–243. https://doi.org/10.1038/334242a0

Gérard, M., Vanderplanck, M., Wood, T., Michez, D., 2020. Global warming and plant–pollinator mismatches. Emerging Topics in Life Sciences 4, 77–86. https://doi.org/10.1042/ETLS20190139

Gilhaus, K., Boch, S., Fischer, M., Hoelzel, N., Kleinebecker, T., Prati, D., Rupprecht, D., Schmitt, B., Klaus, V.H., 2017. Grassland management in Germany: effects on plant diversity and vegetation composition. Tuexenia 37, 379–397.

Gossner, M.M., Weisser, W.W., Meyer, S.T., 2014. Invertebrate herbivory decreases along a gradient of increasing land-use intensity in German grasslands. Basic and Applied Ecology 15, 347–352. https://doi.org/10.1016/j.baae.2014.03.003

Griffin-Nolan, R.J., Blumenthal, D.M., Collins, S.L., Farkas, T.E., Hoffman, A.M., Mueller, K.E., Ocheltree, T.W., Smith, M.D., Whitney, K.D., Knapp, A.K., 2019. Shifts in plant functional composition following long-term drought in grasslands. Journal of Ecology 107, 2133–2148. https://doi.org/10.1111/1365-2745.13252

Hedges, L.V., Gurevitch, J., Curtis, P.S., 1999. The Meta-Analysis of Response Ratios in Experimental Ecology. Ecology 80, 1150–1156. https://doi.org/10.1890/0012-9658(1999)080[1150:TMAORR]2.0.CO;2

Hegland, S.J., Nielsen, A., Lázaro, A., Bjerknes, A.-L., Totland, Ø., 2009. How does climate warming affect plant-pollinator interactions? Ecology Letters 12, 184–195. https://doi.org/10.1111/j.1461-0248.2008.01269.x

Herz, K., Dietz, S., Haider, S., Jandt, U., Scheel, D., Bruelheide, H., 2017. Predicting individual plant performance in grasslands. Ecology and Evolution 7, 8958–8965. https://doi.org/10.1002/ece3.3393

Horbach, S., Rauschkolb, R., Römermann, C., 2023. Flowering and leaf phenology are more variable and stronger associated to functional traits in herbaceous compared to tree species. Flora 300, 152218. https://doi.org/10.1016/j.flora.2023.152218

Huang, L., Koubek, T., Weiser, M., Herben, T., 2018. Environmental drivers and phylogenetic constraints of growth phenologies across a large set of herbaceous species. Journal of Ecology 106, 1621–1633. https://doi.org/10.1111/1365-2745.12927

Jäger, E., 2016. Rothmaler - Exkursionsflora von Deutschland. Gefäßpflanzen: Grundband, 21st ed. Springer Berlin Heidelberg.

Jentsch, A., Kreyling, J., Boettcher-Treschkow, J., Beierkuhnlein, C., 2009. Beyond gradual warming: extreme weather events alter flower phenology of European grassland and heath species. Global Change Biology 15, 837–849. https://doi.org/10.1111/j.1365-2486.2008.01690.x

Kattge, J., Bönisch, G., Díaz, S., Lavorel, S., Prentice, I.C., Leadley, P., Tautenhahn, S., Werner, G.D.A.,(…), Wirth, C., et al. 2020. TRY plant trait database – enhanced coverage and open access. Global Change Biology 26, 119–188. https://doi.org/10.1111/gcb.14904

Klotz, S., Kühn, I., Durka, W., 2002. BiolFlor: Eine Datenbank mit biologisch-ökologischen Merkmalen zur Flora von Deutschland. Schriftenreihe für Vegetationskunde, Bonn: Bundesamt für Naturschutz.

König, P., Tautenhahn, S., Cornelissen, J.H.C., Kattge, J., Bönisch, G., Römermann, C., 2018. Advances in flowering phenology across the Northern Hemisphere are explained by functional traits. Global Ecology and Biogeography 27, 310–321. https://doi.org/10.1111/geb.12696

Korell, L., Auge, H., Chase, J.M., Harpole, S., Knight, T.M., 2020. We need more realistic climate change experiments for understanding ecosystems of the future. Global Change Biology 26, 325–327. https://doi.org/10.1111/gcb.14797

Korner-Nievergelt, F. et al. (2015) ‘blmeco: Data Files and Functions Accompanying the Book “Bayesian Data Analysis in Ecology using R, BUGS and Stan”’. Available at: https://CRAN.R-project.org/package=blmeco (Accessed: 26 March 2024).

Lauder, J.D., Moran, E.V., Hart, S.C., 2019. Fight or flight? Potential tradeoffs between drought defense and reproduction in conifers. Tree Physiology 39, 1071–1085. https://doi.org/10.1093/treephys/tpz031

Lemmer, J., Andrzejak, M., Compagnoni, A., Knight, T.M., Korell, L., 2021. Climate change and grassland management interactively influence the population dynamics of Bromus erectus (Poaceae). Basic and Applied Ecology 56, 226–238. https://doi.org/10.1016/j.baae.2021.06.012

Lenth, R.V., 2022. emmeans: Estimated Marginal Means, aka Least-Squares Means.

Lesica, P., Kittelson, P.M., 2010. Precipitation and temperature are associated with advanced flowering phenology in a semi-arid grassland. Journal of Arid Environments 74, 1013–1017. https://doi.org/10.1016/j.jaridenv.2010.02.002

Lezama, F., Paruelo, J.M., 2016. Disentangling grazing effects: trampling, defoliation and urine deposition. Applied Vegetation Science 19, 557–566. https://doi.org/10.1111/avsc.12250

Liu, Y., Li, G., Wu, X., Niklas, K.J., Yang, Z., Sun, S., 2021. Linkage between species traits and plant phenology in an alpine meadow. Oecologia 195, 409–419. https://doi.org/10.1007/s00442-020-04846-y

Llorens, L., Peñuelas, J., 2005. Experimental Evidence of Future Drier and Warmer Conditions Affecting Flowering of Two Co-occurring Mediterranean Shrubs. International Journal of Plant Sciences 166, 235–245. https://doi.org/10.1086/427480

Memmott, J., Craze, P.G., Waser, N.M., Price, M.V., 2007. Global warming and the disruption of plant–pollinator interactions. Ecology Letters 10, 710–717. https://doi.org/10.1111/j.1461-0248.2007.01061.x

Meng, L. et al. (2021) ‘Photoperiod decelerates the advance of spring phenology of six deciduous tree species under climate warming’, Global Change Biology, 27(12), pp. 2914–2927. Available at: https://doi.org/10.1111/gcb.15575.

Menzel, A., Fabian, P., 1999. Growing season extended in Europe. Nature 397, 659. https://doi.org/10.1038/17709

Menzel, A., Sparks, T.H., Estrella, N., Koch, E., Aasa, A., Ahas, R., Alm-Kübler, K., Bissolli, P., Braslavská, O., Briede, A., Chmielewski, F.M., Crepinsek, Z., Curnel, Y., Dahl, Å., Defila, C., Donnelly, A., Filella, Y., Jatczak, K., Måge, F., Mestre, A., Nordli, Ø., Peñuelas, J., Pirinen, P., Remišová, V., Scheifinger, H., Striz, M., Susnik, A., Van Vliet, A.J.H., Wielgolaski, F.-E., Zach, S., Zust, A., 2006. European phenological response to climate change matches the warming pattern. Global Change Biology 12, 1969–1976. https://doi.org/10.1111/j.1365-2486.2006.01193.x

Miller-Rushing, A.J., Primack, R.B., 2008. Global Warming and Flowering Times in Thoreau’s Concord: A Community Perspective. Ecology 89, 332–341. https://doi.org/10.1890/07-0068.1

Moles, A.T., Warton, D.I., Warman, L., Swenson, N.G., Laffan, S.W., Zanne, A.E., Pitman, A., Hemmings, F.A., Leishman, M.R., 2009. Global patterns in plant height. Journal of Ecology 97, 923–932. https://doi.org/10.1111/j.1365-2745.2009.01526.x

Nordt, B., Hensen, I., Bucher, S.F., Freiberg, M., Primack, R.B., Stevens, A.-D., Bonn, A., Wirth, C., Jakubka, D., Plos, C., Sporbert, M., Römermann, C., 2021. The PhenObs initiative: A standardised protocol for monitoring phenological responses to climate change using herbaceous plant species in botanical gardens. Functional Ecology 35, 821–834. https://doi.org/10.1111/1365-2435.13747

Parmesan, C., 2007. Influences of species, latitudes and methodologies on estimates of phenological response to global warming. Global Change Biology 13, 1860–1872. https://doi.org/10.1111/j.1365-2486.2007.01404.x

Pau, S., Wolkovich, E.M., Cook, B.I., Davies, T.J., Kraft, N.J.B., Bolmgren, K., Betancourt, J.L., Cleland, E.E., 2011. Predicting phenology by integrating ecology, evolution and climate science. Global Change Biology 17, 3633–3643. https://doi.org/10.1111/j.1365-2486.2011.02515.x

Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., Bret-Harte, M.S., Cornwell, W.K., Craine, J.M., Gurvich, D.E., Urcelay, C., Veneklaas, E.J., Reich, P.B., Poorter, L., Wright, I.J., Ray, P., Enrico, L., Pausas, J.G., Vos, A.C. de, Buchmann, N., Funes, G., Quétier, F., Hodgson, J.G., Thompson, K., Morgan, H.D., Steege, H. ter, Sack, L., Blonder, B., Poschlod, P., Vaieretti, M.V., Conti, G., Staver, A.C., Aquino, S., Cornelissen, J.H.C., 2016. Corrigendum to: New handbook for standardised measurement of plant functional traits worldwide. Aust. J. Bot. 64, 715–716. https://doi.org/10.1071/bt12225_co

Piao, S., Liu, Q., Chen, A., Janssens, I.A., Fu, Y., Dai, J., Liu, L., Lian, X., Shen, M., Zhu, X., 2019. Plant phenology and global climate change: Current progresses and challenges. Global Change Biology 25, 1922–1940. https://doi.org/10.1111/gcb.14619

R Core Team (2022) 'R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria', http://www.R-project.org/

Rauschkolb, R., Bucher, S.F., Hensen, I., Ahrends, A., Fernández-Pascual, E., Heubach, K., Jakubka, D., Jiménez-Alfaro, B., König, A., Koubek, T., Kehl, A., Khuroo, A.A., Lindstädter, A., Shafee, F., Mašková, T., Platonova, E., Panico, P., Plos, C., Primack, R., Rosche, C., Shah, M.A., Sporbert, M., Stevens, A.-D., Tarquini, F., Tielbörger, K., Träger, S., Vange, V., Weigelt, P., Bonn, A., Freiberg, M., Knickmann, B., Nordt, B., Wirth, C., Römermann, C. (2024) Spatial variability in herbaceous plant phenology is mostly explained by variability in temperature but also by photoperiod and functional traits. International Journal of Biometeorology. https://doi.org/10.1007/s00484-024-02621-9

Rauschkolb, R., Li, Z., Godefroid, S., Dixon, L., Durka, W., Májeková, M., Bossdorf, O., Ensslin, A., Scheepens, J.F., 2022. Evolution of plant drought strategies and herbivore tolerance after two decades of climate change. New Phytologist 235, 773–785. https://doi.org/10.1111/nph.18125

Reich, P.B., Walters, M.B., Ellsworth, D.S., 1997. From tropics to tundra: Global convergence in plant functioning. Proceedings of the National Academy of Sciences 94, 13730–13734. https://doi.org/10.1073/pnas.94.25.13730

Reisch, C., Poschlod, P., 2011. Morphology and phenology of Scabiosa columbaria from mown and grazed habitats – Results of a simulation experiment. Flora - Morphology, Distribution, Functional Ecology of Plants 206, 887–891. https://doi.org/10.1016/j.flora.2011.05.005

Reisch, C., Poschlod, P., 2009. Land use affects flowering time: seasonal and genetic differentiation in the grassland plant Scabiosa columbaria. Evol Ecol 23, 753–764. https://doi.org/10.1007/s10682-008-9270-4

Römermann, C., Bernhardt-Römermann, M., Kleyer, M., Poschlod, P., 2009. Substitutes for grazing in semi-natural grasslands – do mowing or mulching represent valuable alternatives to maintain vegetation structure? Journal of Vegetation Science 20, 1086–1098. https://doi.org/10.1111/j.1654-1103.2009.01106.x

Root, T.L., Price, J.T., Hall, K.R., Schneider, S.H., Rosenzweig, C., Pounds, J.A., 2003. Fingerprints of global warming on wild animals and plants. Nature 421, 57–60. https://doi.org/10.1038/nature01333

Schädler, M., Buscot, F., Klotz, S., Reitz, T., Durka, W., Bumberger, J., Merbach, I., Michalski, S.G., Kirsch, K., Remmler, P., Schulz, E., Auge, H., 2019. Investigating the consequences of climate change under different land-use regimes: a novel experimental infrastructure. Ecosphere 10, e02635. https://doi.org/10.1002/ecs2.2635

Segrestin, J., Navas, M.-L., Garnier, E., 2020. Reproductive phenology as a dimension of the phenotypic space in 139 plant species from the Mediterranean. New Phytologist 225, 740–753. https://doi.org/10.1111/nph.16165

Sporbert, M., Jakubka, D., Bucher, S.F., Hensen, I., Freiberg, M., Heubach, K., König, A., Nordt, B., Plos, C., Blinova, I., Bonn, A., Knickmann, B., Koubek, T., Linstädter, A., Mašková, T., Primack, R.B., Rosche, C., Shah, M.A., Stevens, A.-D., Tielbörger, K., Träger, S., Wirth, C., Römermann, C., 2022. Functional traits influence patterns in vegetative and reproductive plant phenology – a multi-botanical garden study. New Phytologist 235, 2199–2210. https://doi.org/10.1111/nph.18345

Steyn, H.M., van Rooyen, N., van Rooyen, M.W., Theron, G.K., 1996. The phenology of Namaqualand ephemeral species. The effect of water stress. Journal of Arid Environments 33, 49–62. https://doi.org/10.1006/jare.1996.0045

Sun, S., Frelich, L.E., 2011. Flowering phenology and height growth pattern are associated with maximum plant height, relative growth rate and stem tissue mass density in herbaceous grassland species. Journal of Ecology 99, 991–1000. https://doi.org/10.1111/j.1365-2745.2011.01830.x

Tadey, M., 2020. Reshaping phenology: Grazing has stronger effects than climate on flowering and fruiting phenology in desert plants. Perspectives in Plant Ecology, Evolution and Systematics 42, 125501. https://doi.org/10.1016/j.ppees.2019.125501

Tälle, M., Deák, B., Poschlod, P., Valkó, O., Westerberg, L., Milberg, P., 2016. Grazing vs. mowing: A meta-analysis of biodiversity benefits for grassland management. Agriculture, Ecosystems & Environment 222, 200–212. https://doi.org/10.1016/j.agee.2016.02.008

Van Tienderen, P.H., van der Toorn, J., 1991. Genetic Differentiation Between Populations of Plantago Lanceolata. I. Local Adaptation in Three Contrasting Habitats. Journal of Ecology 79, 27–42. https://doi.org/10.2307/2260782

Visakorpi, K., Block, S., Pellissier, L., Levine, J.M., Alexander, J., 2023. Eco-physiological and morphological traits explain alpine plant species’ response to warming. Functional Ecology 37, 287–301. https://doi.org/10.1111/1365-2435.14228

Völler, E., Auge, H., Bossdorf, O., Prati, D., 2013. Land use causes genetic differentiation of life-history traits in Bromus hordeaceus. Global Change Biology 19, 892–899. https://doi.org/10.1111/gcb.12087

Völler, E., Bossdorf, O., Prati, D., Auge, H., 2017. Evolutionary responses to land use in eight common grassland plants. Journal of Ecology 105, 1290–1297. https://doi.org/10.1111/1365-2745.12746

Wilson, J.B., Peet, R.K., Dengler, J., Pärtel, M., 2012. Plant species richness: the world records. Journal of Vegetation Science 23, 796–802. https://doi.org/10.1111/j.1654-1103.2012.01400.x

Wolkovich, E.M., Cleland, E.E., 2011. The phenology of plant invasions: a community ecology perspective. Frontiers in Ecology and the Environment 9, 287–294. https://doi.org/10.1890/100033

Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J.H.C., Diemer, M., Flexas, J., Garnier, E., Groom, P.K., Gulias, J., Hikosaka, K., Lamont, B.B., Lee, T., Lee, W., Lusk, C., Midgley, J.J., Navas, M.-L., Niinemets, Ü., Oleksyn, J., Osada, N., Poorter, H., Poot, P., Prior, L., Pyankov, V.I., Roumet, C., Thomas, S.C., Tjoelker, M.G., Veneklaas, E.J., Villar, R., 2004. The worldwide leaf economics spectrum. Nature 428, 821–827. https://doi.org/10.1038/nature02403

Zhang, B., Hautier, Y., Tan, X., You, C., Cadotte, M.W., Chu, C., Jiang, L., Sui, X., Ren, T., Han, X., Chen, S., 2020. Species responses to changing precipitation depend on trait plasticity rather than trait means and intraspecific variation. Functional Ecology 34, 2622–2633. https://doi.org/10.1111/1365-2435.13675

Zhang, X. et al. (2023) ‘Resource-acquisitive species have greater plasticity in leaf functional traits than resource-conservative species in response to nitrogen addition in subtropical China’, Science of The Total Environment, 903, p. 166177. Available at: https://doi.org/10.1016/j.scitotenv.2023.166177.

Zhu, J., Zhang, Y., Liu, Y., 2016. Effects of short-term grazing exclusion on plant phenology and reproductive succession in a Tibetan alpine meadow. Sci Rep 6, 27781. https://doi.org/10.1038/srep27781

Zopfi, H.-J., 1993. Ecotypic variation in Rhinanthus alectorolophus (Scopoli) Pollich (Scrophulariaceae) in relation to grassland management: I. Morphological delimitations and habitats of seasonal ecotypes. Flora 188, 15–39. https://doi.org/10.1016/S0367-2530(17)32244-2

Supplementary Material (S III)

Title: Plant species phenology differs between climate and land-use scenarios and relates to plant-functional traits

Authors: Carolin Plos, Isabell Hensen, Lotte Korell, Harald Auge, Christine Römermann

Journal: *Ecology and Evolution*

Appendix S III.1 – Figures

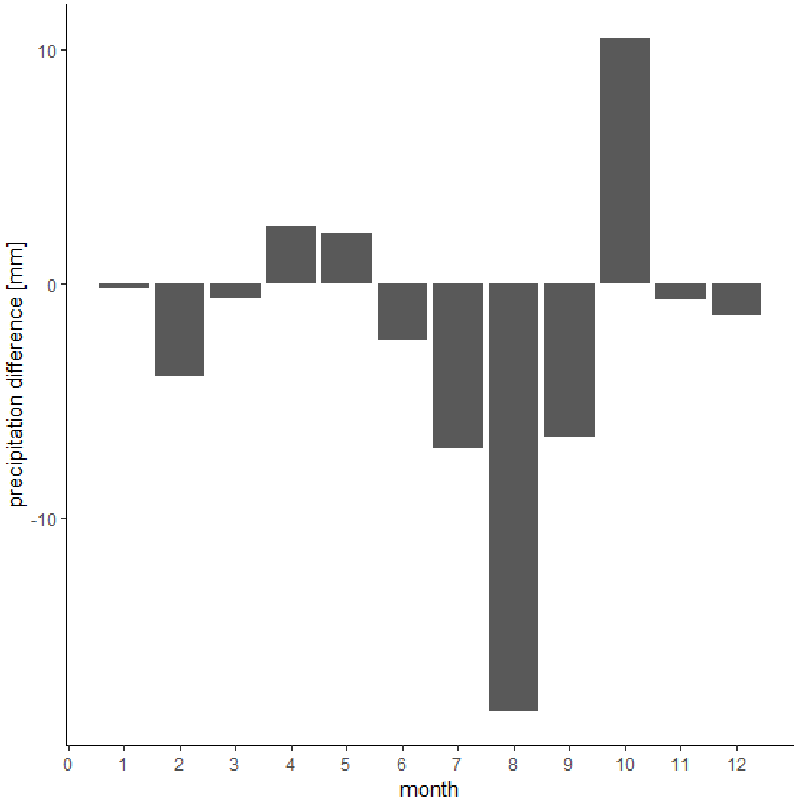


Figure S III.1: Realized precipitation difference in mm of future plots compared to ambient plots, summarized for each month across the study year 2020.

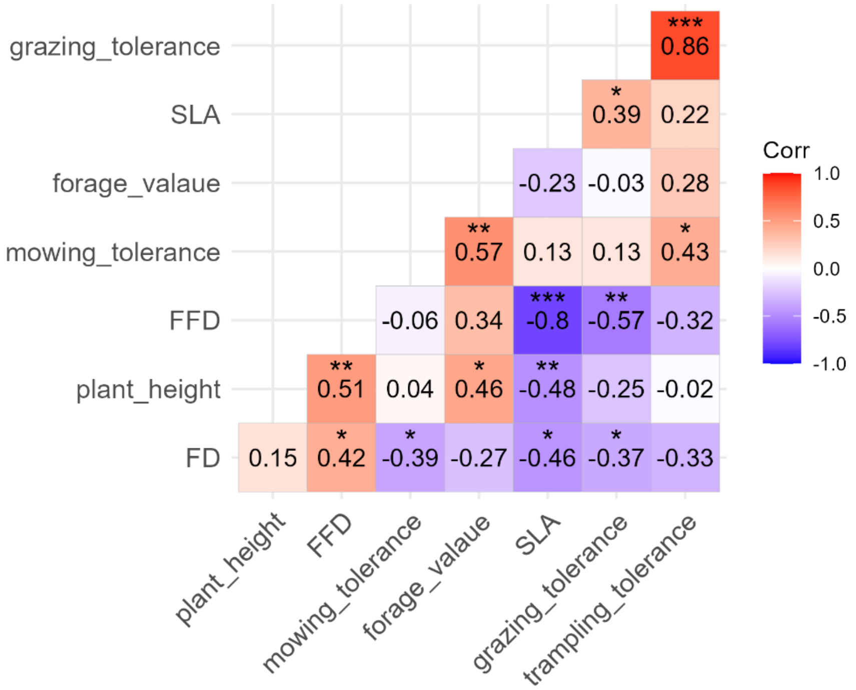
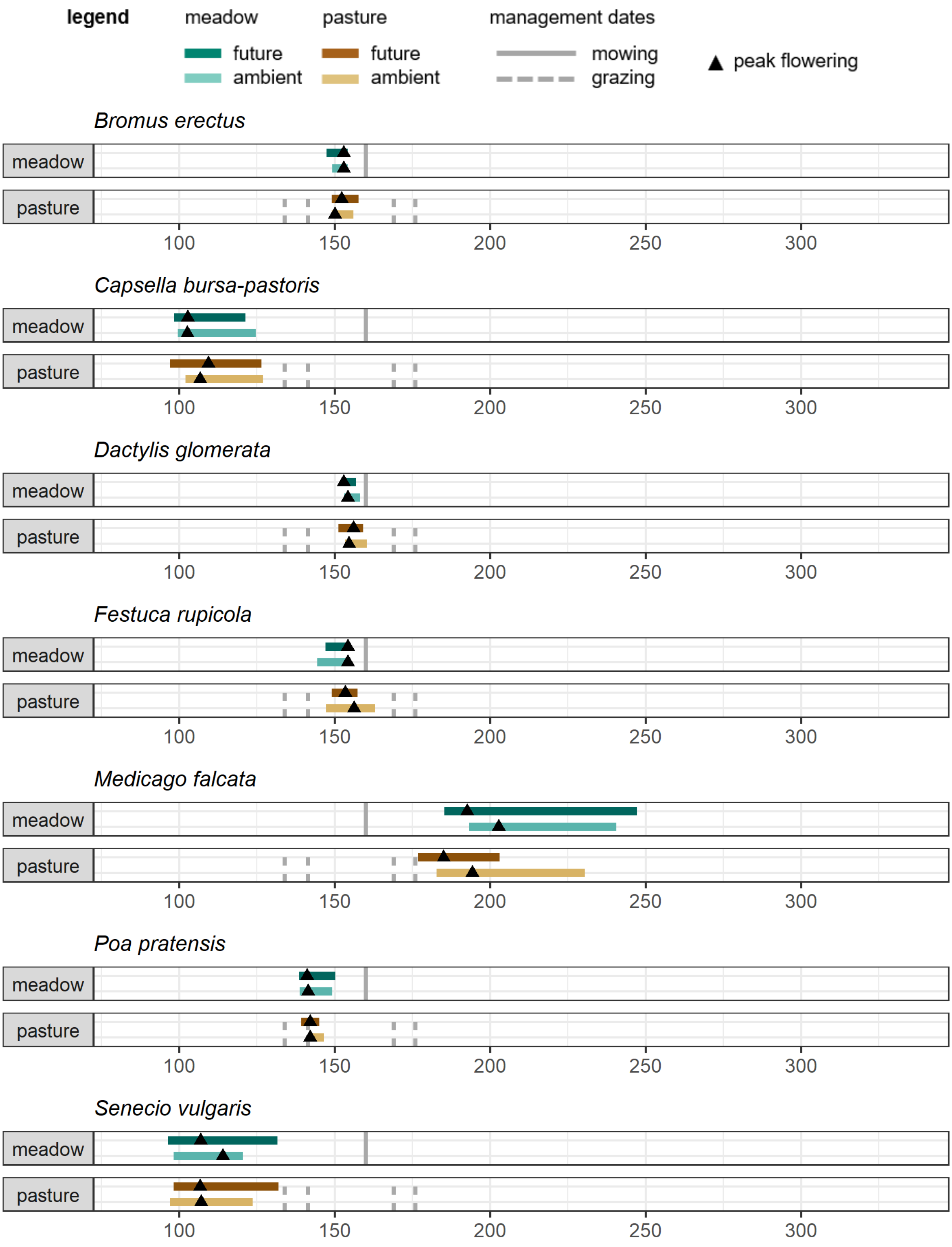
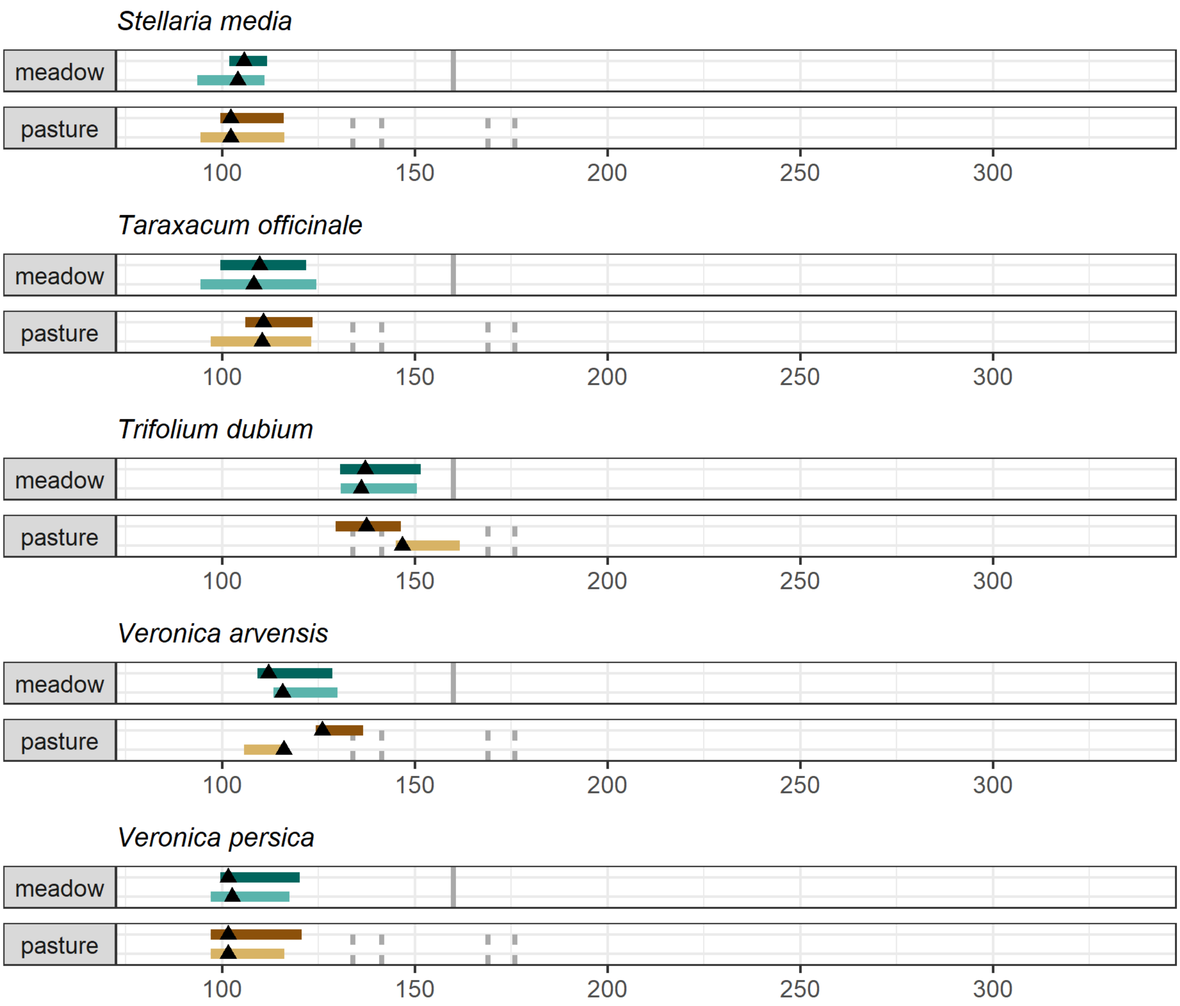


Figure S III.2: Correlation matrix of functional traits, based on Pearson correlations, including the correlation coefficients (*r*) and significance levels (* p < 0.05, ** p < 0.01, *** p < 0.001) of all pairwise combinations of functional traits. Abbreviations: SLA – specific leaf area, FFD – timing of phenological niche measured as first flowering day, FD – length of phenological niche measured as flowering duration in days.

Figure S III.3: Flowering times and timing of land management (mowing or grazing) across all treatments. Strips summarize the mean FFD, LFD and day of peak flowering per treatment, the x-axis shows day of the year (doy). Please note that five species (*A. millefolium, D. carthusianorum, G. album, G. verum, S. ochroleuca*) are already presented in Figure III.1 in the main text and are thus not presented here.




Stellaria media
meadow
pasture
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Taraxacum officinale
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Trifolium dubium
meadow
pasture
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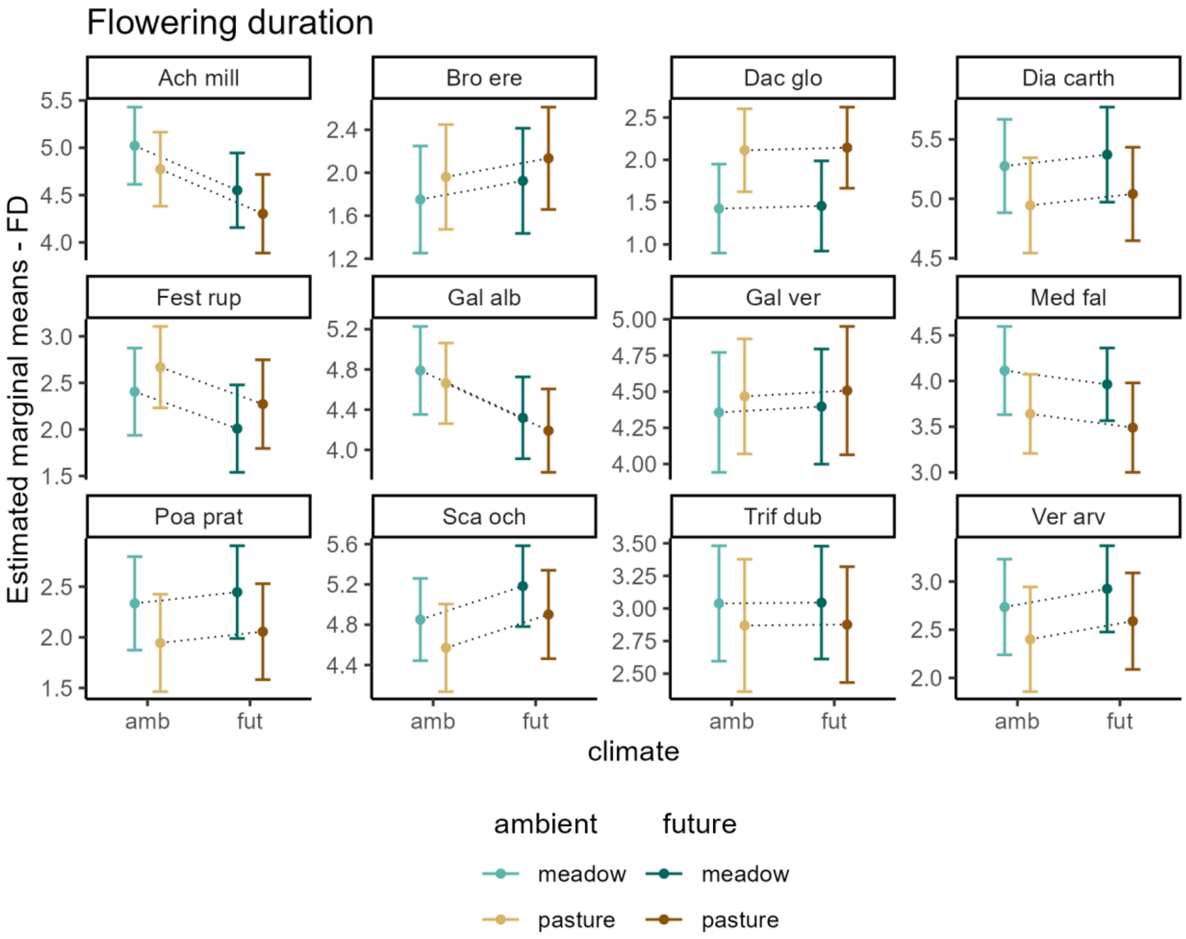

Figure S III.4: Effects of climate and land-use on the flowering duration. Shown are estimated marginal means of peak flowering with the 95% confidence intervals, revealed from the generalized linear mixed model. Results compare the flowering duration between ambient and future climate on meadows and pastures for each species. Letters indicate significant differences between treatments. If no letters are shown, no significant difference between treatment groups was found. Dotted lines are only shown for better interpretation of interactive effects of climate and land-use.

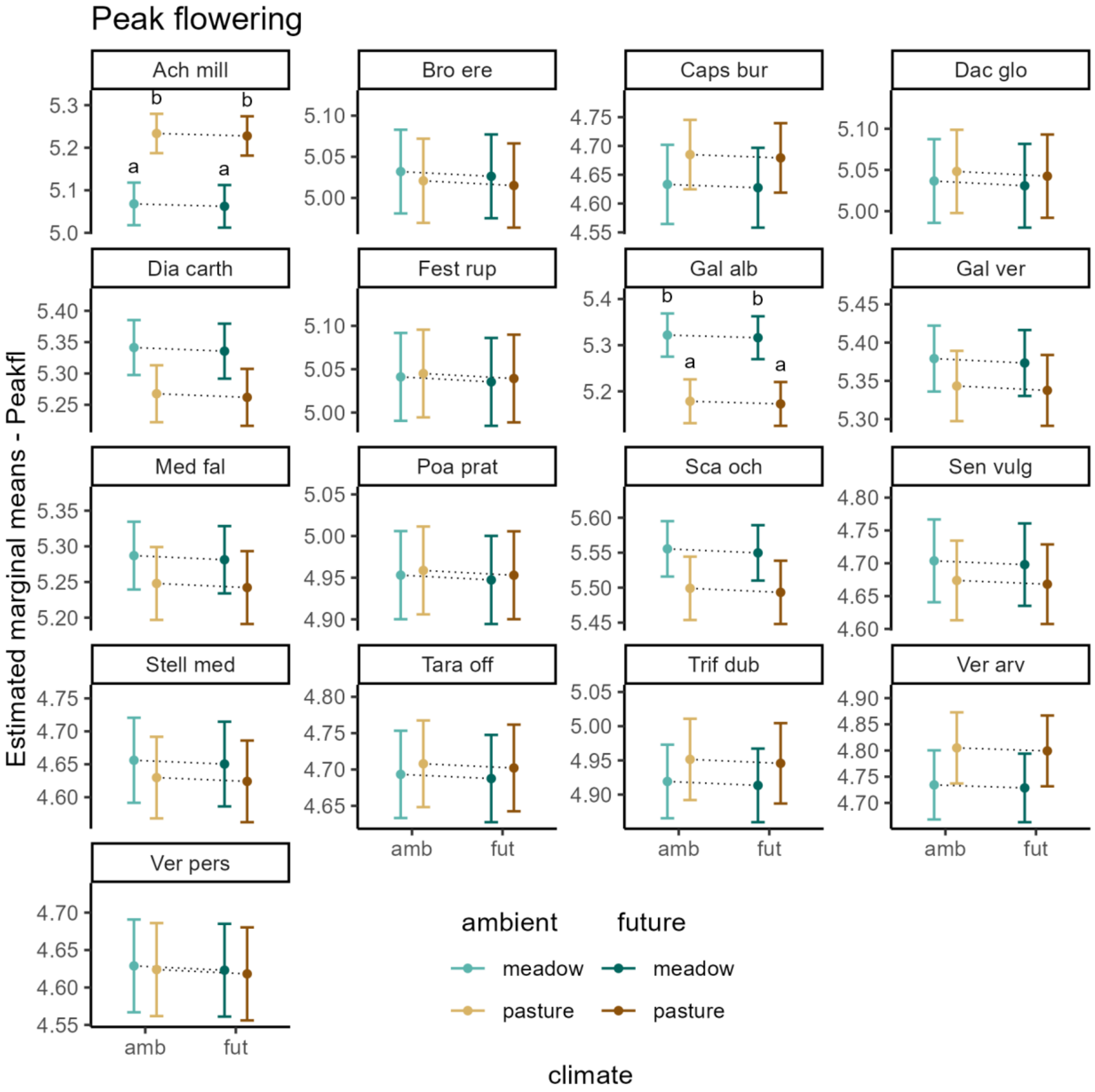

Figure S III.5: Effects of climate and land-use on the day of peak flowering. Shown are estimated marginal means of peak flowering with the 95% confidence intervals, revealed from the generalized linear mixed model. Results compare the day of peak flowering between ambient and future climate on meadows and pastures for each species. Letters indicate significant differences between treatments. If no letters are shown, no significant difference between treatment groups was found. Dotted lines are only shown for better interpretation of interactive effects of climate and land-use.

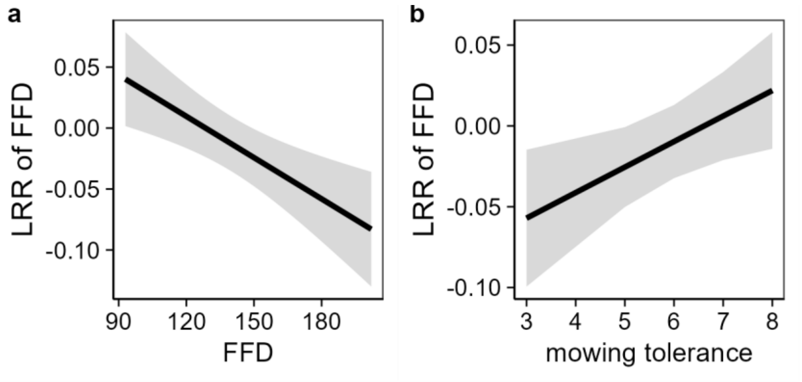

Figure S III.6: Relationships between traits and the shift in first flowering day due to future climate (Log response ratio, LRR), as predicted by the linear model. See also Table III.3 for model results. Traits are: mean first flowering day (from ambient plots) (FFD) and mowing tolerance derived from BiolFlor.

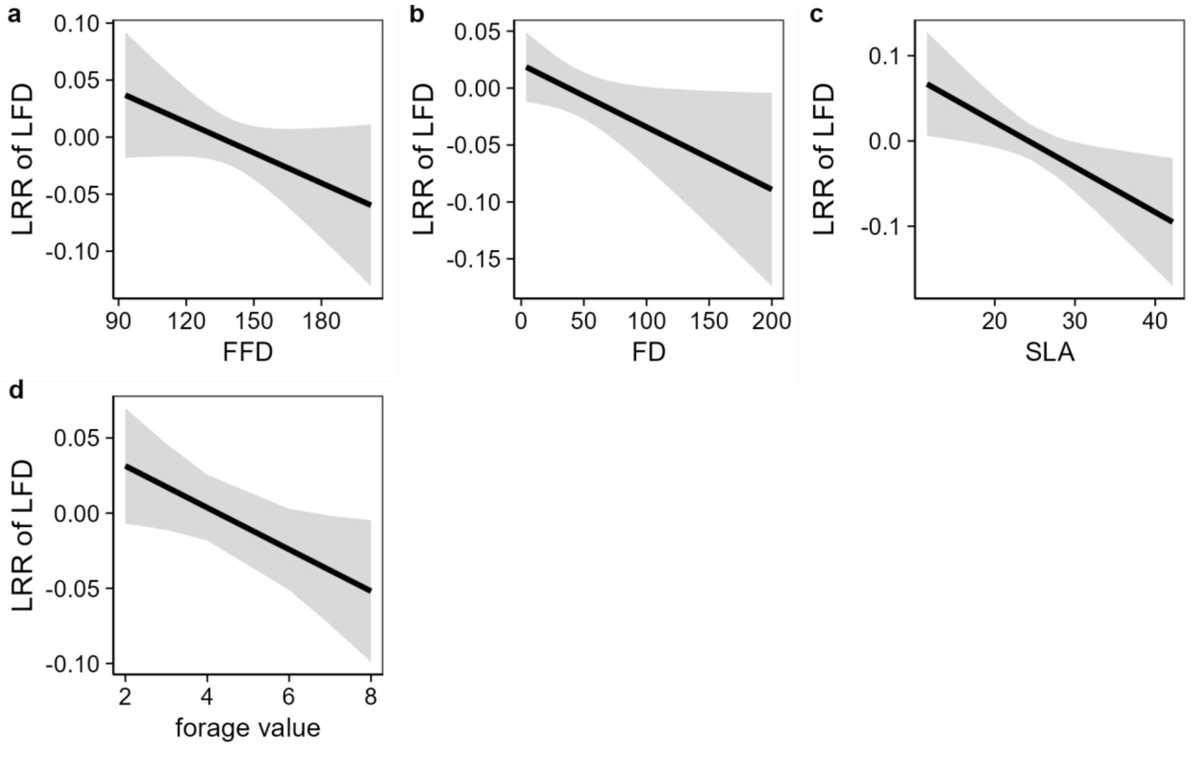

Figure S III.7: Relationships between traits and the shift in last flowering day (LFD) due to future climate (Log response ratio, LRR), as predicted by the linear model. See also Table III.3 for model results. Traits are: mean first flowering day (from ambient plots) (FFD), mean flowering duration in days (from ambient plots) (FD), mean SLA derived from TRY (SLA) and forage value derived from BiolFlor.

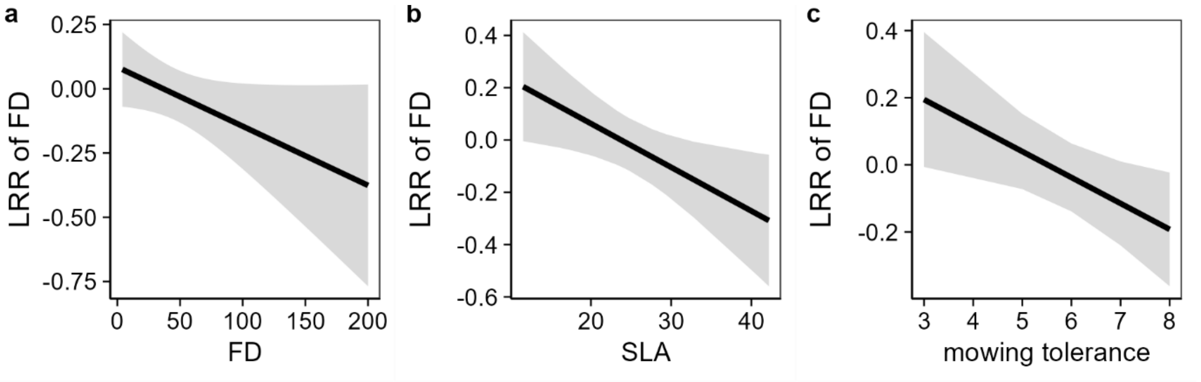

Figure S III.8: Relationships between traits and the shift in flowering duration (FD) due to future climate (Log response ratio, LRR), as predicted by the linear model. See also Table III.3 for model results. Traits are: mean flowering duration in days (from ambient plots) (FD), mean SLA derived from TRY (SLA) and mowing tolerance derived from BiolFlor.

The coverage of open soil (%) and litter (%) was estimated weekly for each permanent plot (3m x 3m), across the monitoring season of 2020. Different proportions of litter cover and open soil were observed across land-use types and climate treatments, with pastures generally having larger proportions of open soil that remarkably increased under future climate conditions after the second grazing event in summer while on meadows the proportion of open soil was generally smaller and tended to decrease under future climate (Figure S III.9). In contrast, litter cover on meadows tended to increase more strongly under future climate than observed for pastures (Figure S III.10), although the patterns were more comparable between the land-use types.

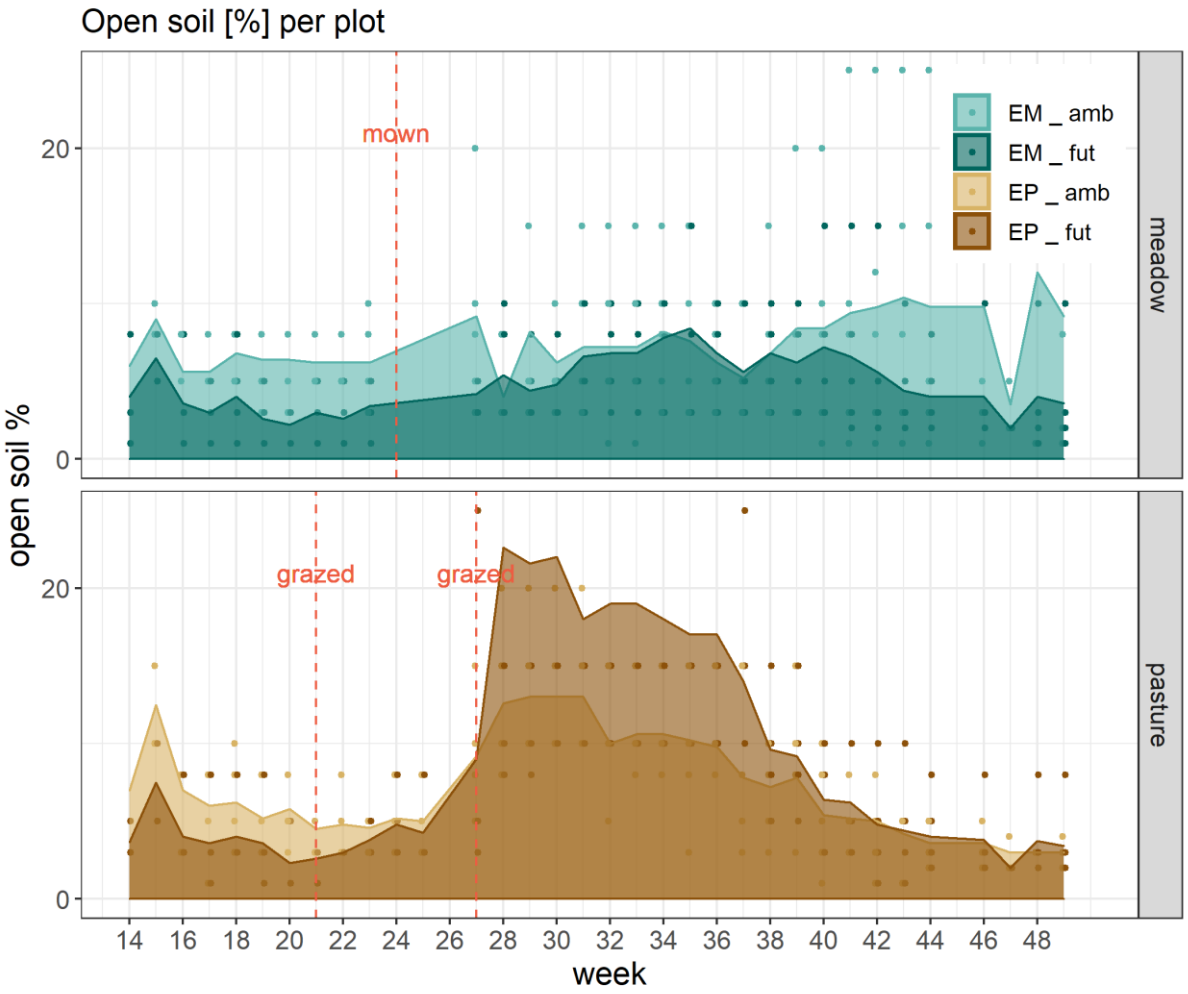

Figure S III.9: Percentage open soil cover per plot and timing of land management throughout the monitoring season in 2020 compared between meadows (EM) and pastures (EP) under ambient and future climate. Dots indicate the weekly open soil cover per plot, the ribbons indicate the mean weekly open soil cover across plots of the same treatment. Dashed vertical lines indicate the timing of the land use events (i.e. mowing or grazing). First grazing occurred in week 21 and 22 respectively, and second grazing in week 27 and 28 respectively, as every plot (n = 10) was grazed for 24 hours.

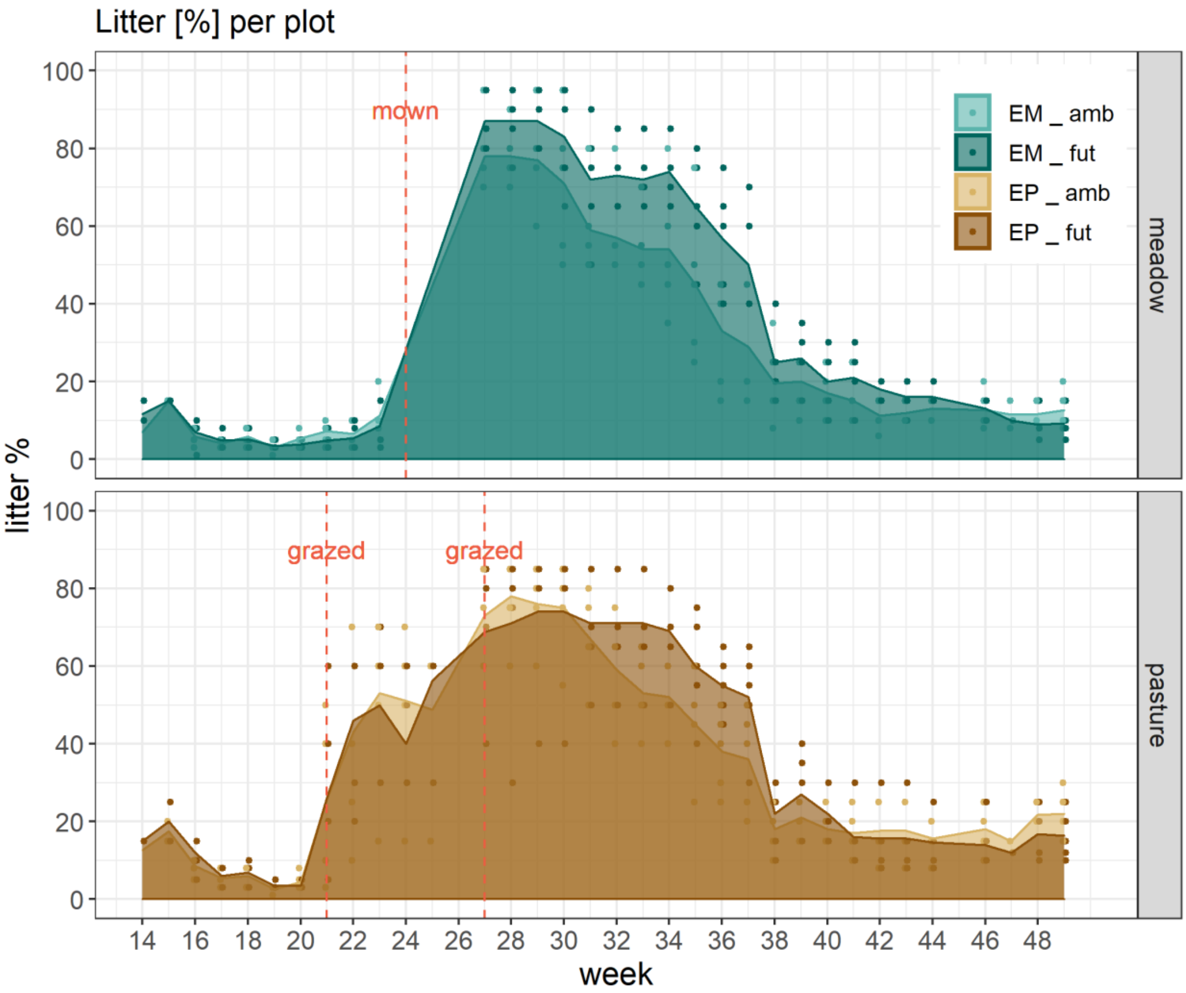

Figure S III.10: Percentage litter cover per plot and timing of land management throughout the monitoring season compared between meadows (EM) and pastures (EP) under ambient and future climate. Dots indicate the weekly litter cover per plot, the ribbons indicate the mean weekly litter cover. Dashed vertical lines indicate the timing of the land use events (i.e. mowing or grazing). First grazing stretched through week 21 and 22 respectively, and second grazing through week 27 and 28 respectively, as every plot (n = 10) was grazed for 24 hours.

Temperature and soil moisture were measured daily within each plot. Details on temperature and soil moisture measurements can be found in Schädler et al. (2019) and in Appendix S5 of the respective publication. Figure S III.11 shows that especially in the summer months the daily minimum temperature was higher under future climate regardless of land-use (a), while daily maximum temperature was generally higher in pastures (b), overall increasing mean daily temperatures on future pastures (c). Soil moisture was lower under future climate and lowest on future pastures with this effect increasing with soil depth (Figure S III.12).

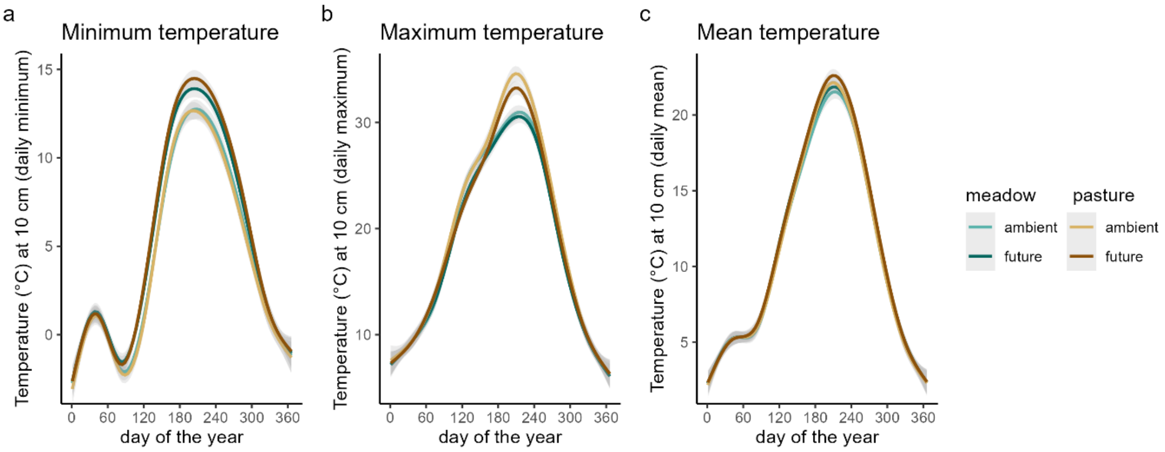

Figure S III.11: Daily temperatures a) minimum, b) maximum, c) mean, measured 10 cm above the ground across all meadow and pasture plots under ambient and future climate for 2020.

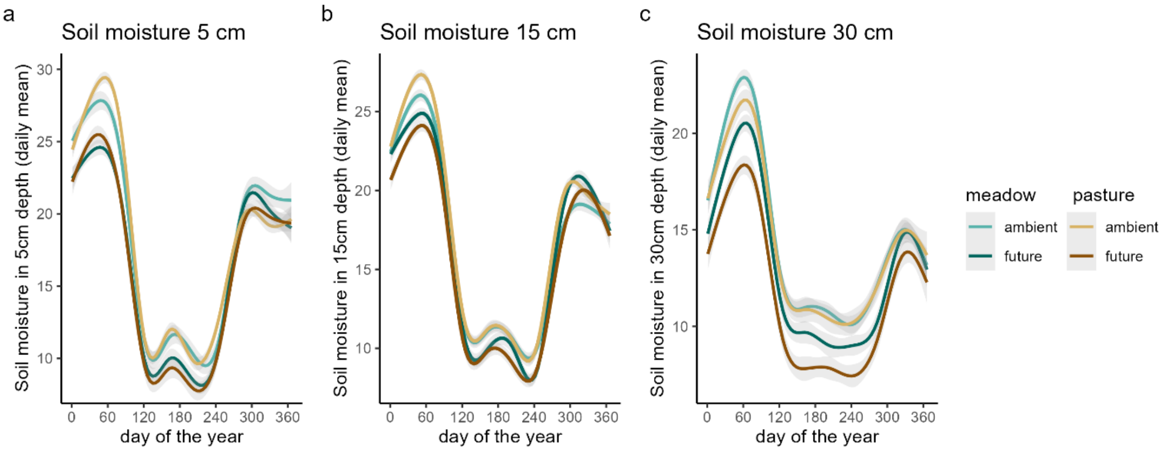

Figure S III.12: Mean daily soil moisture measured in a) 5 cm, b) 15 cm and c) 30 cm depth across all meadow and pasture plots under ambient and future climate for 2020.

Appendix S III.2 – Tables

Table S III.1: Model selection table explaining shifts in first flowering day (FFD shift) to future climate by functional traits, grassland indicator values and land-use type. The table shows the best models according to AICc with a deltaAIC < 2 derived by the *dredge* function (*MuMIn* package, Bartoń, 2023). Numbers (i.e. estimates) indicate traits that were included in the final models. Empty cells refer to traits that were excluded from the models.

Intercept	land use	forage value	FD	FFD	height	SLA	mowing tolerance	trampling tolerance	df	logLik	AICc	delta	weight
-0.012				-0.038			0.028		4	43.41	-77.2	0	0.234
-0.012				-0.044			0.036	-0.020	5	44.79	-77.1	0.13	0.218
-0.012				-0.053	0.014		0.036	-0.022	6	45.55	-75.4	1.78	0.096

Table S III.2: Model selection table explaining shifts in last flowering day (LFD shift) to future climate by testing functional traits, grassland indicator values and land-use type. The table shows the best models according to AICc with a deltaAIC < 2 derived by the *dredge* function (*MuMIn* package, Bartoń, 2023). Numbers (i.e. estimates) indicate traits that were included in the final models. Empty cells refer to traits that were excluded from the models.

Intercept	land use	forage value	FD	FFD	height	SLA	mowing tolerance	land use : FFD	land use : SLA	df	logLik	AICc	delta	weight
-0.005		-0.028	-0.027	-0.030		-0.045				6	47.41	-79.2	0	0.096
-0.005		-0.035	-0.032			-0.024				5	45.83	-79.2	0.02	0.095
0.004	+			0.001	-0.021	-0.017		+	+	8	50.85	-78.8	0.34	0.081
-0.005				-0.039	-0.021	-0.043				5	45.49	-78.5	0.7	0.068
0.004	+			-0.005		-0.012		+	+	7	48.73	-78.4	0.8	0.064
-0.005				-0.04699		-0.0392				4	43.90	-78.2	0.97	0.059
-0.005		-0.028	-0.031		-0.018	-0.031				6	46.92	-78.2	1	0.058
-0.005		-0.026	-0.019							4	43.86	-78.1	1.05	0.057
0.005	+	-0.027	-0.026	-0.013		-0.046		+		8	50.37	-77.9	1.3	0.05
-0.005		-0.021								3	42.36	-77.8	1.38	0.048
0.003	+			-0.021	-0.021	-0.046		+		7	48.39	-77.7	1.49	0.046
-0.005					-0.020					3	42.29	-77.7	1.53	0.045
-0.005		-0.022	-0.026	-0.028	-0.015	-0.049				7	48.30	-77.5	1.66	0.042
-0.005			-0.016	-0.036	-0.023	-0.049				6	46.54	-77.4	1.74	0.04
-0.005		-0.016		-0.040		-0.037				5	44.95	-77.4	1.77	0.04
0.003	+			-0.028		-0.041		+		6	46.51	-77.4	1.82	0.039
0.004	+	-0.015		0.0003		-0.011		+	+	8	50.03	-77.2	1.97	0.036

Table S III.3: Model selection table explaining shifts in flowering duration (FD shift) to future climate by testing functional traits, grassland indicator values and land-use type. The table shows the best models according to AICc with a deltaAIC < 2 derived by the *dredge* function (*MuMIn* package, Bartoń, 2023). Numbers (i.e. estimates) indicate traits that were included in the final models. Empty cells refer to traits that were excluded from the models.

Intercept	land use	forage value	FD	FFD	SLA	mowing tolerance	trampling tolerance	df	logLik	AICc	delta	weight
-0.022			-0.115		-0.142	-0.138		5	-0.82	14.1	0	0.203
-0.022			-0.105		-0.151	-0.165	0.076	6	0.25	15.1	0.99	0.124
-0.022					-0.095	-0.099		4	-2.80	15.2	1.07	0.119
-0.022			-0.104	-0.1072	-0.225	-0.129		6	0.13	15.4	1.24	0.109
-0.022					-0.109	-0.135	0.088	5	-1.48	15.5	1.32	0.105
-0.022				-0.1281	-0.197	-0.093		5	-1.57	15.6	1.5	0.096
-0.022						-0.112		3	-4.51	16	1.81	0.082
0.029	+		-0.119		-0.144	-0.139		6	-0.17	16	1.84	0.081
-0.022		-0.125	-0.116		-0.190			5	-1.75	16	1.85	0.08

Table S III.4: Model selection table explaining shifts in peak flowering (Peakfl shift) to future climate by testing functional traits, grassland indicator values and land-use type. The table shows the best models according to AICc with a deltaAIC < 2 derived by the *dredge* function (*MuMIn* package, Bartoń, 2023). Numbers (i.e. estimates) indicate traits that were included in the final models. Empty cells refer to traits that were excluded from the models.

Intercept	land use	forage value	FD	FFD	height	SLA	mowing tolerance	trampling tolerance	df	logLik	AICc	delta	weight
-0.002									2	49.13	-93.8	0	0.232
-0.011	+								3	49.69	-92.5	1.35	0.118
-0.002								0.008	3	49.65	-92.4	1.44	0.113
-0.002		-0.008							3	49.59	-92.3	1.55	0.107

Chapter IV

Abiotic conditions affect nectar properties and flower visitation in four herbaceous plant species

This chapter is published in *Flora* as

Plos, C., Stelbrink, N., Römermann, C., Knight, T.M., Hensen, I., 2023. Abiotic conditions affect nectar properties and flower visitation in four herbaceous plant species. Flora 303, 152279. https://doi.org/10.1016/j.flora.2023.152279

Abstract

Both plant nectar production and insect activity are highly dependent on abiotic environmental conditions. Furthermore, the foraging behaviour of insect pollinators can be affected by nectar properties. In the context of climate change, it is important to understand how plant-pollinator interactions respond to temperature and other abiotic factors. We investigated the effect of natural variation in temperature and solar radiation on nectar quantity (nectar volume) and quality (sucrose concentration and sucrose mass) and on flower visitation rates in four herbaceous plant species (*Dictamnus albus, Lamium album, Salvia officinalis, Vincetoxicum hirundinaria*) in the Botanical Garden Halle (Germany). Temperature affected nectar properties in all four species. Solar radiation affected nectar quantity and quality in two species, most likely by affecting flower temperature. The number of flower visits was unimodally related to temperature for two species and positively related to solar radiation in another. The variable responses across plant species in the effects of abiotic factors on nectar properties and flower visitation patterns may be due to differences in flower shape and colour, to differences in the composition of flower visitors, or due to other unmeasured extrinsic factors that vary across patches where these species occur. Our study highlights the importance of considering direct and indirect effects of climate factors on pollinator visitation in multiple plant species.

Keywords: Botanical garden, environmental factors, flower traits, nectar volume, pollinators, sucrose concentration

Introduction

Pollination is among the most important ecosystem services for both natural and agricultural systems (Klein et al., 2007), as the majority of plant species require animal visitation in order to successfully reproduce (Ollerton et al., 2011; Rodger et al., 2021). Climate change has the potential to significantly threaten this critical interaction (González-Varo et al., 2013). Climate can directly affect insect flower visitors because insects have species-specific temperature optima for foraging (Corbet et al., 1993; Stone and Willmer, 1989; Zoller et al., 2020), and indirectly influence flower visitors by altering the rewards (e.g., nectar volume and sucrose amount) that plants offer (Descamps et al., 2018). To develop a general understanding of how climate change may alter pollination, it is important to understand how each of these components will change in response to abiotic factors such as temperature and solar radiation (Maron et al., 2014), as these factors are likely to be affected by climate change (Rapp, 2014).

For a given community of potential flower visitors, the visitation rate and composition of visitor communities to flowering plants depends on the characteristics of the plant species. Plant species differ in their floral traits, such as the size, shape and colour of the corolla, scent and nectar composition, which are associated with their pollination syndrome (Faegri and Pijl, 1979; Rosas - Guerrero et al., 2014). These traits might differ significantly across even closely related plants (e.g. Basnett et al., 2021; Comba, 1999; Mačukanović-Jocić et al., 2011). For example, *Salvia officinalis* L. and *Lamium album* L. are both plant species in the Lamiaceae family that attract bees with their bilabiate corollas and nectar rewards. However, only bees with a long proboscis are able to reach the nectar of *Lamium album* (Lye et al., 2009), whereas the nectar of *Salvia officinalis* is accessible to both long-tongued and short-tongued bees (Comba, 1999; Inouye, 1980; Mačukanović-Jocić et al., 2011).

Flower visitation rates are often mediated by rewards offered by the plant, which might also be affected by abiotic factors. Floral resources that plants produce, such as nectar, are directly affected by abiotic factors, such as temperature and solar radiation (Petanidou and Smets, 1996; Silva et al., 2004; Takkis et al., 2018). Nectar production measured at a certain site has been shown to be low at both low and high temperatures and to peak at intermediate temperatures forming a unimodal relationship with temperature (Petanidou, 2007; Takkis et al., 2018), and sugar concentration of nectar increases with temperature due to higher evapotranspiration (Corbet, 1990). Rapid evaporation due to high temperatures though might lead to nectar concentrations that are higher than those preferred by pollinators (Corbet, 1990), increasing the risk of plant-pollinator mismatches at high temperatures (Gérard et al., 2020). Solar radiation mediates photosynthetic activity of plants, which is associated with increasing nectar volume and sugar concentrations (Boose, 1997; Cawoy et al., 2008; Southwick, 1984). Furthermore, solar radiation can affect flower temperature more than ambient temperature itself and thus might also play an important role in influencing nectar properties in that way (Petanidou and Smets, 1996). Animal pollinators are known to adapt their foraging behaviour in response to the quantity and quality of floral rewards (Abrol, 2006; Fowler et al., 2016; Thomson, 1988; Waddington et al., 1981) and thus we would expect associations between nectar quantity and quality and flower visitation. In this way abiotic factors can have indirect effects on flower visitation rates.

Abiotic factors can also have a direct influence on pollinator activity and thus on potential flower visitation (direct effects). Temperature influences the activity patterns of insect pollinators due to species-specific thermal tolerances (Corbet, 1990; Corbet et al., 1993; Kühsel and Blüthgen, 2015; Stone and Willmer, 1989) and desiccation tolerances (Burdine and McCluney, 2019). Most insect pollinators are not active below a certain temperature and reduce their activity again when temperatures are too high, forming a unimodal relationship (Corbet et al., 1993; Kühsel and Blüthgen, 2015). Fewer studies investigated the effect of solar radiation on pollinator behaviour (e.g. Arnold and Chittka, 2012, focusing on artificial light;

Kilkenny and Galloway, 2008, using a field study), but those that have typically observed reduced visitation of plants shaded compared to those that are sun-exposed.

The current state of our knowledge on the direct and indirect effects of abiotic factors on the visitation rate of pollinators is typically limited to studies focused on single plant species or crop plants (e.g., Abrol, 2010; Boose, 1997; Carroll et al., 2001; del Rio and Burquez, 1986; Silva et al., 2004), a single pollinator group or species (e.g., Corbet et al., 1993; Descamps et al., 2021; Kovac and Stabentheiner, 2011; Vicens and Bosch, 2000), and/or a single abiotic factor (e.g., Boose, 1997; Huber, 1956; Petanidou and Smets, 1996) or considering only plant or insect responses (e.g., Boose, 1997; Carroll et al., 2001; Vicens and Bosch, 2000). This is likely because collecting data on pollinator observations and nectar properties across abiotic environments is time consuming. However, examining responses across many plant species, pollinator groups and abiotic factors is critical to disentangle these complex interactions and relationships and for developing a general understanding of the patterns and their context dependence. Thus, this study goes one step further compared to existing studies by collecting a comprehensive dataset on (a) temperature and solar radiation, (b) flower visitations, (c) nectar quantity and quality, all measured simultaneously on four selected plant species growing under comparable soil, light, and climatic conditions in a botanical garden. While plants occur in different patches in the garden that might differ in external conditions, the otherwise similar conditions of the larger garden setting allow us to cautiously discuss differences across the investigated plant species in their responses of nectar properties or flower visitation associated to variation in abiotic conditions.

Based on the literature discussed above, we set up the following hypotheses: 1) The nectar quantity (i.e. nectar volume) of our study plants responds to temperature in a unimodal way and is positively related to solar radiation. The nectar quality (i.e. sucrose concentration and sucrose mass) is positively related to temperature and solar radiation. 2) Flower visitation rates are related to temperature in a unimodal way and are positively related to solar radiation. 3) Flower visitation rates are influenced by nectar quantity and quality. With this approach we aim to better understand the direct and indirect (i.e., through changing nectar properties) effects of abiotic drivers on pollinator visitation. This study is a basis for a better understanding on how plant-pollinator interactions might be affected by changes in climate and which role flower traits and pollinator composition might play in shaping these biotic interactions.

Materials and Methods

Study site

The study was conducted in the Botanical Garden Halle (Saale) in Germany. In the study year (2020), the mean annual temperature of Halle (Saale) was 12 °C with a total annual precipitation of 401 mm (Deutscher Wetterdienst (DWD) Climate Data Center (CDC), 2021). All observations and measurements were conducted between mid-May and end of June, covering the main flowering period of the study species. Precipitation in the study months was 40 mm in May and 26 mm in June (Deutscher Wetterdienst (DWD) Climate Data Center (CDC), 2021). Thus, plants required additional irrigation that was applied consistently to all four species when required. Plants were growing in distinct monospecific patches of approximately 1 m². All four observed plant species grew closely together in the systematic part of the botanical garden (see also Figure S IV.1), where plants grow in an open and plane area and in the same soil substrate (chernozem) with even soil depth (>100cm). The distance between two patches ranged from ~10 to ~25 m. Thus, plants occurred in a similar background of abiotic conditions regarding climate, soil, exposure to wind and of other flowering plant species and had access to the same community of animal pollinators.

Study species

Four plant species were investigated: *Dictamnus albus* L., *Lamium album* L., *Salvia officinalis* L., *Vincetoxicum hirundinaria* MEDIK. (for more species information, see Table IV.1). The species were chosen as they all provide measurable amounts of nectar, had enough flowers to conduct a study with repeated nectar measurements and had overlapping flowering periods.

Abiotic factors

Our study considers the effects of natural variation in abiotic factors on our response variables rather than experimental manipulation of these factors. Considering natural variation has the advantage that animal pollinator responses, which will occur at larger spatial grains than most experiments can consider, will be influenced by this same natural variation in temperature and solar radiation. However, this method has the disadvantage that unmeasured factors might covary with our focal abiotic factors, and thus our inference is more limited. Temperature was measured with HOBO Loggers (Onset, HOBO Pro v2 (U23-001)) at 30 cm height every 10 minutes. Loggers were equipped with sun shields and were placed directly next to the plants during flower visitor observations to measure the local microclimate experienced by the plant. Photosynthetic active radiation (PAR) was used as a measure of solar radiation intensity and was measured after every flower visitor observation interval approximately 1.5 m above the ground with a photometer in µmol/m²s (HD2102.2, DeltaOhm). For an overview of the microsite conditions (Temperature and PAR) measured at the four observed plant species see Figure S IV.2 in the supplements).

Table IV.1: Overview of the studied plant species and their characteristics as derived from [1] the BiolFlor Database (Klotz et al., 2002), [2] FloraWeb (BfN, 2011), [3] PhenObs Data (Sporbert et al., 2022) and [4] own measurements (see Methods section).

	Lamium album L.	*Dictamnus albus* L.	*Salvia officinalis* L.	*Vincetoxicum hirundinaria* Medik.
Family	Lamiaceae	Rutaceae	Lamiaceae	Apocynaceae
Flower shape [1]	true lip flowers, hymenoptere flower	hymenoptere flowers, lip flowers (Verbascum type)	true lip flowers, hymenoptere flowers	clamp trap flowers
Flower colour	white	pink	purple	yellowish white
Flowering time [1]	April - October	May - June	May - July	May - August
Flowering time 2020 [3]	07.04.-29.09.20 (peak flowering until 12.05.20)	25.05.-10.06.20	12.05.-28.07.20 (peak flowering until 24.06.20)	20.05.-16.09.20 (first peak until 24.06.20)
Main pollinators [1]	hymenoptera	hymenoptera	hymenoptera	diptera, hymenoptera
Habitat [2]	nutrient rich, ruderal	dry and warm	dry and warm, calcareous soils	dry and warm
Native Range [1]	Europe to Asia	Europe to Asia	Europe	Europe to western Asia
Temperature during observations [4] min T max T mean T	 13.16 °C 31.50 °C 20.82 °C	 12.94 °C 31.07 °C 20.70 °C	 12.44 °C 29.46 °C 21.16 °C	 12.79 °C 28.67 °C 21.20 °C

Nectar measurements and flower availability

To measure nectar properties, we sampled nectar three times a day in the morning between 9 am and 10 am, at midday between 12 am and 1 pm and in the afternoon between 3 pm and 4 pm on 13-18 days per plant species. To avoid nectar consumption by flower visitors prior to sampling, at least five flowers per population were covered with fine mesh bags for at least one hour (Corbet, 2003). After conducting flower visitor observations on all four study plants, nectar samples were taken with 1 µl micro capillaries (minicaps®, Hirschmann®) from five of the bagged flowers. All nectar was taken from each sampled flower. Care was taken not to sample the same flower multiple times to avoid errors due to possibly damaged flowers. The nectar volume in the capillary was measured with a ruler in mm and then calculated to µl. Nectar samples were placed in 2 ml Eppendorf tubes and were stored at -20°C until further analysis. In case of starting rain (which occurred on five sampling days), nectar measurements were stopped for that day as nectar can be diluted by rain (Corbet and Delfosse, 1984). The sucrose concentration (in % or g/100g) of the nectar samples was measured using a handheld refractometer modified for small volumes (Eclipse, Bellingham & Stanley). Using the calibration table of Kearns and Inouye (1993) the sucrose mass concentration (mg/µl) of the nectar samples was calculated. From this the mean sucrose mass per flower (mg/flower) was calculated. The mean values over the five sampled flowers were calculated for nectar amount, sucrose concentration and sucrose mass.

As previous studies reported that flower visitations are strongly influenced by flower availability (Arroyo-Correa et al., 2021; Barbir et al., 2016; Grindeland et al., 2005; Ohashi and Yahara, 1998), we also assessed the flower availability of our focal species. The number of open flowers of an individual plant or a plant population will correlate to the total amount of available floral resources (e.g. total nectar volume and total sugar mass) (Mueller et al., 2020) and furthermore increases flower attractiveness (flower display/total flower display) for potential pollinators (Descamps et al., 2021; Potts et al., 2003). The number of all open flowers of the observed plant patch was counted on each sampling day. In case of very large numbers of flowers as observed for *S. officinalis* (max. 7900 flowers) the flowers of a quarter of the patch were counted and extrapolated.

Flower visitor observations

All flower visitors of the four plant species were observed on 13-18 days each, covering the main flowering period of the investigated species. In case of starting rain, observations were stopped for that day. Observations were conducted three times a day in the morning between 9 am and 10 am, at midday between 12 am and 1 pm and in the afternoon between 3 pm and 4 pm. Flower visits of every insect were counted for 10 minutes per plant species considering the whole plant patch (~1 m^2). The number of flower visits in the 10-minute observation interval was considered as the visitation rate in this study.

Visiting insects were identified to morphotypes leading to different levels of determination: Honey bees (*Apis mellifera*) and bumble bees (*Bombus sp.*) were identified to species level. All Brachycera (suborder) specimens excluding syrphid flies (Syrphidae, family) were considered *flies*. Furthermore, we distinguished between *hover flies* (Syrphidae), *wasps* (Vespoidea, superfamily), *beetles* (Coleoptera, order) and *wild bees* (Apiformes without *Apis mellifera* and *Bombus* species). In total 168 observation intervals were conducted with on average 42 observation intervals per plant species.

Statistical analysis

Nectar properties

To better understand the mechanisms driving variation in nectar properties, nectar amount, sucrose concentration and sucrose mass were tested for correlation using Pearson's correlation (function *cor.test*) for each plant species. To test the hypothesis that nectar properties are unimodally associated to temperature and positively associated to solar radiation, per plant species we assessed the effect of these abiotic factors on a) nectar amount per flower, b) sucrose concentration and sucrose mass per flower using linear mixed effect models (package *lmerTest*, function *lmer*) (Kuznetsova et al., 2017). Due to the relatively low number of replicates we were not able to jointly model the predictor effects across all species by including species as covariate. Thus, we decided to run separate models per species and to compare the estimates. To test for a unimodal relationship between temperature and nectar properties, we included the quadratic term of temperature in the models. Observation day was included as a random factor to account for non-independence of the data (temporal autocorrelation). To identify the factors (temperature and/ or solar radiation) that were associated to changes in nectar properties of each plant species, the models were simplified step-wise until the most parsimonious model for each plant species was identified. The explanatory variables temperature and solar radiation were tested for correlation using Pearson’s correlation (function *cor.test*) before analysis ($r = 0.21; p = 0.01$).

Flower visitation

To visualize how flower visitor composition varied across the focal plant species and identify significant pollinator groups to each plant species, we used non-metric multidimensional scaling (NMDS). Pairwise dissimilarity across observation intervals was calculated using the function *metaMDS* from the R package *vegan* (Oksanen et al., 2020) using Bray-Curtis distance and 999 iterations.

Because 31 of our 168 observation intervals had no flower visitors, we first tested whether the presence or absence of flower visitors during an observation interval was driven by abiotic factors using a generalized linear mixed effects model (family binomial) with all abiotic factors (temperature, the quadratic term of temperature and solar radiation) and plant species as explanatory variables and the number of flowers as a covariate (see more details in Table S IV.1, Figure S IV.3, supplements). As there was no significant effect of any of the explanatory variables on the presence/absence of flower visitors, zero observations were excluded in further analyses (Table S IV.1, Figure S IV.3).

Next, to test the hypothesis that the number of flower visits relates to temperature in a unimodal way and is positively associated to solar radiation, per plant species we performed generalized linear mixed effects models (family quasipoisson) using the package *lme4* and the function *glmer.nb* (Bates et al., 2015). As above, due to the relatively low number of replicates we were not able to jointly model the predictor effects across all species by including species as covariate and decided to run separate models per species and to compare the estimates. Temperature, the quadratic term of temperature and solar radiation (measured as PAR) served as explanatory variables and the number of flowers on the observation day was included as covariate. To identify the factors (temperature and/ or solar radiation) that were associated to changes in the flower visitation rate of each plant species, the models were simplified step-wise until the most parsimonious model for each plant species was identified. As above, observation day was included as a random factor to account for non-independence of the data (temporal autocorrelation). The explanatory variables temperature and solar radiation were tested for correlation using Pearson's correlation (function *cor.test*) before analysis ($r = 0.21; p = 0.01$).

Correlation between nectar production and flower visits

To investigate whether and to what extend flower visitation rates were correlated to nectar quantity and quality of the different focal plants, we tested for correlation of both variables using Pearson's correlation (function *cor.test*) for each plant species separately.

All statistical analyses were performed in R version 4.0.4 (R Core Team, 2021).

Results

Correlation between nectar properties

Nectar properties were partly correlated with one another (Table S IV.2, Figure S IV.4, supplements). A strong positive correlation was found for nectar volume and sucrose mass per flower for all species. Nectar volume and sucrose concentration were significantly negatively correlated for all species. Sucrose mass and sucrose concentration were not correlated with each other for any of the plant species. An overview about general differences in the nectar properties between the investigated plant species is given in the supplements (Figure S IV.5).

Effect of abiotic factors on nectar quantity and quality

Temperature was an important factor explaining variation in nectar quantity and quality. Nectar volume significantly decreased with temperature for three out of four studied species and significantly decreased with solar radiation for one species (Figure IV.1). The most parsimonious models describing variation in nectar volume of *D. albus* and *V. hirundinaria* only contained temperature as explanatory variable (*D. albus*: $estimate_{Temp} = -0.45, p = 0.005, n = 31$); *V. hirundinaria*: $estimate_{Temp} = -0.03, p = 0.002, n = 46$) (Figure IV.1a). For *L. album* the most parsimonious model contained temperature ($estimate_{Temp} = -0.26, p = 0.04, n = 45$) (Figure IV.1a) and the quadratic term of temperature with a marginally significant effect ($estimate_{Temp^2} = 0.15, p = 0.06, n = 45$). The most parsimonious model describing variation in nectar volume of *S. officinalis* only contained PAR. Nectar volume of *S. officinalis* was negatively associated with PAR ($estimate_{PAR} = -0.33, p = 0.025, n = 41$) (Figure IV.1 d).

The abiotic factors that explained changes in sucrose concentration varied across plant species. The most parsimonious model explaining the variation in sucrose concentration contained only solar radiation for *D. albus* ($estimate_{PAR} = 56.66, p = 0.08, n = 31$) (Figure IV.1e), only temperature for *L. album* ($estimate_{Temp} = 33.22, p = 0.09, n = 45$) (Figure IV.1 b), both temperature and solar radiation for *S. officinalis* ($estimate_{Temp} = 73.00, p = 0.06, n = 41$; $estimate_{PAR} = 78.52, p = 0.03, n = 41$) (Figure IV.1 b, e), and temperature and the quadratic term of temperature for *V. hirundinaria* ($estimate_{Temp} = 50.56, p = 0.07, n = 46; estimate_{Temp^2} = -44.81, p = 0.06, n = 0.06, n = 46$) describing an overall unimodal relationship (Figure IV.1 b).

The sucrose mass per flower [mg] significantly decreased with temperature for *D. albus* ($estimate_{Temp} = -0.31, p = 0.03, n = 31$) (Figure IV.1 c) while PAR did not affect sucrose mass (most parsimonious model). Sucrose mass of the other investigated species was not affected by temperature and PAR (Figure IV.1 c, f).

Composition of flower visitors

The four observed plant species showed different but partly overlapping pollinator communities (Figure IV.2). *Dictamnus albus* was mostly visited by honey bees (*Apis mellifera*) (~93 % of visits). *Salvia officinalis* was mostly visited by wild bees (47 % of visits) and bumblebees (40% of visits) (Figure IV.2). A single species of bumblebee, *Bombus pascorum,* accounted for about 22 % of all visits to *S. officinalis*, followed by *B. sylvarum* (7 %), *B. terrestris* (7 %) and *B. hypnorum* (3 %). *L. album* had the fewest visits, and these visits were by bumblebees (81%), wild bees (12 %), and syrphid flies (Syrphidae) (5 %). Most frequent bumblebee species visitors were *B. pascorum* (54 % of all visits) and *B. hypnorum* (21 % of all visits). *Vincetoxicum hirundinaria* was mainly visited by honey bees (52 %), flies (Diptera) (30 %) and syrphid flies (Syrphidae) (9 %). The proportion of visits made by each pollinator group to each plant species is given in Figure IV.2.

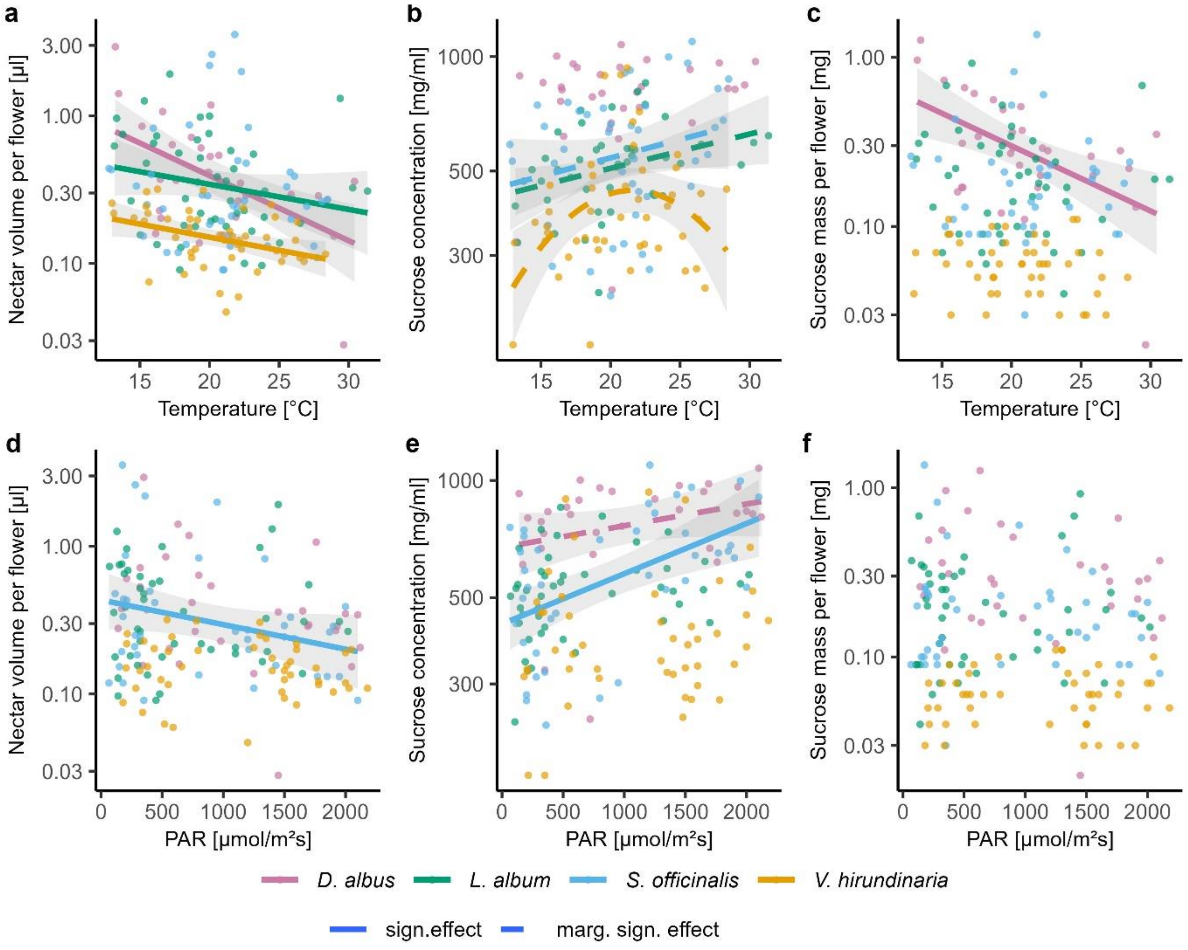

Figure IV.1: Effect of abiotic factors temperature and solar radiation (PAR) on the nectar volume per flower [µl] (a, d), the sucrose concentration of nectar [mg/ml] (b, e) and the sucrose mass per flower [mg] (c, f). Colours indicate different plant species. Solid lines indicate significant effects ($p < 0.05$), dashed lines indicate marginal significant effects ($p < 0.1$ and > 0.05).

Effects of abiotic factors on flower visitation rates

The different plant species showed different patterns in how the measured abiotic factors affected the number of flower visits. For each plant species the results only from the most parsimonious models are reported. Temperature affected the number of flower visits in the hypothesized unimodal manner for *D. albus* (*$estimate_{Temp} = 0.45$, $p = 0.009$, $estimate_{Temp^2} = -0.36$, $p = 0.005$, $n = 27$*) and *L. album* (*$estimate_{Temp^2} = -0.41$, p 0.02, $n = 25$*) (Figure IV.3 a). However, no effect of temperature on the visitation of *S. officinalis* and *V. hirundinaria* was found (Figure IV.3 a). Solar radiation (measured as PAR) affected the number of flower visits only for *S. officinalis* (*$estimate_{PAR}= 0.24$, $p= 0.006$, $n = 43$*) describing a positive relationship

(Figure IV.3 b). The number of flowers of the observed population positively affected the number of visits for *D. albus* ($estimate_{No\ of\ flowers} = 1.11, p < 0.001, n = 27$), *L. album* ($estimate_{No\ of\ flowers} = 0.46, p = 0.007, n = 25$) and *S. officinalis* ($estimate_{No\ of\ flowers} = 0.45, p = 0.001, n = 43$) (Figure IV.3 c). No effect of the number of flowers on the number of visits was found for *V. hirundinaria* (Figure IV.3 c).

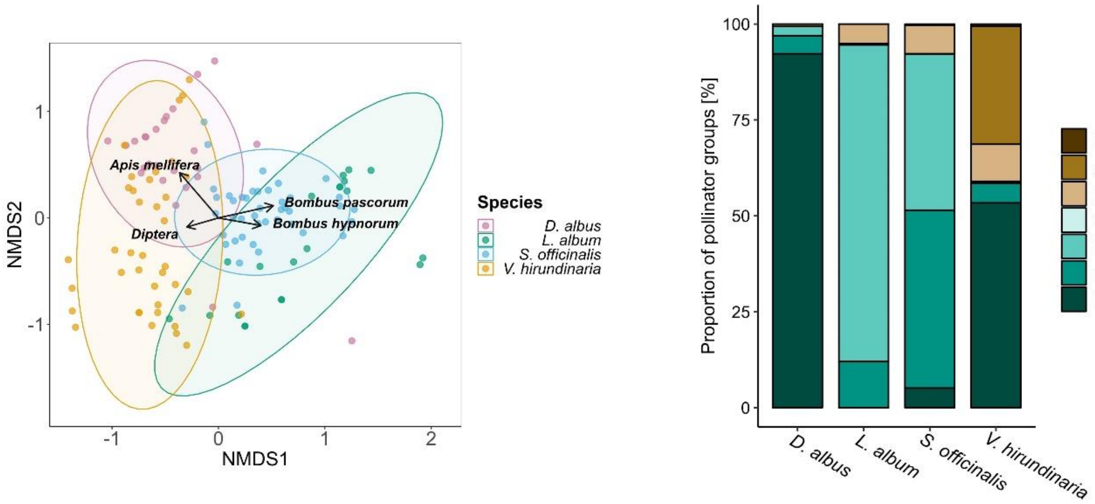

Figure IV.2: Left: NMDS of the composition of flower visitors observed at the four focal plant species in the Botanical Garden Halle. Each point describes the visitor community of one 10 min observation interval per plant species. Colours indicate target plant species. Arrows indicate flower visitors that were significantly correlated with the axes. Right: Proportion of pollinator groups that were observed at the focal plant species.

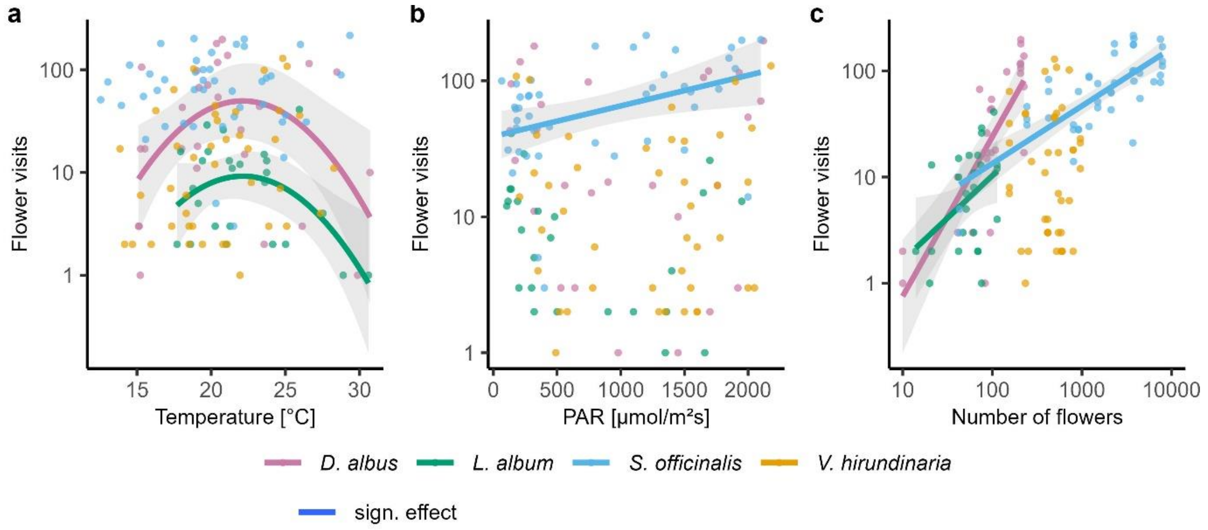

Figure IV.3: Relationship between a) temperature, b) solar radiation, c) the number of flowers with the number of flower visits observed at each plant species. Colours indicate different plant species. Solid lines indicate significant effects (p<0.05).

Correlation between nectar properties and flower visits

There was no clear pattern of correlation between nectar properties and flower visits. Nectar amount was negatively correlated to flower visits for *V. hirundinaria* (*r= -0.42; p= 0.006*) (Figure IV.4 a, Table IV.2). Other tested plant species showed no correlation of nectar amount and flower visits. Sucrose concentration was significantly correlated to flower visitation for two out of four species. *Salvia officinalis* showed a positive relationship between sucrose concentration and flower visits (*r = 0.48, p=0.001*; Figure IV.4 b), while visits of *L. album* were negatively related to sucrose concentration (*r = -0.43, p=0.02*, Figure IV.4 b). Sucrose mass per flower showed a significant correlation with flower visits only for *V. hirundinaria* with a negative correlation (*r = -0.39, p=0.02*, Figure IV.4 c).

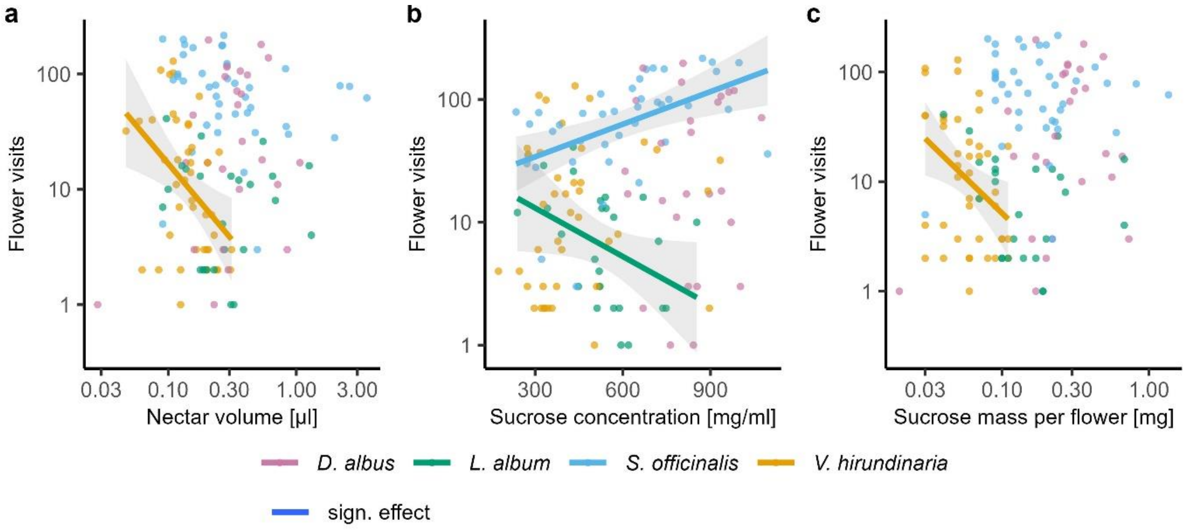

Figure IV.4: Correlation between nectar properties and insect visitation, solid lines indicate significant correlations.

Table IV.2: Pearson's correlation coefficients *r* and significance levels for the correlation between nectar properties and flower visits of the respective plant species

	nectar amount [µl]		sucrose concentration [mg/ml]		sucrose mass [mg]	
flower visits of:	*r*	*p-value*	*r*	*p-value*	*r*	*p-value*
Dictamnus albus	0.31	n.s.	0.07	n.s.	0.35	n.s.
Lamium album	-0.02	n.s.	-0.43	0.02	-0.2	n.s.
Salvia officinalis	-0.21	n.s.	0.48	0.001	-0.01	n.s.
Vincetoxicum hirundinaria	-0.42	0.006	0.13	n.s.	-0.39	0.02

Discussion

The objective of this study was to investigate the direct and indirect effects (through nectar quantity and quality) of temperature and solar radiation on the visitation of pollinators of four focal plant species. We found that temperature was an important abiotic factor, affecting nectar volume and sucrose concentration of three plant species while solar radiation (PAR) influenced the nectar volume and sucrose concentration of only one species (Figure IV.1). Temperature was unimodally related to the visitation of pollinators for two plant species and PAR was positively related to pollinator visitation for one species (Figure IV.2). Surprisingly, we found that flower visitation rate was not consistently affected by nectar quantity and quality (Figure IV.4). Interestingly, the flower-visitor interactions of the four species responded differently to abiotic factors. We are limited in our ability to conclusively test mechanisms for species differences, due to the limited number of species and the fact that the species were studied in four distinct locations within the garden (see Figure S IV.1 for an overview of the study site). However, we discuss the potential roles of differences across species in floral traits and the types of floral visitors. This research should hopefully motivate more case studies to build towards a larger comprehensive survey of floral traits, nectar properties, flower visitors and their response to abiotic conditions.

Effect of abiotic factors on nectar quantity and quality

In contrast to our expectation that nectar quantity and quality respond unimodally to temperature, we found linear negative responses (Figure IV.1a,c). One explanation for this result could be that we lacked days with very cold temperatures, which were rare during our study period. Similar results were found by Adjaloo et al. (2015), where temperatures were never very cold (minimum 28°C) but included very hot sampling days (maximum 42°C). Only in *V. hirundinaria,* we found a quadratic relationship between sucrose concentration and temperature (Figure IV.1b). The increase in sucrose concentration could be explained by evaporation of nectar with increasing temperatures (Corbet, 1990), and beyond certain temperatures, physiological stress due to high temperatures could in turn explain decreasing sucrose concentrations (Pacini and Nepi, 2007; Petanidou and Smets, 1996; Scaven and Rafferty, 2013). Sucrose mass of nectar was mostly unaffected by temperature or solar radiation (Figure IV.1c,f). This could be due to the fact that sucrose mass per flower is relatively constant in many plant species (Nicolson and Thornburg, 2007; Schwerdtfeger, 1996) - it may even be genetically fixed (Klinkhamer and Wijk, 1999; Mitchell and Shaw, 1993). This coincides with the foraging preferences of the most frequent pollinators (pollinator classes) (Nicolson and Thornburg, 2007; Schwerdtfeger, 1996). For. *D. albus* effects of temperature on sucrose mass reflected the same patterns as found for nectar volume (Figure

IV.1 a,c), what may reflect a change in overall nectar production due to temperature (Pacini and Nepi, 2007; Petanidou and Smets, 1996; Scaven and Rafferty, 2013) as sucrose amount and nectar volume were strongly correlated (Figure S IV.4 a).

Nectar volume decreased with increasing temperature or solar radiation while for most species, sucrose concentration increased in parallel (Figure IV.1), indicating higher evapotranspiration of nectar (Corbet, 1990, Fowler et al., 2016; Nicolson and Thornburg, 2007). Furthermore, nectar volume and sucrose concentration were negatively correlated for all four species (Figure S IV.4 b) which supports the assumption that higher evaporation at higher (flower) temperatures is the mechanism explaining our observed patterns (Fowler et al., 2016; Nicolson and Thornburg, 2007).

Temperature affected nectar properties more strongly than solar radiation in our investigated plant species (Figure IV.1). Whether the change in nectar properties was stronger associated to temperature or solar radiation could be mainly related to the flower traits of our studied species. Solar radiation can increase flower temperature even more than ambient temperature (Hanan, 1970; Rougerie-Durocher et al., 2020) and could therefore override direct temperature effects. That might play a role especially for darker coloured flowers (*S. officinalis*, *D. albus*) as flower temperature of light-coloured flowers (*L. album*, *V. hirundinaria*) is less affected by radiation than by ambient temperature (McKee and Richards, 1998). Furthermore, nectar in open flowers (*D. albus*) is more susceptible to evapotranspiration than nectar in flowers with deep corollas (Corbet, 1978; Plowright, 1987). The effect of solar radiation on nectar properties might overrule the effect of ambient temperature depending on flower colour and shape. Thus, flower colour and shape might help explaining differing response patterns in nectar properties to abiotic conditions like temperature or solar radiation.

The plant species we selected yielded small but measurable amounts of nectar on average ranging from 0.2 µl (*V. hirundinaria*) to about 0.5 µl in the other three species (Figure S IV.5). We would expect that plants with very small nectar amounts that were not included in our study due to practicability reasons would be even stronger affected by high temperatures and solar radiation (Corbet, 2003). However, since nectar measurements are very difficult to make for these species (but see Aronne and Malara, 2019), not much is known about these relationships.

The direct and indirect effect of abiotic factors on flower visitation rates

In our study, flower visitation was explained by a combination of direct and indirect (nectar quantity and quality) effects of temperature and solar radiation. Our results were species specific, which might be explained by 1) the different ways in which nectar resources were shaped by abiotic conditions and 2) different flower visitor compositions observed at the studied plant species that might have different needs and adaptations to abiotic conditions and nectar rewards. As in other studies, visitation was positively driven by the number of flowers (Barbir et al., 2016; Descamps et al., 2021; Fowler et al., 2016; Grindeland et al., 2005; Mueller et al., 2020). In our study, this phenomenon is also evident, wherein the impact of the number of flowers is notably strong (Figure IV.3 c), potentially obscuring the influence of abiotic factors to some degree.

In two species, we found the expected unimodal relationship between flower visitation and temperature (*D. albus*, *L. album*; Figure IV.3 a), which might be explained by the thermal tolerances of honeybees and bumblebees (Corbet et al., 1993) that were their main visitors (Figure IV.2). No relationship between flower visitation and temperature was found for *S. officinalis* and *V. hirundinaria* that both had a more diverse composition of flower visitors compared to the other two species (Figure IV.2). Their very diverse composition of flower visitors (a variety of wild bees and bumblebees at *S. officinalis*; honeybees, flies incl. syrphid flies at *V. hirundinaria*) might explain the absence of a relationship between temperature and visitation as visitors might show high thermal niche complementarity (Kühsel and Blüthgen, 2015). A positive association between solar radiation and flower visitations was only found in one species (*S. officinalis*), where heat gain due to solar radiation might be more important for their flower visitors than ambient temperatures (Kovac and Stabentheiner, 2011).

Flower visits were not consistently correlated to nectar properties as expected (Figure IV.4). Depending on the flower visitor community observed at our target plant species (Figure IV.2) we might differently interpret our findings. For example, honeybees (main visitors of *D. albus*) are known to respond rapidly to changes in nectar availability (Seeley et al., 1991). Thus, the decreases in flower visitation and nectar volumes at higher temperatures can be interpreted as an indirect effect of temperature on flower visitation. Other visitor groups ,like for example flies (important visitors of *V. hirundinaria*), might be less able to respond to changes in nectar availability (Fowler et al., 2016 , Hendriksma et al., 2019; Inouye et al., 2015). The negative correlation between nectar volume and sucrose mass, respectively, with flower visits found for *V. hirundinaria* (Figure IV.4) seems counterintuitive but might reflect the consumption pattern of nectar foragers, meaning that we observe low standing-crops when many flower visitors are present as plants are able to modify nectar secretion as a function of the removals (Zimmerman and Pyke, 1986). Pollinator exclusion from flowers was conducted one hour prior sampling, what might have been not enough to secrete new nectar for *V. hirundinaria*. It might be that this species reproduces nectar on a slower rate than the other tested plant species and the result is due to our methodology. Our general intention regarding the nectar sampling was to measure the nectar quantity and quality as it is available to the pollinators (standing crop) (Corbet, 2003). To ensure that our sampled flowers were not emptied right before nectar sampling we chose the one-hour covering to balance sampling problems regarding reabsorption or evaporation of the nectar that could arise with longer covering (Corbet, 2003; Kearns and Inouye, 1993). Generally, the produced nectar volumes of *V. hirundinaria* were rather small (<0.2µl) and therefore conclusions on the causality for those negative correlations are hard to draw and patterns could also be random. Flower visitation of *L. album* and S*. officinalis* was oppositely correlated to increases in sucrose concentration (Figure IV.4 b). On the one hand, rapid evaporation of nectar due to high temperatures might lead to nectar concentrations higher than those preferred by pollinators (Corbet, 1990) as well as increase nectar viscosity that might hinder nectar uptake by bumblebees (main visitors of *L. album)* (Harder, 1986). On the other hand, increasing sucrose concentrations might increase attractiveness for flower visitors (Kim et al., 2011; Krömer et al., 2008; Nicolson, 2007), as bees usually adapt their foraging behaviour to maximise nutritional uptake (Pyke, 1984), which can be achieved at higher nectar concentrations (Hendriksma et al., 2019). Thus, parts of our observed visitation patterns may reflect indirect effects of temperature or solar radiation mediated by altered nectar properties.

There may be further reasons why insect visitation might be indirectly affected by temperature and solar radiation that are not related to the nectar properties we measured: First, flower visitors might not primarily be attracted by nectar but by floral volatiles (Jürgens et al., 2008) or are foraging primarily for pollen. Volatile emission of flowers increases with temperature and radiation (Jakobsen and Olsen, 1994), increasing flower attractiveness for pollinators. Second, higher flower and nectar temperatures increase the attractiveness for foragers, even though sucrose concentration seems to stronger drive forager choice (Whitney et al., 2008). Moreover, colour perception differs between different visitor groups and might be differently affected by changing ambient light conditions (Chittka et al., 2014; Lunau, 2014; van der Kooi et al., 2021). Future studies should incorporate these aspects to provide a more holistic view of flower traits and their influence on pollinator attractiveness in the context of changing climate conditions (Junker and Parachnowitsch, 2015).

Besides the indirect effects of temperature and solar radiation on flower visitation, abiotic conditions can also directly impact distinct visitor communities in unique ways, owing to variations in their thermal tolerances (Corbet et al., 1993) and the complementarity of their thermal niches (Kühsel and Blüthgen, 2015). The combination of direct and indirect effects on flower visitation might explain the absence of a consistent correlation pattern between visits and nectar quantity and quality in our investigated plant species.

Conclusion

This research contributes to a better understanding of direct and indirect effects of environmental conditions on flower visitation patterns, which can affect the reproductive success of plants. Temperature and solar radiation affected nectar quantity and quality differently, and our results suggest that this might be due to differences in flower traits of plant species. However, observations on a larger set of plant species covering a wider range of flower shapes and colours as well as a more controlled study design like a common garden would be necessary to confirm this hypothesis. Flower visitation patterns were shaped by a combination of direct effects of temperature on pollinator activity and indirect effects of temperature and solar radiation on nectar quantity and quality. Additionally, the composition of flower visitors that were observed at the focal plant species influenced these direct and indirect responses, as different insect groups have different requirements and adaptations to temperature and nectar quantity and quality. Botanical gardens offer good opportunities to study flower visitation on various plant species, as many plant as well as pollinator species co-occur in a small area and under comparable conditions (Nordt et al., 2021; Vilella-Arnizaut et al., 2022). In order to understand impacts of climate change on pollination we need to consider that flower traits and pollinator composition might be crucial aspects that will influence species-specific responses to changing abiotic conditions. Thus, this study contributes to a better understanding of the factors influencing biotic interactions (i.e. pollination), which is essential for understanding and predicting the impacts of climate change. More experimental studies (like e.g. Descamps et al., 2021) on a variety of plant species, covering different functional groups and flower types investigating the effects of climate change on plant-pollinator interactions are needed to estimate the manifold impacts of changing abiotic conditions on plants, their flower visitors as well as plant-pollinator interactions.

References

Abrol, D.P., 2010. Foraging behaviour of Apis florea F., an important pollinator of Allium cepa L. Journal of Apicultural Research 49, 318–325. https://doi.org/10.3896/IBRA.1.49.4.04

Abrol, D.P., 2006. Foraging Behaviour of Bees as Influenced by Quality and Quantity of Rewards from Flowers. Journal of Asia-Pacific Entomology 9, 145–148. https://doi.org/10.1016/S1226-8615(08)60285-X

Adjaloo, M.K., Ankomah, A.A., Yeboah-Gyan, K., Dzomeku, B.M., 2015. Nectar production dynamics in two melliferous plant species. Genetics and Plant Physiology 5, 145–161.

Arnold, S.E.J., Chittka, L., 2012. Illumination preference, illumination constancy and colour discrimination by bumblebees in an environment with patchy light. Journal of Experimental Biology 215, 2173–2180. https://doi.org/10.1242/jeb.065565

Aronne, G., Malara, P., 2019. Fiber-optic refractometer for in vivo sugar concentration measurements of low-nectar-producing flowers. New Phytologist 224, 987–993. https://doi.org/10.1111/nph.16084

Arroyo-Correa, B., Bartomeus, I., Jordano, P., 2021. Individual-based plant–pollinator networks are structured by phenotypic and microsite plant traits. Journal of Ecology 109, 2832–2844. https://doi.org/10.1111/1365-2745.13694

Barbir, J., Azpiazu, C., Badenes-Pérez, F.R., Fernández-Quintanilla, C., Dorado, J., 2016. Functionality of Selected Aromatic Lamiaceae in Attracting Pollinators in Central Spain. Journal of Economic Entomology 109, 529–536. https://doi.org/10.1093/jee/tow004

Basnett, S., Nagaraju, S.K., Hart, R., Devy, S.M., 2021. Floral traits and community phylogenetic structure shape plant-pollinator interactions in co-occurring Rhododendrons in the Himalaya. Perspectives in Plant Ecology, Evolution and Systematics 53, 125646. https://doi.org/10.1016/j.ppees.2021.125646

Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software 67, 1–48. https://doi.org/10.18637/jss.v067.i01

BfN, 2011. FloraWeb: Daten und Informationen zu Wildpflanzen und zur Vegetation Deutschlands, Bundesamt für Naturschutz. https://www.floraweb.de/ [accessed 07.06.2022]

Boose, D.L., 1997. Sources of variation in floral nectar production rate in Epilobium canum (Onagraceae): implications for natural selection. Oecologia 110, 493–500. https://doi.org/10.1007/s004420050185

Burdine, J.D., McCluney, K.E., 2019. Differential sensitivity of bees to urbanization-driven changes in body temperature and water content. Sci Rep 9, 1643. https://doi.org/10.1038/s41598-018-38338-0

Carroll, A.B., Pallardy, S.G., Galen, C., 2001. Drought stress, plant water status, and floral trait expression in fireweed, Epilobium angustifolium (Onagraceae). American Journal of Botany 88, 438–446. https://doi.org/10.2307/2657108

Cawoy, V., Kinet, J.-M., Jacquemart, A.-L., 2008. Morphology of Nectaries and Biology of Nectar Production in the Distylous Species Fagopyrum esculentum. Ann Bot 102, 675–684. https://doi.org/10.1093/aob/mcn150

Chittka, L., Faruq, S., Skorupski, P., Werner, A., 2014. Colour constancy in insects. J. Comp. Physiol. A 200, 435–448. https://doi.org/10.1007/s00359-014-0897-z

Comba, L., 1999. Flowers, Nectar and Insect Visits: Evaluating British Plant Species for Pollinator-friendly Gardens. Annals of Botany 83, 369–383. https://doi.org/10.1006/anbo.1998.0835

Corbet, S.A., 2003. Nectar sugar content: estimating standing crop and secretion rate in the field. Apidologie 34, 1–10. https://doi.org/10.1051/apido:2002049

Corbet, S.A., 1990. Pollination and the weather. Israel Journal of Plant Sciences 39, 13–30. https://doi.org/10.1080/0021213X.1990.10677131

Corbet, S.A., 1978. Bee visits and the nectar of Echium vulgare L. and Sinapis alba L. Ecological Entomology 3, 25–37. https://doi.org/10.1111/j.1365-2311.1978.tb00900.x

Corbet, S.A., Delfosse, E.S., 1984. Honeybees and the nectar of Echium plantagineum L. in southeastern Australia. Australian Journal of Ecology 9, 125–139. https://doi.org/10.1111/j.1442-9993.1984.tb01351.x

Corbet, S.A., Fussell, M., Ake, R., Fraser, A., Gunson, C., Savage, A., Smith, K., 1993. Temperature and the pollinating activity of social bees. Ecological Entomology 18, 17–30. https://doi.org/10.1111/j.1365-2311.1993.tb01075.x

del Rio, C.M., Burquez, A., 1986. Nectar Production and Temperature Dependent Pollination in Mirabilis jalapa L. Biotropica 18, 28–31. https://doi.org/10.2307/2388358

Descamps, C., Jambrek, A., Quinet, M., Jacquemart, A.-L., 2021. Warm Temperatures Reduce Flower Attractiveness and Bumblebee Foraging. Insects 12, 493. https://doi.org/10.3390/insects12060493

Descamps, C., Quinet, M., Baijot, A., Jacquemart, A.-L., 2018. Temperature and water stress affect plant–pollinator interactions in Borago officinalis (Boraginaceae). Ecology and Evolution 8, 3443–3456. https://doi.org/10.1002/ece3.3914

Deutscher Wetterdienst (DWD) Climate Data Center (CDC), 2021. OpenData. https://opendata.dwd.de/climate_environment/CDC/observations_germany/climate/monthly/kl/recent/. [accessed 9 December 2021]

Faegri, K., Pijl, L.V.D., 1979. Principles of Pollination Ecology. Elsevier.

Fowler, R.E., Rotheray, E.L., Goulson, D., 2016. Floral abundance and resource quality influence pollinator choice. Insect Conservation and Diversity 9, 481–494. https://doi.org/10.1111/icad.12197

Gérard, M., Vanderplanck, M., Wood, T., Michez, D., 2020. Global warming and plant–pollinator mismatches. Emerging Topics in Life Sciences 4, 77–86. https://doi.org/10.1042/ETLS20190139

González-Varo, J.P., Biesmeijer, J.C., Bommarco, R., Potts, S.G., Schweiger, O., Smith, H.G., Steffan-Dewenter, I., Szentgyörgyi, H., Woyciechowski, M., Vilà, M., 2013. Combined effects of global change pressures on animal-mediated pollination. Trends in Ecology & Evolution 28, 524–530. https://doi.org/10.1016/j.tree.2013.05.008

Grindeland, J.M., Sletvold, N., Ims, R.A., 2005. Effects of floral display size and plant density on pollinator visitation rate in a natural population of Digitalis purpurea. Functional Ecology 19, 383–390. https://doi.org/10.1111/j.1365-2435.2005.00988.x

Hanan, J.J., 1970. Statistical analysis of flower temperatures in the carnation. Journal of the American Society of Horticultural Science 95, 68–73.

Harder, L.D., 1986. Effects of nectar concentration and flower depth on flower handling efficiency of bumble bees. Oecologia 69, 309–315. https://doi.org/10.1007/BF00377639

Hendriksma, H.P., Toth, A.L., Shafir, S., 2019. Individual and Colony Level Foraging Decisions of Bumble Bees and Honey Bees in Relation to Balancing of Nutrient Needs. Frontiers in Ecology and Evolution 7.

Huber, H., 1956. Die Abhängigkeit der Nektarsekretion von Temperatur, Luft- und Bodenfeuchtigkeit. Planta 48, 47–98. https://doi.org/10.1007/BF01911144

Inouye, D.W., 1980. The effect of proboscis and corolla tube lengths on patterns and rates of flower visitation by bumblebees. Oecologia 45, 197–201. https://doi.org/10.1007/BF00346460

Inouye, D.W., Larson, B.M.H., Ssymank, A., Kevan, P.G., 2015. Flies and Flowers III: Ecology of foraging and pollination. Journal of Pollination Ecology 16, 115–133. https://doi.org/10.26786/1920-7603(2015)15

Jakobsen, H.B., Olsen, C.E., 1994. Influence of climatic factors on emission of flower volatiles in situ. Planta 192, 365–371. https://doi.org/10.1007/BF00198572

Junker, R.R., Parachnowitsch, A.L., 2015. Working Towards a Holistic View on Flower Traits— How Floral Scents Mediate Plant–Animal Interactions in Concert with Other Floral Characters. Journal of the Indian Institute of Science 95, 43–68.

Jürgens, A., Dötterl, S., Liede-Schumann, S., Meve, U., 2008. Chemical diversity of floral volatiles in Asclepiadoideae-Asclepiadeae (Apocynaceae). Biochemical Systematics and Ecology 36, 842–852. https://doi.org/10.1016/j.bse.2008.10.005

Kearns, C.A., Inouye, D.W., 1993. Techniques for pollination biologists. Techniques for pollination biologists.

Kilkenny, F.F., Galloway, L.F., 2008. Reproductive success in varying light environments: direct and indirect effects of light on plants and pollinators. Oecologia 155, 247–255. https://doi.org/10.1007/s00442-007-0903-z

Kim, W., Gilet, T., Bush, J.W.M., 2011. Optimal concentrations in nectar feeding. PNAS 108, 16618–16621. https://doi.org/10.1073/pnas.1108642108

Klein, A.-M., Vaissière, B.E., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C., Tscharntke, T., 2007. Importance of pollinators in changing landscapes for world crops. Proceedings of the Royal Society B: Biological Sciences 274, 303–313. https://doi.org/10.1098/rspb.2006.3721

Klinkhamer, P.G.L., Wijk, C.A.M. van der V., 1999. Genetic Variation in Floral Traits of Echium vulgare. Oikos 85, 515–522. https://doi.org/10.2307/3546700

Klotz, S., Kühn, I., Durka, W., 2002. BiolFlor: Eine Datenbank mit biologisch-ökologischen Merkmalen zur Flora von Deutschland. Schriftenreihe für Vegetationskunde, Bonn: Bundesamt für Naturschutz.

Kovac, H., Stabentheiner, A., 2011. Thermoregulation of foraging honeybees on flowering plants: seasonal variability and influence of radiative heat gain. Ecological Entomology 36, 686–699. https://doi.org/10.1111/j.1365-2311.2011.01313.x

Krömer, T., Kessler, M., Lohaus, G., Schmidt-Lebuhn, A.N., 2008. Nectar sugar composition and concentration in relation to pollination syndromes in Bromeliaceae. Plant Biology 10, 502–511. https://doi.org/10.1111/j.1438-8677.2008.00058.x

Kühsel, S., Blüthgen, N., 2015. High diversity stabilizes the thermal resilience of pollinator communities in intensively managed grasslands. Nat Commun 6, 7989. https://doi.org/10.1038/ncomms8989

Kuznetsova, A., Brockhoff, P.B., Christensen, R.H.B., 2017. lmerTest Package: Tests in Linear Mixed Effects Models. Journal of Statistical Software 82, 1–26. https://doi.org/10.18637/jss.v082.i13

Lunau, K., 2014. Visual ecology of flies with particular reference to colour vision and colour preferences. J. Comp. Physiol. A 200, 497–512. https://doi.org/10.1007/s00359-014-0895-1

Lye, G., Park, K., Osborne, J., Holland, J., Goulson, D., 2009. Assessing the value of Rural Stewardship schemes for providing foraging resources and nesting habitat for bumblebee queens (Hymenoptera: Apidae). Biological Conservation 142, 2023–2032. https://doi.org/10.1016/j.biocon.2009.03.032

Mačukanović-Jocić, M., Stevanović, Z.D., Mladenović, M., Jocić, G., 2011. Flower morphophysiology of selected Lamiaceae species in relation to pollinator attraction. Journal of Apicultural Research 50, 89–101. https://doi.org/10.3896/IBRA.1.50.2.01

Maron, J.L., Baer, K.C., Angert, A.L., 2014. Disentangling the drivers of context-dependent plant–animal interactions. Journal of Ecology 102, 1485–1496. https://doi.org/10.1111/1365-2745.12305

McKee, J., Richards, A.J., 1998. Effect of flower structure and flower colour on intrafloral warming and pollen germination and pollen-tube growth in winter flowering Crocus L. (Iridaceae). Botanical Journal of the Linnean Society 128, 369–384. https://doi.org/10.1111/j.1095-8339.1998.tb02127.x

Mitchell, R.J., Shaw, R.G., 1993. Heritability of floral traits for the perennial wild flower Penstemon centranthifolius (Scrophulariaceae): clones and crosses. Heredity 71, 185–192. https://doi.org/10.1038/hdy.1993.123

Mueller, A.L., Berger, C.A., Schittenhelm, S., Stever-Schoo, B., Dauber, J., 2020. Water availability affects nectar sugar production and insect visitation of the cup plant Silphium perfoliatum L. (Asteraceae). Journal of Agronomy and Crop Science 206, 529–537. https://doi.org/10.1111/jac.12406

Nicolson, S.W., 2007. Nectar consumers, in: Nicolson, S.W., Nepi, M., Pacini, E. (Eds.), Nectaries and Nectar. Springer Netherlands, Dordrecht, pp. 289–342. https://doi.org/10.1007/978-1-4020-5937-7_7

Nicolson, S.W., Thornburg, R.W., 2007. Nectar chemistry, in: Nicolson, S.W., Nepi, M., Pacini, E. (Eds.), Nectaries and Nectar. Springer Netherlands, Dordrecht, pp. 215–264. https://doi.org/10.1007/978-1-4020-5937-7_5

Nordt, B., Hensen, I., Bucher, S.F., Freiberg, M., Primack, R.B., Stevens, A.-D., Bonn, A., Wirth, C., Jakubka, D., Plos, C., Sporbert, M., Römermann, C., 2021. The PhenObs initiative: A standardised protocol for monitoring phenological responses to climate change using herbaceous plant species in botanical gardens. Functional Ecology 35, 821–834. https://doi.org/10.1111/1365-2435.13747

Ohashi, K., Yahara, T., 1998. Effects of variation in flower number on pollinator visits in Cirsium purpuratum (Asteraceae). American Journal of Botany 85, 219–224. https://doi.org/10.2307/2446309

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O’Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H., 2020. vegan: Community Ecology Package. R package version 2.5-7.

Ollerton, J., Winfree, R., Tarrant, S., 2011. How many flowering plants are pollinated by animals? Oikos 120, 321–326. https://doi.org/10.1111/j.1600-0706.2010.18644.x

Pacini, E., Nepi, M., 2007. Nectar production and presentation, in: Nicolson, S.W., Nepi, M., Pacini, E. (Eds.), Nectaries and Nectar. Springer Netherlands, Dordrecht, pp. 167–214. https://doi.org/10.1007/978-1-4020-5937-7_4

Petanidou, T., 2007. Ecological and evolutionary aspects of floral nectars in Mediterranean habitats, in: Nicolson, S.W., Nepi, M., Pacini, E. (Eds.), Nectaries and Nectar. Springer Netherlands, Dordrecht, pp. 343–375. https://doi.org/10.1007/978-1-4020-5937-7_8

Petanidou, T., Smets, E., 1996. Does temperature stress induce nectar secretion in Mediterranean plants? New Phytologist 133, 513–518. https://doi.org/10.1111/j.1469-8137.1996.tb01919.x

Plowright, R.C., 1987. Corolla depth and nectar concentration: an experimental study. Can. J. Bot. 65, 1011–1013. https://doi.org/10.1139/b87-139

Potts, S.G., Vulliamy, B., Dafni, A., Ne’eman, G., Willmer, P., 2003. Linking Bees and Flowers: How Do Floral Communities Structure Pollinator Communities? Ecology 84, 2628–2642. https://doi.org/10.1890/02-0136

Pyke, G.H., 1984. Optimal Foraging Theory: A Critical Review. Annual Review of Ecology and Systematics 15, 523–575.

R Core Team, 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rapp, D., 2014. Assessing Climate Change: Temperatures, Solar Radiation and Heat Balance. Springer.

Rodger, J.G., Bennett, J.M., Razanajatovo, M., Knight, T.M., van Kleunen, M., Ashman, T.-L., Steets, J.A., Hui, C., Arceo-Gómez, G., Burd, M., Burkle, L.A., Burns, J.H., Durka, W., Freitas, L., Kemp, J.E., Li, J., Pauw, A., Vamosi, J.C., Wolowski, M., Xia, J., Ellis, A.G., 2021. Widespread vulnerability of flowering plant seed production to pollinator declines. Science Advances 7, eabd3524. https://doi.org/10.1126/sciadv.abd3524

Rosas-Guerrero, V., Aguilar, R., Martén-Rodríguez, S., Ashworth, L., Lopezaraiza-Mikel, M., Bastida, J.M., Quesada, M., 2014. A quantitative review of pollination syndromes: do floral traits predict effective pollinators? Ecology Letters 17, 388–400. https://doi.org/10.1111/ele.12224

Rougerie-Durocher, S., Philion, V., Szalatnay, D., 2020. Measuring and modelling of apple flower stigma temperature as a step towards improved fire blight prediction. Agricultural and Forest Meteorology 295, 108171. https://doi.org/10.1016/j.agrformet.2020.108171

Scaven, V.L., Rafferty, N.E., 2013. Physiological effects of climate warming on flowering plants and insect pollinators and potential consequences for their interactions. Current Zoology 59, 418–426. https://doi.org/10.1093/czoolo/59.3.418

Schwerdtfeger, M., 1996. Die Nektarzusammensetzung der Asteridae und ihre Beziehung zu Blutenokologie und Systematik. Dissertationes Botanicae 264, 1–94.

Seeley, T.D., Camazine, S., Sneyd, J., 1991. Collective decision-making in honey bees: how colonies choose among nectar sources. Behav Ecol Sociobiol 28, 277–290. https://doi.org/10.1007/BF00175101

Silva, E.M., Dean, B.B., Hiller, L., 2004. Patterns of Floral Nectar Production of Onion (Allium cepa L.) and the Effects of Environmental Conditions. Journal of the American Society for Horticultural Science 129, 299–302. https://doi.org/10.21273/JASHS.129.3.0299

Southwick, E.E., 1984. Photosynthate Allocation to Floral Nectar: A Neglected Energy Investment. Ecology 65, 1775–1779. https://doi.org/10.2307/1937773

Sporbert, M., Jakubka, D., Bucher, S.F., Hensen, I., Freiberg, M., Heubach, K., König, A., Nordt, B., Plos, C., Blinova, I., Bonn, A., Knickmann, B., Koubek, T., Linstädter, A., Mašková, T., Primack, R.B., Rosche, C., Shah, M.A., Stevens, A.-D., Tielbörger, K., Träger, S., Wirth, C., Römermann, C., 2022. Functional traits influence patterns in vegetative and reproductive plant phenology – a multi-botanical garden study. New Phytologist 235, 2199–2210. https://doi.org/10.1111/nph.18345

Stone, G.N., Willmer, P.G., 1989. Warm-up rates and body temperatures in bees: The importance of body size, thermal regime and phylogeny. Journal of Experimental Biology 147, 303–328.

Takkis, K., Tscheulin, T., Petanidou, T., 2018. Differential Effects of Climate Warming on the Nectar Secretion of Early- and Late-Flowering Mediterranean Plants. Front. Plant Sci. 9. https://doi.org/10.3389/fpls.2018.00874

Thomson, J.D., 1988. Effects of variation in inflorescence size and floral rewards on the visitation rates of traplining pollinators of Aralia hispida. Evol Ecol 2, 65–76. https://doi.org/10.1007/BF02071589

van der Kooi, C.J., Stavenga, D.G., Arikawa, K., Belušič, G., Kelber, A., 2021. Evolution of Insect Color Vision: From Spectral Sensitivity to Visual Ecology. Annu. Rev. Entomol. 66, 435–461. https://doi.org/10.1146/annurev-ento-061720-071644

Vicens, N., Bosch, J., 2000. Weather-Dependent Pollinator Activity in an Apple Orchard, with Special Reference to Osmia cornuta and Apis mellifera (Hymenoptera: Megachilidae and Apidae). Environmental Entomology 29, 413–420. https://doi.org/10.1603/0046-225X-29.3.413

Vilella-Arnizaut, I.B., Roeder, D.V., Fenster, C.B., 2022. Use of botanical gardens as arks for conserving pollinators and plant-pollinator interactions: A case study from the United States Northern Great Plains. Journal of Pollination Ecology 31, 53–69. https://doi.org/10.26786/1920-7603(2022)645

Waddington, K.D., Allen, T., Heinrich, B., 1981. Floral preferences of bumblebees (Bombus edwardsii) in relation to intermittent versus continuous rewards. Animal Behaviour 29, 779–784. https://doi.org/10.1016/S0003-3472(81)80011-5

Whitney, H.M., Dyer, A., Chittka, L., Rands, S.A., Glover, B.J., 2008. The interaction of temperature and sucrose concentration on foraging preferences in bumblebees. Naturwissenschaften 95, 845–850. https://doi.org/10.1007/s00114-008-0393-9

Zimmerman, M., Pyke, G.H., 1986. Reproduction in Polemonium: Patterns and Implications of Floral Nectar Production and Standing Crops. American Journal of Botany 73, 1405–1415. https://doi.org/10.1002/j.1537-2197.1986.tb10886.x

Zoller, L., Bennett, J.M., Knight, T.M., 2020. Diel-scale temporal dynamics in the abundance and composition of pollinators in the Arctic summer. Sci Rep 10, 21187. https://doi.org/10.1038/s41598-020-78165-w

Supplementary Material (S IV)

Title: Abiotic conditions affect nectar properties and flower visitation in four herbaceous plant species

Authors: Carolin Plos, Niklas Stelbrink, Christine Römermann, Tiffany M. Knight, Isabell Hensen

Journal: *Flora*

Figure S IV.1: Aerial view of the systematic part of the Botanical Garden in Halle (Saale) where the study was conducted. Patches of ~1m² of the study plants are marked.

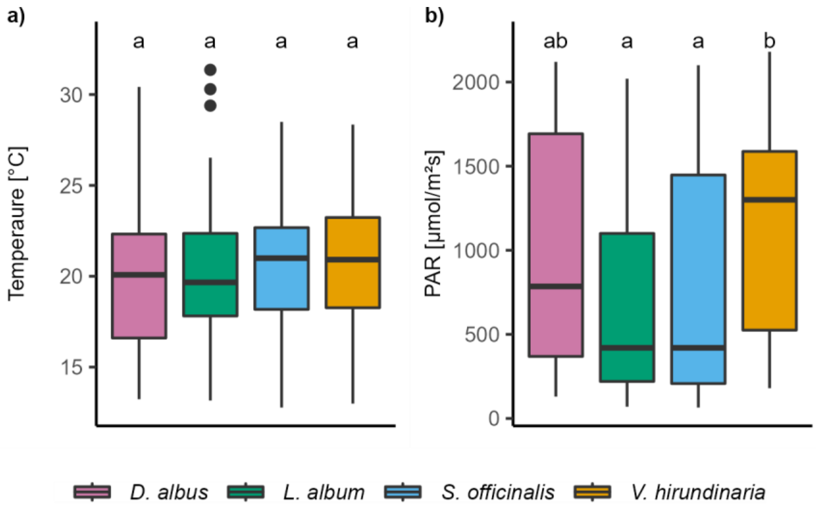

Figure S IV.2: Microsite conditions measured at the four observed plant species. a) Temperature [°C], b) photosynthetic active radiation abbrev. PAR [µmol/m²s]. Letters indicate differences among species patches (derived from a Tukey post hoc test).

Test for the effect of abiotic factors on the presence or absence of flower visitors

We initially tested whether the absence of flower visitors could be explained by abiotic factors. Thus, the data was transformed to presence/absence information (0/1). A generalized linear mixed model (package *lme4*, function *glmer*; family binomial) was used containing visitation (0/1) as response variable and temperature, the quadratic term of temperature and solar radiation (PAR) as explanatory variables. The number of flowers on the observation day was included as co-variate in the model. All explanatory variables were tested in interaction with plant species. Date of the observation was used as random factor.The model explained 99 % of the variation ($R^2_{marginal}$=0.99, $R^2_{conditional}$=0.99). There was no significant effect of the tested abiotic factors temperature and solar radiation (PAR) and the covariate 'number of flowers' on the presence or absence of flower visitors (Figure S IV.3, Table S IV.1). Thus, observation intervals with no flower visitor were excluded from further analysis.

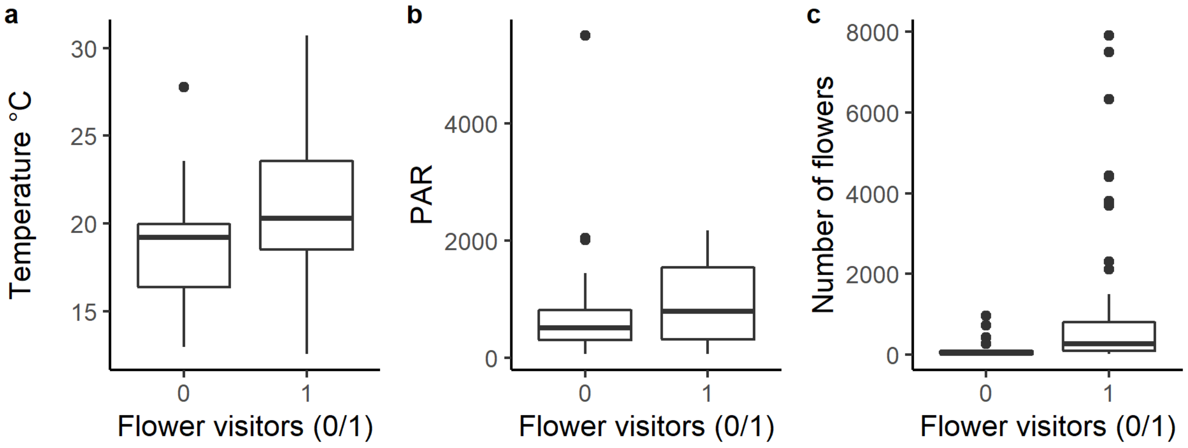

Figure S IV.3: Effect of a) temperature b) PAR and c) the number of flowers on the presence (1) or absence (0) of flower visitors during observation intervals across all plant species.

Table S IV.1: Model output for generalized mixed model (*glmer*) testing the effect of abiotic factors on the presence/absence of flower visitors

	Estimate	Std. error	z Value	p-Value
(Intercept)	3.704e+01	2.084e+01	1.777	0.0755
Temp	1.463e+00	8.700e-01	1.682	0.0925
I((Temp)^2)	-2.582e-01	4.119e-01	-0.627	0.5308
PAR	-6.531e-01	1.352e+00	-0.483	0.6291
No_of_flowers	7.218e+01	4.282e+01	1.686	0.0919
speciesLA	-1.999e+01	2.358e+01	-0.848	0.3965
speciesSO	1.132e+02	5.153e+05	0.000	0.9998
speciesVH	-3.481e+01	2.087e+01	-1.668	0.0954
Temp:speciesLA	-2.141e-01	1.075e+00	-0.199	0.8422
Temp:speciesSO	-6.268e+01	1.619e+06	0.000	1.0000
Temp:speciesVH	3.078e-02	1.728e+00	0.018	0.9858
I((Temp)^2):speciesLA	3.331e-01	6.252e-01	0.533	0.5942
I((Temp)^2):speciesSO	1.169e+02	6.317e+06	0.000	1.0000
I((Temp)^2):speciesVH	1.647e-01	1.010e+00	0.163	0.8704
PAR:speciesLA	3.185e-01	1.408e+00	0.226	0.8211
PAR:speciesSO	1.443e+02	5.147e+05	0.000	0.9998
PAR:speciesVH	3.259e+00	1.921e+00	1.697	0.0898
No_of_flowers:speciesLA	-3.815e+01	4.825e+01	-0.791	0.4291
No_of_flowers:speciesSO	-3.243e+01	3.944e+05	0.000	0.9999
No_of_flowers:speciesVH	-7.968e+01	4.311e+01	-1.848	0.0646

Correlation between nectar properties for the focal plant species

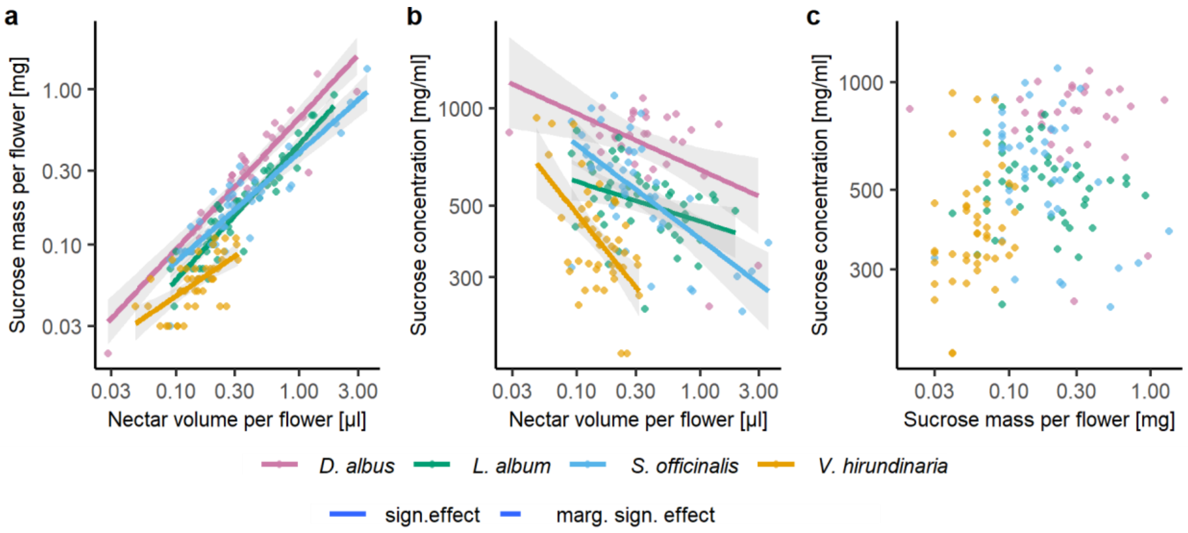

Figure S IV.4: Correlation between nectar parameters, solid lines indicate significant correlations (see also Table S IV.2).

Table S IV.2: Results of Pearson´s correlation test between nectar properties for each plant species

Dictamnus albus			
nectar volume	**0.93**	**-0.45**	
sucrose concentr.	-0.11		**
sucrose mass		n.s.	***
	sucrose mass	sucrose concentr.	nectar volume

Lamium album			
nectar volume	**0.94**	**-0.40**	
sucrose concentr.	-0.07		**
sucrose mass		n.s.	***
	sucrose mass	sucrose concentr.	nectar volume

Salvia officinalis			
nectar volume	**0.91**	**-0.64**	
sucrose concentr.	-0.26		***
sucrose mass		n.s.	***
	sucrose mass	sucrose concentr.	nectar volume

Vincetoxicum hirundinaria			
nectar volume	**0.63**	**-0.61**	
sucrose concentr.	0.20		***
sucrose mass		n.s.	***
	sucrose mass	sucrose concentr.	nectar volume

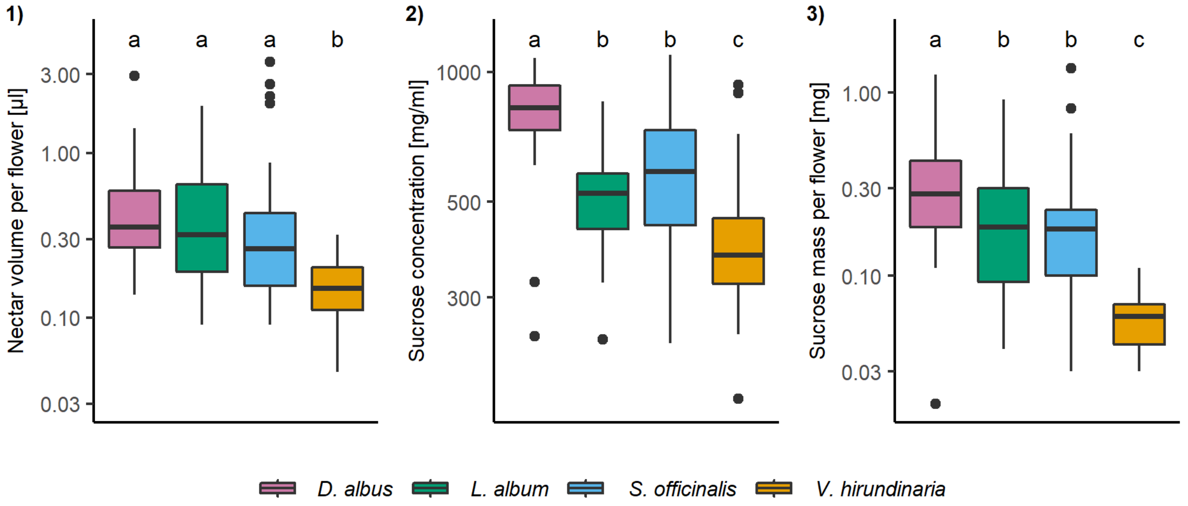

Figure S IV.5: Differences in nectar properties among the four observed plant species. 1) nectar volume per flower in µl, 2) sucrose concentration in mg/ml, 3) sucrose mass per flower in mg. Letters indicate species differences (derived from the Tukey post hoc test)

Chapter V

Synthesis

In this thesis, I investigated the relationship between phenology and functional traits, with a special focus on floral traits, to understand patterns of interspecific phenological variation and phenological shifts due to changing climate in herbaceous plant species. To further assess potential consequences of changing climate for plant-pollinator interactions direct effects of abiotic conditions on floral resources and pollinator visitation rates were observed. The main findings of this thesis and connections between the Chapters are summarized in Figure V.1.

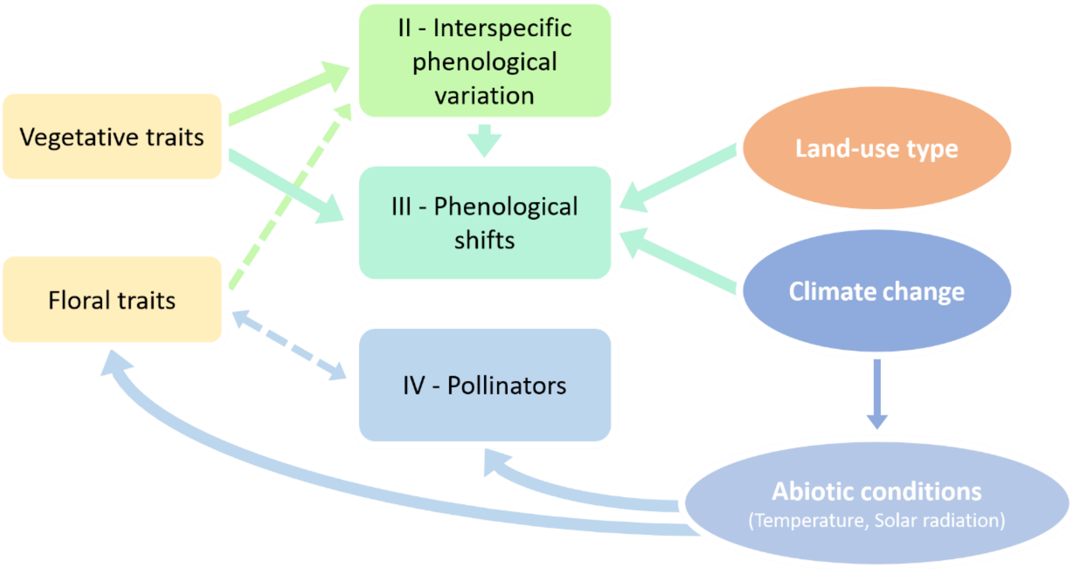

Figure V.1: Graphical overview of the main results of this thesis. Colored boxes in the middle refer to chapters II-IV and arrow colors correspond to the results of the respective chapters. The arrows indicate the identified relationships between the investigated variables and drivers with solid lines indicating pronounced and dashed lined indicating weak relationships.

Summary of Results

In **Chapter II**, I examined the **relative importance of floral and vegetative traits in explaining interspecific phenological variation.** I could show that traits played a significant role in explaining interspecific phenological variation and were generally more influential than phylogenetic relatedness. Among the investigated traits, vegetative traits were stronger predictors of phenological patterns than floral traits (Figure V.1). Plant height emerged as a key trait, showing a strong positive relationship with both flowering and fruiting phenology, explaining a substantial proportion of the variation. Leaf senescence was more strongly associated with LDMC, indicating that resource conservation strategies influenced the timing of late-season phenological events. Floral traits contributed to explain phenological variation but were of overall minor importance. Phenology-trait relationships were consistent across different environmental backgrounds represented by the Botanical Gardens.

In **Chapter III**, I investigated **interacting effects of climate and land-use type on the flowering phenology** of herbaceous plants and the **role of functional traits** in **mediating phenological responses**. First, I found that climate and land-use type (mowing or grazing) individually affected the flowering phenology of herbaceous plants in very species-specific ways (Figure V.1). Second, phenological climate responses were not modulated by land-use type. However, microclimatic conditions on meadows and pastures were affected differently by future climate scenarios, suggesting the potential for interactive effects of climate and land use on plant phenology. Third, phenological shifts under future climate were explained by traits related to an acquisitive growth strategy (e.g. SLA) and the phenological niche (i.e. flowering time and duration), with acquisitive, late and long flowering species showing decreases in flowering duration (Figure V.1).

In **Chapter IV**, I investigated how **temperature** and **solar radiation influence plant-pollinator interactions** by affecting **nectar traits** and **flower visitation rates**. Nectar quantity and quality responded species-specifically to abiotic conditions, with nectar volume generally decreasing under higher temperatures or increased solar radiation. The species-specific patterns are potentially influenced by floral traits such as flower shape and color. Similarly, flower visitation rates responded species-specifically to abiotic conditions but were primarily driven by flower abundance (Figure V.1). While nectar traits played a secondary role in shaping insect visitation patterns, their influence likely depended on the pollinator composition associated with each plant species. Furthermore, the lack of a clear correlation pattern between nectar traits and flower visitations may result from the complex interplay of direct and indirect effects of abiotic factors influencing pollinator activity.

General discussion

Phenology-trait relationships in the face of climate change

Functional traits serve as proxies for key ecological strategies, reflecting plant growth dynamics and resource use efficiency (Díaz et al., 2016; Westoby et al., 2002). This thesis highlights that **plant height** and **growth strategy-related traits** were crucial in explaining interspecific variation in phenology (Chapters II and III, Figure S III.2) and species-specific phenological shifts in response to climate change (Chapter III). Especially **plant height** that positively related to later reproductive phenology was a **key trait** for explaining interspecific phenological variation in Chapter II and III, confirming previous research (Bolmgren and D. Cowan, 2008; Du and Qi, 2010; E-Vojtkó et al., 2022; Huang et al., 2018; Jia et al., 2011; Segrestin et al., 2020; Sporbert et al., 2022; Sun and Frelich, 2011a). This frequently observed relationship reflects a time-size trade-off, where taller plants require more time to reach reproductive height and, as a result, flower later (Bolmgren and D. Cowan, 2008; Sun and Frelich, 2011a). The "time-size" trade-off involves balancing the benefits of growing larger before reproduction or reproducing earlier, with early flowering leading to a smaller plant size but offering more time for seed development, germination, and juvenile growth (Bolmgren and D. Cowan, 2008). Huang et al. (2018) propose plant size (involving height and foliage volume) as most important trait to consider in phenological studies, especially regarding phenological niche differentiation, as it is the key factor influencing biotic interactions, determining an individual’s survival and reproduction. While considering a large variety of traits including floral traits, my findings underscore the key role of plant height in mediating phenological patterns. It must be noted that the relationship between plant height and phenology varies by growth form (König et al., 2018). This thesis focuses on herbaceous species, where the relationship is evident, while in woody species, it was observed to be weaker, absent, or inverse (Bolmgren and D. Cowan, 2008; Du and Qi, 2010; König et al., 2018). The phenological stages primarily explained by plant height were mainly associated with reproductive phenology, while vegetative stages were more closely linked to different traits or were more strongly influenced by phylogenetic relatedness (Chapter II), suggesting that distinct processes govern vegetative and reproductive phenology. While plant height well explained interspecific phenological variation it did not play a role for explaining phenological shifts explored in Chapter III. This contrasts to König et al. (2018) that found that smaller plants stronger advanced flowering under climate change, indicating other traits, such as leaf economics, being more important for mediating phenological responses in the investigated grassland system.

This thesis demonstrates the **importance of growth strategy-related traits** in explaining phenological variation and shifts. Traits associated with the fast-slow growth and high-low resistance continua, such as SLA, LDMC, and mowing tolerance (Bucher et al., 2019; Pérez-Harguindeguy et al., 2016; Reich, 2014; Wright et al., 2004), explained interspecific variation in phenology (Chapter II) and responses to climate (Chapter III). An **acquisitive growth strategy**, characterized by fast growth and high resource use efficiency, was linked to earlier flowering (Chapters II, III; Figure SIII.2) and stronger phenological shifts under changing climate conditions (Chapter III), a pattern also reported in other studies (Bucher et al., 2018; Dorji et al., 2013; König et al., 2018). From this I conclude that the greater plasticity associated with acquisitive strategies (Atkin et al., 2006; Zhang et al., 2023) may facilitate a higher phenological responsiveness to climate change. In contrast, **conservative growth strategies**—associated with slower growth, longer leaf lifespan, and higher stress resistance (Pérez-Harguindeguy et al., 2016) —were linked to later flowering, fruiting, and senescence (Chapter II) (see also Bucher and Römermann, 2021) and exhibited weaker phenological shifts (Chapter III). Notably, some species with conservative traits were even able to extend their flowering duration under future climate conditions (Chapter III, Box 1), suggesting that drought-resistant species may have an advantage when drought limits the growth and development of acquisitive plants.

Grassland indicator values (Briemle et al., 2002) proved to be useful tools for understanding phenological responses in grassland systems, as they integrate traits related to growth capacity, plant height, and nutrient content—key components of plant growth strategies. However, these values are currently available only for common Central European grassland species, limiting their applicability to other regions. However, if indicator values are not available for the target species, key traits such as SLA, LDMC, plant height, growth form and nutrient content— which are encompassed within these indicators—could be used as alternatives in similar analyses.

The timing and duration of flowering summarized as the **phenological niche** played a key role in determining the extent and direction of phenological shifts under future climate conditions (Chapter III). While previous studies have found that early-flowering species exhibit the strongest advances in phenology (Fitter and Fitter, 2002; Lesica and Kittelson, 2010; Menzel et al., 2006; Miller-Rushing and Primack, 2008), this thesis identified an opposite pattern. Advances in early-flowering species are typically linked to early season warming and earlier snowmelt (linked to increased water availability), which individually or interactively accelerate plant development and flowering (Abu-Asab et al., 2001; Cornelius et al., 2013; Lesica and Kittelson, 2010; Rosbakh et al., 2021; Sherry et al., 2007; Stuble et al., 2021). However, in Chapter III, the warming treatment (~0.55°C mean increase) was relatively modest compared to regional climate projections (~2°C mean increase) (Schädler et al., 2019), likely limiting its influence on plant growth and phenology. In contrast, altered precipitation patterns—including increased rainfall in spring and autumn (~10% increase) and reduced summer precipitation (~20% decrease)—likely had a stronger impact by promoting spring growth while imposing summer drought stress that constrained plant development and flowering.

The most pronounced phenological shifts were observed in late and long-flowering species, suggesting that drought, rather than temperature, was the primary driver of phenological responses. While the combined effects of temperature and precipitation changes cannot be fully disentangled due to the experimental setup, the results indicate a phenological drought escape strategy, where summer-flowering species shortened their flowering duration to enhance survival under drought conditions. These findings underscore that a species' phenological niche determines which climatic factors most strongly constrain its growth relevant for flowering (e.g., warming in spring vs. drought in summer), thereby shaping its phenological response to climate change. Overall, the findings of this thesis suggest that a **species' phenological response** is highly context-dependent, driven by the interaction between its **functional traits (e.g., growth strategy, phenological niche)** and the **predominant limiting factor** (e.g., temperature, water, light, nutrients) at or preceding the time of flowering.

Floral traits played a **secondary role** for explaining phenological variation (Chapter II) and were not affected by climate and land-use in two plant species (Box 1). Chapter II presents a comprehensive assessment of floral traits, examining their coordination with widely studied vegetative traits and their relationship to detailed year-round phenological patterns. While previous studies have explored floral trait coordination, they have largely relied on database information or focused on different trait sets (E-Vojtkó et al., 2022). In contrast, this study integrates a diverse range of floral traits, including pollen and nectar traits, with detailed phenological data on the same plants, offering novel insights into trait-phenology relationships that have not been extensively investigated before.

The weak relationship between floral traits and phenology highlights the dominant role of vegetative traits in regulating plant growth, development, and consequently, phenology and phenological responses (Chapter II, III). My findings support the idea that the leaf and flower economic spectra are largely decoupled (E-Vojtkó et al., 2022), likely due to the lower evolvability of floral traits compared to vegetative traits (Opedal, 2019) and the distinct selective pressures acting on them (E-Vojtkó et al., 2022; Murren, 2002; Zhang et al., 2017). However, floral organs remain physiologically integrated within the vegetative plant body, requiring resources for development and maintenance, they cannot be considered independently of vegetative traits (Galen, 1999). This integration is evident in the correlation patterns observed between vegetative and floral traits (Chapter II), also observed by E-Vojtkó et al. (2022).

While abiotic factors undoubtedly influence floral traits, their evolution is primarily shaped by pollinator-mediated selection (Caruso et al., 2019; Galen, 1999), making them relatively decoupled from environmental constraints other than pollination. Pollination type—whether self- vs. cross-pollination or wind- vs. insect pollination—seems to shape flowering phenology and its responsiveness to climate change, with pollinator-dependent plants exhibiting stronger phenological shifts (E-Vojtkó et al., 2022; Fitter and Fitter, 2002; König et al., 2018; Segrestin et al., 2018). Thus, incorporating categorical traits like mating system and pollination type could improve our understanding of phenological patterns and climate responses in future assessments. Additionally, including size-related floral traits as presented in Chapter II provides insights into a plant's resource allocation between reproductive and vegetative structures, refining our understanding of different growth strategies (see also recommendations by Roddy et al., 2021).

Box 1: **Trait responses to climate and land use**: Functional traits can respond to changes in climate (Kuppler and Kotowska, 2021; Valencia et al., 2016) and land-use practices (Díaz et al., 2007, 2001). While Chapter III focused on phenological responses, examining how climate change and land use influence functional traits could improve predictions of plant community dynamics under future conditions. Initially, this thesis aimed to assess *in situ* trait responses, including floral traits, at the GCEF (see Chapter III for details on the experimental setup). However, due to space limitations caused by side experiments in the GCEF plots and unbalanced species distributions across treatments (see also Box 3), adequate sampling was only possible for two species (*Scabiosa ochroleuca* L. and *Taraxacum officinale* L.). Flower size (diameter of flower head), the number of flowers (flower heads) and floral display size (i.e., flower size x flower number) were assessed on two individuals per plot (4 treatment combinations future vs. ambient climate x meadow vs. pasture x 5 repetitions per treatment = 20 plots x 2 individuals = 40 individuals). For both species, flower size, number, and display size were not significantly affected by climate or land use, contrasting with previous findings (Kuppler et al., 2021; Kuppler and Kotowska, 2021) that reported reductions in flower size and number under drought conditions.

However, when accounting for species abundance (number of flowers per individual weighted for species abundance = flower abundance), *S. ochroleuca* exhibited increased flower abundance in meadows under future climate but a decline in pastures, indicating an interactive effect of climate and land use (climate x land use interaction, $p < 0.01$). In contrast, *T. officinale* showed lower flower abundance in pastures (land use effect, $p < 0.001$) and a marginally significant decline under future climate (climate effect, $p = 0.052$), without an interaction effect (Figure V.2). As the number of flowers of both species were not significantly affected by climate or land-use type these patterns were driven by differences in species abundance rather than direct trait responses. These findings highlight that while the investigated floral traits may not be directly affected by climate or land-use type, flower abundance—a key determinant of pollinator resources—can be influenced by these factors. Consequently, species abundance serves as a useful proxy for estimating floral resource availability under changing environmental conditions as for example shown by Baude et al. (2016) for Great Britain.

S. ochroleuca appears to benefit from future climate conditions, particularly in meadows, where it exhibits increased flower abundance (Figure V.2). While Chapter III linked acquisitive growth strategies to shortened flowering under future climate conditions, *S. ochroleuca* follows a more resource-conservative strategy, characterized by low SLA (Table III.1), which enhances its resistance to water-limited conditions. Consequently, this species was able to advance and extend its flowering period under future climate scenarios marked by summer drought (Figure III.1, III.2). These findings suggest that drought-resistant species with conservative growth strategies may be more resilient to climate change, whereas acquisitive species relying on drought escape strategies may be disadvantaged, particularly if flowering duration serves as a proxy for pollination success.

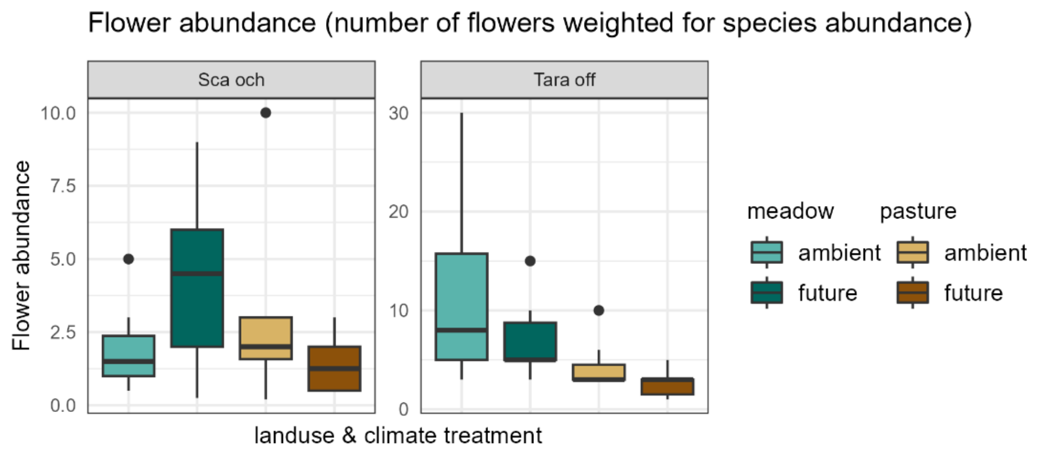

Figure V.2: Flower abundance of *Scabiosa ochroleuca* (left) and *Taraxacum officinale* (right) across climate and land-use treatments within the Global Change Experimental Facility (GCEF). Flower abundance is the number of flowers weighted for the species abundance (% cover) observed in the central 3m x 3m plot of the GCEF plots. For details on the experimental setup see Chapter III and Schädler et al. (2019).

Identifying Relevant Traits for Phenology-Trait Research

This thesis demonstrates that **plant height** and key **leaf traits** such as SLA and LDMC proof to work well for explaining interspecific phenological variation, and that the **phenological niche** and **growth-strategy** related traits such as SLA explain climate-driven phenological shifts in herbaceous species. However, for a more comprehensive understanding of phenological shifts pollination type should also be considered in future studies as discussed above. All these traits are widely available in floras and trait databases such as TRY, LEDA or BiolFlor (Kattge et al., 2020; Kleyer et al., 2008; Klotz et al., 2002), while vegetative traits are additionally easy and quick to assess, highlighting their broad applicability in phenology-trait studies. Additional traits that could be of interest for studying phenology-trait relationships, which were not addressed in this thesis, along with relevant practical considerations, are discussed in the following paragraphs.

Floral traits did not show strong relationships with phenology as presented in Chapter II. As floral traits are still comparably time consuming to assess they should be wisely selected according to the respective research questions. To get, for example, a perspective on a plants' resource investment in floral structures flower size, flower mass per area and flower longevity representing the main dimensions of the recently proposed **flower economic spectrum** (FES) could be used as baseline traits (Roddy et al., 2021). However, assessing flower mass per area is a destructive approach that incorporates the dry mass of the flower and might thus not be applicable in all contexts. It was, for example, not possible to sample whole inflorescences within the Botanical Gardens (Chapter II). In contrast, flower longevity is more time consuming to assess as single flowers need to be tagged and observed throughout days or weeks. As the goal within this thesis was to include as many species as possible this approach was unfortunately not feasible within the scope of this thesis.

Pollen traits showed no strong associations with phenological patterns (Chapter II), and the functional significance of their remarkable diversity remains poorly understood (Pacini and Franchi, 2020). However, pollen performance is a crucial determinant of reproductive success and is highly sensitive to temperature, making it particularly relevant in the context of climate change (Rosbakh et al., 2018). Future research should explore how the pollen traits examined in Chapter II influence pollen performance under varying abiotic conditions for a better understanding of the various functions of pollen traits.

The relationship between visually attractive floral traits, such as **flower color**, and phenology remains largely unclear. However, some evidence suggests that flower color may be linked to flowering phenology (Berrached et al., 2017; Wang et al., 2020). E-Vojtkó et al. (2022) found a relationship between flower color and pollination vector and type, with blue colored, nectar rewarding flowers being associated to insect pollination while rather inconspicuous flowers were associated to abiotic pollination. It could be assumed that the phenological sequence of flower colors appearing throughout the season will be tightly linked to the phenology of the most important pollinators in natural communities, reflecting their interactions. Furthermore, Chapter IV suggests that flower color and shape may influence how abiotic conditions such as temperature affect nectar properties, though this pattern requires validation across a broader range of species. Color perception largely differs between humans and insect pollinators and categorial information from floras or databases would neglect relevant aspects of the color spectrum (Chittka, 1997; Chittka and Menzel, 1992; Peitsch et al., 1992). To measure flower color in a meaningful way, i.e. by assessing the whole floral spectrum relevant to insect pollinator vision including UV patterns, spectroscopy techniques should be employed (see for example Sooraj et al., 2019). Detailed information on floral reflectance is still only available for a limited number of species, but databases like the Floral Reflectance Database (FReD) are constantly developing (Arnold et al., 2010), and might allow larger assessments of the relationships between phenology and flower color in the near future.

The presence and degree of **preformation in overwintering buds** have only recently been explored within a broader ecological context (Schnablová et al., 2024, 2021). The degree to which a plant species preforms leaves and inflorescences within its renewal buds plays a crucial role in shaping its phenology—for instance, species with highly preformed inflorescences tend to flower earlier (Schnablová et al., 2024, 2021). Given its potential influence on phenological responses, bud preformation should be investigated across a wider range of species and integrated into future studies on phenological shifts.

Belowground traits, particularly **root traits**, play a fundamental role in resource acquisition, storage, and plant growth (Freschet et al., 2021; Nord and Lynch, 2009), making them highly interesting traits when aiming at understanding interspecific phenological variation and plant responses to climate change. Despite their ecological significance, belowground traits have historically been underrepresented in studies on phenology-trait relationships, likely due to the methodological challenges and labor-intensive nature of their measurement (but see Berrached et al. (2017), Gahleitner et al. (2024)). However, recent years have seen increasing recognition of their importance, supported by the development of belowground trait databases and advancements in root trait research (Berrached et al., 2017; Guerrero-Ramírez et al., 2021; Iversen et al., 2017).

Findings from Chapter II suggest that belowground traits might contribute to explaining certain phenological patterns. Specifically, initial growth, flowering duration, and senescence were more strongly influenced by phylogenetic relatedness, likely due to differences between monocotyledonous spring geophytes—characterized by early growth onset, short flowering periods, and early senescence—and dicotyledonous species, which exhibited more variable phenological patterns within the investigated species set. Spring geophytes, which possess storage organs such as bulbs, tubers, or rhizomes, store carbohydrates that enable them to initiate growth and flowering early in the season, even before optimal growing conditions are established (Sheikh et al., 2022). In contrast, species lacking these storage structures must first accumulate carbohydrates under favorable conditions, often resulting in delayed growth and flowering. This distinction underscores the ecological advantage of storage organs in responding to seasonal changes (see also Schnablová et al. (2024). While the observed pattern in Chapter II remains a chance discovery requiring validation across a broader species set and phylogenetic gradient, it suggests a potential relevance of belowground traits in phenological research.

Despite the scarcity of phenological studies integrating root traits, recent research highlights their potential importance. A case study on two herbaceous species within the PhenObs network (Nordt et al., 2021) identified strong correlations between root traits—such as specific root length, root diameter, root branching density, specific root area, and root tips per dry weight—and phenological timing, with the strongest relationships occurring with reproductive stages (Gahleitner et al., 2024). Similarly, a study by Ye et al. (2024) reported a relationship between root dry matter content (RDMC) and autumn phenology, where high RDMC delayed senescence, analogous to the relationship observed for leaf dry matter content (LDMC) (Bucher and Römermann, 2021). These findings suggest that root traits, like leaf traits, align along an acquisitive-conservative spectrum, where acquisitive root traits facilitate rapid resource uptake, while conservative traits enhance resource retention strategies (Weigelt et al., 2021; Ye et al., 2024). Based on this framework, I hypothesize that plants with acquisitive root traits will be more strongly affected by climate-driven changes in resource availability, particularly water, leading to pronounced shifts in phenology—similar to patterns observed for leaf traits (see Chapter III). However, emerging research suggests that aboveground and belowground trait coordination may be largely independent (Carmona et al., 2021). While this remains a topic of debate, it appears to hold at least with respect to the 'fungal collaboration gradient' (Weigelt et al., 2023, 2021). This independence suggests that studies focusing solely on aboveground traits may overlook key belowground processes influencing phenology.

In light of the 'fungal collaboration gradient' proposed by Bergmann et al. (2020), I further speculate that plants associated with mycorrhizal symbiosis—characterized by large root diameters—may be less affected by resource fluctuations and thus exhibit weaker phenological responses to climate change. In contrast, species lacking mycorrhizal associations, typically exhibiting high specific root length, must acquire all essential resources independently and may therefore show stronger phenological shifts in response to climate variability. Incorporating root traits into phenology-trait studies will likely enhance our understanding of plant phenological responses to environmental change, help explain previously unexplained variation, and improve predictions of climate change impacts on plant life cycles.

While aboveground phenology is well studied, belowground phenological processes have received less attention. However, growing research highlights their importance, particularly in the context of climate change, where mismatches between above- and belowground phenology may have significant ecological consequences (Liu et al., 2022; Schwieger et al., 2019; Xin-Yi et al., 2023). To fully understand climate change impacts on plants and ecosystems, future research should also emphasize belowground phenology.

Box 2: Temporal flower availability under future climate on meadows and pastures: As demonstrated in Chapter III, flowering phenology species-specifically responded to climate and land-use type. However, to assess the overall effect of climate and land use on the temporal availability of floral resources within the plant community, it is necessary to combine the flowering phenology with information on the species abundance and flowering intensity. The metric of 'flower cover' combines the weekly observed species abundances (% cover) with their respective flowering intensities (%), using the formula: flower cover (%) = (abundance [%] * flowering intensity [%]) / 100. The 'total flower cover' is derived by summing the species-specific flower cover across all species present. When tracking this measure throughout the year, it is evident that pastures consistently show lower flower cover than meadows (Figure V.3). Following land management in early summer, flower cover remains low in both land-use types, although meadows show a better recovery than pastures. Notably, pastures under ambient climate conditions exhibit an additional flowering peak in late summer, which is absent under future climate scenarios (Figure V.3). This suggests that floral resource availability is influenced by the interaction between climate and land-use type, with future climate conditions potentially reducing floral resources, particularly in pastures.

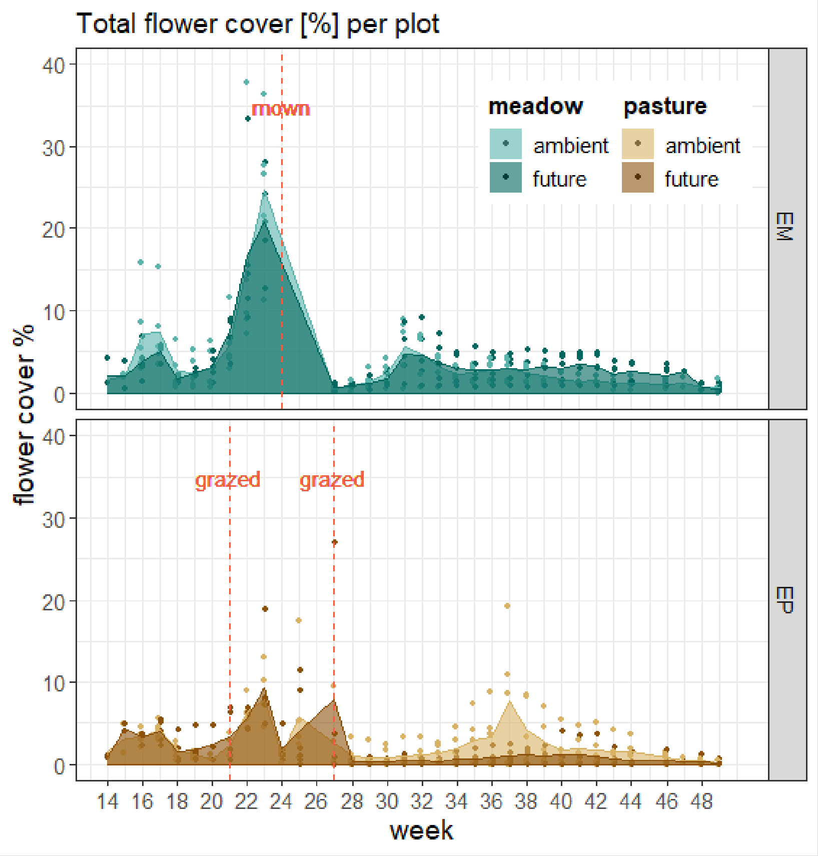

Figure V.3: Temporal flower availability throughout the season on meadows and pastures under ambient and future climate. Shown is the flower cover that considers the species abundance (% cover) on the observed 3m x 3m plot and combines it with the weekly observed flowering intensity (%) of each species occurring in the same plot. The total flower cover shown here sums up these values for all occurring species per plot and gives a measure for the percentage of area covered by flowers.

Implications for pollinators

Insect pollinators are in decline, facing multiple threats including climate and land-use change (Goulson et al., 2015; Hallmann et al., 2017; Potts et al., 2010; Vanbergen and the Insect Pollinators Initiative, 2013). While both plants and pollinators exhibit phenological shifts in response to climate change, research on plant-pollinator mismatches has yielded mixed results. Some studies suggest that synchronized shifts may minimize mismatches (Forrest, 2015; Hegland et al., 2009; Ovaskainen et al., 2013), whereas others emphasize a greater risk, particularly due to temporal gaps in floral resource availability (Høye et al., 2013; Ogilvie et al., 2017; Ogilvie and Forrest, 2017).

This thesis highlights the multiple ways in which climate and land use interact to shape flowering phenology and floral resource availability across different scales, including species-level phenology, species and community-level flower abundances, and species-level nectar properties (Box 1, Figure V.2; Box 2, Figure V.3; Chapter III, IV). Climate projections indicate increasing temperatures, reduced summer precipitation and increased drought frequency in temperate biomes (European Environment Agency, 2015; Intergovernmental Panel on Climate Change (IPCC), 2023), a trend also reflected in the future climate scenario at the GCEF (see Chapter III, Figures S III.1, S III.12). The findings of this thesis suggest that climate change, **particularly increased summer drought, will reduce the floral resource availability** in temperate grasslands, with potential consequences for pollinators. First, the phenological responses observed in Chapter III suggest that particularly acquisitive and late-flowering plant species, may shorten their flowering period as a strategy of drought escape. Second, flower abundance declined under future climate conditions, particularly in pastures, where disturbance through grazing likely intensifies the effects of drought stress (Box 1, Figure V.2; Box 2, Figure V.3). Many species despite commonly occurring across treatments did only rarely or never flower, a pattern that was especially pronounced on pastures that were characterized by a combination of disturbance through grazing and warmer and drier conditions (Box 3). While no significant effect of climate on flower size and number were detected (Box 1), changes in species abundances and flowering intensities influenced the overall floral resource availability (Box 1 and 2). In Chapter IV I showed that flower visitation by insects was mainly driven by flower abundance. Thus, decreased flower abundances on the species and community level may might lead to pollen limitation through fewer flower visits (Knight et al., 2005). Additionally, on the level of the individual plants nectar volume decreased with temperature and solar radiation, further limiting essential pollinator resources (Chapter IV).

Box 3: Flowering frequency of common species across climate and land-use types: Of the 95 species observed across the GCEF plots, 35 species occurred commonly across treatments, being present in at least 17 out of the 20 plots. However, only half of these species were flowering across plots and treatments, making them eligible for further analysis (see Chapter III). From Figure V.4 it is apparent that most of the rarely flowering species still flower in meadows but less often in the pasture plots particularly under future climate. An ANOVA testing the effect of climate and land-use type on the proportion of flowering plots revealed no climate but a land-use effect (estimated difference $_{\text{pasture-meadow}}$ = - 0.19; *F-value* = 6.29, *p-value* = 0.014, Figure V.5). The observed pattern may be linked to land management practices that occurred too early for some plants to flower, particularly since the first grazing took place earlier than the mowing. Additionally, the combination of grazing disturbances and drought-induced stress may have hindered the growth of certain species, preventing them from flowering.

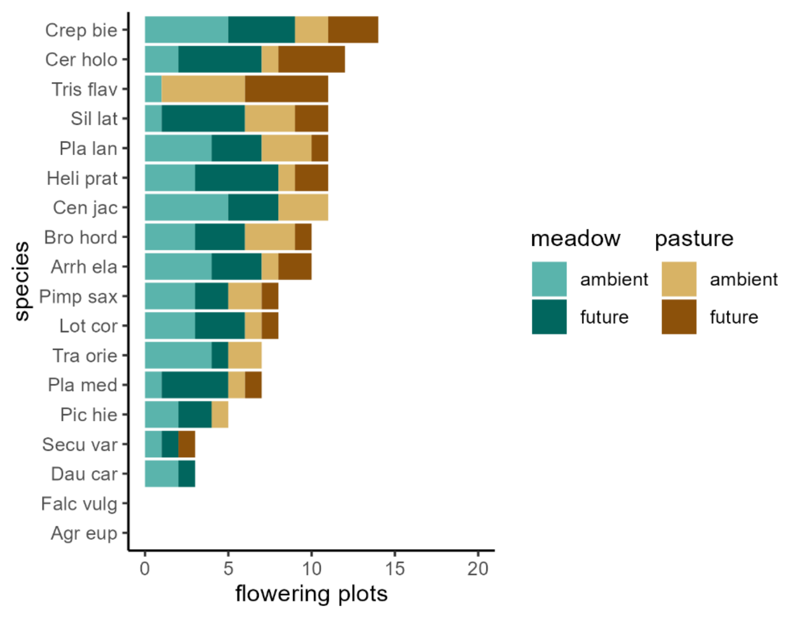

Figure V.4: Species that commonly occurred (in ≥17/20 plots) but rarely flowered (in ≤15 plots), making them ineligible for analysis in Chapter III (18/35 most common species). Bars show the number of plots where each species flowered (five repetitions per treatment). Colors represent GCEF treatments. Two species (*Falcaria vulgaris* Bernh., *Agrimonia eupatoria* L.) never flowered despite widely occurring.

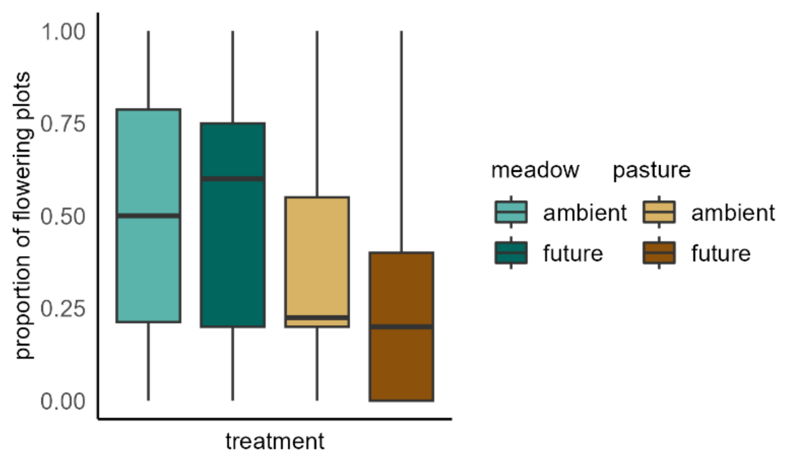

Figure V.5: Proportion of plots were common but rarely flowering species were flowering per treatment (compare Figure V.4). The proportion of flowering plots was significantly lower in pastures. For more details on the experiment and observation setup see Chapter III.

Altogether, my findings suggest a **decline in pollinator resources under future climate** by reducing and shifting the flower availability in the considered grasslands, especially on pastures (Chapter III, Box 1, 2, 3) and by changes in nectar properties through warming (Chapter IV). Pollinators could therefore be at least indirectly affected by climate change, as they have fewer floral resources available. Even though severe drought events, such as in 2018 and subsequent years, can led to local (quasi-)extinctions of plant species (Andrzejak et al., 2025), plant communities in extensively managed grasslands are expected to remain relatively stable under changing climatic conditions (Korell et al., 2024). Andrzejak et al. (2025) found that perennial plants in the same study system (GCEF) still exhibited positive population growth rates despite their reproduction being constrained by climate and land-use pressures, suggesting their ability to persist even under increasingly stressful environmental conditions. In contrast, pollinators may experience earlier and more direct negative effects due to reduced floral resources. Ogilvie et al. (2017) demonstrated that interannual pollinator abundance is strongly driven by indirect effects of climate on the floral resource phenology. They showed that particularly the number of floral days (i.e., number of days above a certain flower density threshold), that is primarily influenced by precipitation, explained changes in bumblebee abundances. Given that pollinators are generally more vulnerable to declines in floral resources than plants are to pollinator decline, the reductions in flower availability observed within this thesis may disproportionately impact pollinator populations (Davila et al., 2012; Høye et al., 2013; Ogilvie et al., 2017; Schleuning et al., 2016).

Limitations

The findings of this thesis are limited to **herbaceous species** within the **temperate biome**. The magnitude of phenological shifts was shown to differ among growth forms (Ge et al., 2015; König et al., 2018). König et al. (2018) showed that additionally phenology-trait relationships differ among growth forms and that the magnitude of phenological shifts also depends on the climatic zone especially in herbaceous plants. Thus, the transferability of the found phenology-trait relationships to other growth forms or other climatic zones is not clear and could be investigated in subsequent studies. The patterns observed in this thesis generally align with findings from previous research on herbaceous plants in temperate biomes, reinforcing the robustness of the thesis' conclusions (Bucher et al., 2018; E-Vojtkó et al., 2022; König et al., 2018; Sporbert et al., 2022; Sun and Frelich, 2011b).

The herbaceous species examined in this thesis are predominantly **perennials**. In contrast to annual species were growth and phenology responds more rapidly to changing climate, and evolutionary rates are faster due to the short generation cycles, perennial species might respond delayed or to a lesser degree to changing climate and being rather influenced by legacy effects from previous years e.g., related to warming or droughts (Fitter and Fitter, 2002; König et al., 2018; Nord and Lynch, 2009; Stuble et al., 2021). Although the effects of resource acquisition are expected to be similar between annuals and perennials, stored resources may play a more significant role than resources acquired in the current season for perennial plants (Bolmgren and D. Cowan, 2008; Nord and Lynch, 2009). Additionally, unlike annual species, perennial species are not reliant on flowering and reproduction within the same year. They can persist even in the absence of sexual reproduction, allowing them to withstand periods of limited reproduction over extended durations. This is in line with findings from a demography study on perennial plants within the GCEF. Andrzejak et al. (2025) showed that population growth rates were mainly positive under climate change while reproduction was identified as the key life stage mediating population growth. Additionally, many perennials are able of vegetative (clonal) reproduction and might favor vegetative before sexual reproduction especially under unfavorable conditions (Herben et al., 2015).

Recommendations for practical implementation

The following practical recommendations can be cautiously formulated from the results of this work. **Land management practices** like mowing or grazing and especially their **timing** and **frequency** should be **adapted to the local climatic conditions** to allow plants to flower and reproduce. Andrzejak et al. (2025) showed within the same experiment, the GCEF, that reproduction is the most crucial phase for long-term population growth rates and should thus be the focus of conservation practices. From the insights gained in Chapter III, were a big proportion of common species did not flower (50% of the 35 most common species flowered in <1/3 of the plots, two species never flowered, Box 3), I would recommend delaying land management in dry years (as was the study year 2020) to allow flowering and fruiting of more species. As the summer was characterized by drought that additionally constrained flowering of many species this decision needs to be carefully balanced (not too late, not to early). Also, the frequency of land management might need to be reduced according to drought conditions to allow recovery of the plant community and decrease local extinctions, as described by Andrzejak et al. (2025). It is important to note that my study was not designed to compare different intensities of land management. Therefore, this recommendation should be considered within the context of the specific land management practices and local climatic conditions at the GCEF in Bad Lauchstädt.

Plant phenology influences species interactions and coexistence and thus community assembly (Cleland and Wolkovich, 2024; Rudolf, 2019). In Chapter III I identified acquisitive growth strategies and the phenological niche as key traits that mediate phenological shifts to changing climate in a grassland system. Recent research has identified a potential link between phenological responses to warming and species performance, with species that exhibit greater phenological shifts tending to perform better under warmer conditions (Alexander and Levine, 2019; Cleland et al., 2012; Kotilainen et al., 2024; Macgregor et al., 2019). Thus, one could conclude that **acquisitive plants might have a competitive advantage** in future plant communities, while **conservative plants might exhibit enhanced stability in flowering** despite stressful conditions. When aiming at **restoring grassland habitats** these findings could be considered e.g., for selecting suitable species that represent diversity of strategy types.

Conclusion and future perspectives

This thesis highlights the central role of vegetative traits in shaping plant phenology. While plant height was the strongest predictor of interspecific phenological variation, traits associated with the growth strategy and phenological niche primarily mediated phenological shifts. Although floral traits played a secondary role in mediating interspecific phenological variation, their inclusion provides insight into an often-overlooked aspect of plant trait space, contributing to a broader understanding of the plant economic spectrum. Given the importance of leaf economics in phenological shifts, integrating floral traits from the flower economic spectrum (Roddy et al., 2021) could clarify whether flower economics are linked to leaf economics and contribute to phenological response strategies. Additionally, incorporating belowground traits—such as storage organs, root diameter, and specific root length—could provide a more comprehensive understanding of how resource-use strategies influence phenological patterns.

The findings of this thesis further suggest that pollinators may be negatively affected by future climate conditions due to declines in floral resources at multiple scales, including shifts in species-level phenology, species and community-level flower abundances, and species-level nectar properties. Understanding how these factors interact with plant functional traits is crucial for predicting the ecological consequences of climate change.

Future research should take a holistic approach by integrating key reproductive, vegetative, and belowground traits across the major axes of plant form and function as discussed above (para. Identifying Relevant Traits for Phenology-Trait Research). This would offer deeper insights into how traits collectively shape phenological variation, climate-induced phenological shifts, and their cascading effects on plant-pollinator interactions.

References

Abu-Asab, M.S., Peterson, P.M., Shetler, S.G., Orli, S.S., 2001. Earlier plant flowering in spring as a response to global warming in the Washington, DC, area. Biodiversity and Conservation 10, 597–612. https://doi.org/10.1023/A:1016667125469

Alexander, J.M., Levine, J.M., 2019. Earlier phenology of a nonnative plant increases impacts on native competitors. Proceedings of the National Academy of Sciences 116, 6199–6204. https://doi.org/10.1073/pnas.1820569116

Andrzejak, M., Knight, T.M., Plos, C., Korell, L., 2025. Changes in reproduction mediate the effects of climate change and grassland management on plant population dynamics. Ecological Applications 35, e3063. https://doi.org/10.1002/eap.3063

Arnold, S.E.J., Faruq, S., Savolainen, V., McOwan, P.W., Chittka, L., 2010. FReD: The Floral Reflectance Database — A Web Portal for Analyses of Flower Colour. PLOS ONE 5, e14287. https://doi.org/10.1371/journal.pone.0014287

Atkin, O.K., Loveys, B.R., Atkinson, L.J., Pons, T.L., 2006. Phenotypic plasticity and growth temperature: understanding interspecific variability. Journal of Experimental Botany 57, 267–281. https://doi.org/10.1093/jxb/erj029

Bergmann, J., Weigelt, A., van der Plas, F., Laughlin, D.C., Kuyper, T.W., Guerrero-Ramirez, N., Valverde-Barrantes, O.J., Bruelheide, H., Freschet, G.T., Iversen, C.M., Kattge, J., McCormack, M.L., Meier, I.C., Rillig, M.C., Roumet, C., Semchenko, M., Sweeney, C.J., van Ruijven, J., York, L.M., Mommer, L., 2020. The fungal collaboration gradient dominates the root economics space in plants. Science Advances 6, eaba3756. https://doi.org/10.1126/sciadv.aba3756

Berrached, R., Kadik, L., Mouheb, H.A., Prinzing, A., 2017. Deep roots delay flowering and relax the impact of floral traits and associated pollinators in steppe plants. PLOS ONE 12, e0173921. https://doi.org/10.1371/journal.pone.0173921

Bolmgren, K., D. Cowan, P., 2008. Time – size tradeoffs: a phylogenetic comparative study of flowering time, plant height and seed mass in a north-temperate flora. Oikos 117, 424–429. https://doi.org/10.1111/j.2007.0030-1299.16142.x

Briemle, G., Nitsche, S., Nitsche, L., 2002. Nutzungswertzahlen für Gefäßpflanzen des Grünlandes. Schriftenreihe für Vegetationskunde, Bundesamt für Naturschutz, Bonn 38, 203–225.

Bucher, S.F., Feiler, R., Buchner, O., Neuner, G., Rosbakh, S., Leiterer, M., Römermann, C., 2019. Temporal and spatial trade-offs between resistance and performance traits in herbaceous plant species. Environmental and Experimental Botany 157, 187–196. https://doi.org/10.1016/j.envexpbot.2018.10.015

Bucher, S.F., König, P., Menzel, A., Migliavacca, M., Ewald, J., Römermann, C., 2018. Traits and climate are associated with first flowering day in herbaceous species along elevational gradients. Ecology and Evolution 8, 1147–1158. https://doi.org/10.1002/ece3.3720

Bucher, S.F., Römermann, C., 2021. The timing of leaf senescence relates to flowering phenology and functional traits in 17 herbaceous species along elevational gradients. Journal of Ecology 109, 1537–1548. https://doi.org/10.1111/1365-2745.13577

Carmona, C.P., Bueno, C.G., Toussaint, A., Träger, S., Díaz, S., Moora, M., Munson, A.D., Pärtel, M., Zobel, M., Tamme, R., 2021. Fine-root traits in the global spectrum of plant form and function. Nature 597, 683–687. https://doi.org/10.1038/s41586-021-03871-y

Caruso, C.M., Eisen, K.E., Martin, R.A., Sletvold, N., 2019. A meta-analysis of the agents of selection on floral traits. Evolution 73, 4–14. https://doi.org/10.1111/evo.13639

Chittka, L., 1997. BEE COLOR VISION IS OPTIMAL FOR CODING FLOWER COLOR, BUT FLOWER COLORS ARE NOT OPTIMAL FOR BEING CODED—WHY? Israel Journal of Plant Sciences 45, 115–127. https://doi.org/10.1080/07929978.1997.10676678

Chittka, L., Menzel, R., 1992. The evolutionary adaptation of flower colours and the insect pollinators' colour vision. J Comp Physiol A 171, 171–181. https://doi.org/10.1007/BF00188925

Cleland, E.E., Allen, J.M., Crimmins, T.M., Dunne, J.A., Pau, S., Travers, S.E., Zavaleta, E.S., Wolkovich, E.M., 2012. Phenological tracking enables positive species responses to climate change. Ecology 93, 1765–1771. https://doi.org/10.1890/11-1912.1

Cleland, E.E., Wolkovich, E.M., 2024. Effects of Phenology on Plant Community Assembly and Structure. Annual Review of Ecology, Evolution, and Systematics 55, 471–492. https://doi.org/10.1146/annurev-ecolsys-102722-011653

Cornelius, C., Leingärtner, A., Hoiss, B., Krauss, J., Steffan-Dewenter, I., Menzel, A., 2013. Phenological response of grassland species to manipulative snowmelt and drought along an altitudinal gradient. Journal of Experimental Botany 64, 241–251. https://doi.org/10.1093/jxb/ers321

Davila, Y.C., Elle, E., Vamosi, J.C., Hermanutz, L., Kerr, J.T., Lortie, C.J., Westwood, A.R., Woodcock, T.S., Worley, A.C., 2012. Ecosystem services of pollinator diversity: a review of the relationship with pollen limitation of plant reproduction1This article is part of a Special Issue entitled "Pollination biology research in Canada: Perspectives on a mutualism at different scales". Botany 90, 535–543. https://doi.org/10.1139/b2012-017

Díaz, S., Kattge, J., Cornelissen, J.H.C., Wright, I.J., Lavorel, S., Dray, S., Reu, B., Kleyer, M., Wirth, C., Colin Prentice, I., Garnier, E., Bönisch, G., Westoby, M., Poorter, H., Reich, P.B., Moles, A.T., Dickie, J., Gillison, A.N., Zanne, A.E., Chave, J., Joseph Wright, S., Sheremet'ev, S.N., Jactel, H., Baraloto, C., Cerabolini, B., Pierce, S., Shipley, B., Kirkup, D., Casanoves, F., Joswig, J.S., Günther, A., Falczuk, V., Rüger, N., Mahecha, M.D., Gorné, L.D., 2016. The global spectrum of plant form and function. Nature 529, 167–171. https://doi.org/10.1038/nature16489

Díaz, S., Lavorel, S., McINTYRE, S., Falczuk, V., Casanoves, F., Milchunas, D.G., Skarpe, C., Rusch, G., Sternberg, M., Noy-Meir, I., Landsberg, J., Zhang, W., Clark, H., Campbell, B.D., 2007. Plant trait responses to grazing – a global synthesis. Global Change Biology 13, 313–341. https://doi.org/10.1111/j.1365-2486.2006.01288.x

Díaz, S., Noy-Meir, I., Cabido, M., 2001. Can grazing response of herbaceous plants be predicted from simple vegetative traits? Journal of Applied Ecology 38, 497–508. https://doi.org/10.1046/j.1365-2664.2001.00635.x

Dorji, T., Totland, Ø., Moe, S.R., Hopping, K.A., Pan, J., Klein, J.A., 2013. Plant functional traits mediate reproductive phenology and success in response to experimental warming and snow addition in Tibet. Global Change Biology 19, 459–472. https://doi.org/10.1111/gcb.12059

Du, G., Qi, W., 2010. Trade-offs between flowering time, plant height, and seed size within and across 11 communities of a QingHai-Tibetan flora. Plant Ecol 209, 321–333. https://doi.org/10.1007/s11258-010-9763-4

European Environment Agency, 2015. Climate change impacts and adaptation.

E-Vojtkó, A., Junker, R.R., de Bello, F., Götzenberger, L., 2022. Floral and reproductive traits are an independent dimension within the plant economic spectrum of temperate central Europe. New Phytologist 236, 1964–1975. https://doi.org/10.1111/nph.18386

Fitter, A.H., Fitter, R.S.R., 2002. Rapid Changes in Flowering Time in British Plants. Science 296, 1689–1691. https://doi.org/10.1126/science.1071617

Forrest, J.R.K., 2015. Plant–pollinator interactions and phenological change: what can we learn about climate impacts from experiments and observations? Oikos 124, 4–13. https://doi.org/10.1111/oik.01386

Freschet, G.T., Roumet, C., Comas, L.H., Weemstra, M., Bengough, A.G., Rewald, B., Bardgett, R.D., De Deyn, G.B., Johnson, D., Klimešová, J., Lukac, M., McCormack, M.L., Meier, I.C., Pagès, L., Poorter, H., Prieto, I., Wurzburger, N., Zadworny, M., Bagniewska-Zadworna, A., Blancaflor, E.B., Brunner, I., Gessler, A., Hobbie, S.E., Iversen, C.M., Mommer, L., Picon-Cochard, C., Postma, J.A., Rose, L., Ryser, P., Scherer-Lorenzen, M., Soudzilovskaia, N.A., Sun, T., Valverde-Barrantes, O.J., Weigelt, A., York, L.M., Stokes, A., 2021. Root traits as drivers of plant and ecosystem functioning: current understanding, pitfalls and future research needs. New Phytologist 232, 1123–1158. https://doi.org/10.1111/nph.17072

Gahleitner, S., Krause, L., Rauschkolb, R., Ioni, S., Reichl, J., Knickmann, B., Lang, I., 2024. Two herbaceous plants and their root systems' association to phenology and weather across botanical gardens.

Galen, C., 1999. Why Do Flowers Vary?: The functional ecology of variation in flower size and form within natural plant populations. BioScience 49, 631–640. https://doi.org/10.2307/1313439

Ge, Q., Wang, H., Rutishauser, T., Dai, J., 2015. Phenological response to climate change in China: a meta-analysis. Global Change Biology 21, 265–274. https://doi.org/10.1111/gcb.12648

Goulson, D., Nicholls, E., Botías, C., Rotheray, E.L., 2015. Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. Science 347, 1255957. https://doi.org/10.1126/science.1255957

Guerrero-Ramírez, N.R., Mommer, L., Freschet, G.T., Iversen, C.M., McCormack, M.L., Kattge, J., Poorter, H., van der Plas, F., Bergmann, J., Kuyper, T.W., York, L.M., Bruelheide, H., Laughlin, D.C., Meier, I.C., Roumet, C., Semchenko, M., Sweeney, C.J., van Ruijven, J., Valverde-Barrantes, O.J., Aubin, I., Catford, J.A., Manning, P., Martin, A., Milla, R., Minden, V., Pausas, J.G., Smith, S.W., Soudzilovskaia, N.A., Ammer, C., Butterfield, B., Craine, J., Cornelissen, J.H.C., de Vries, F.T., Isaac, M.E., Kramer, K., König, C., Lamb, E.G., Onipchenko, V.G., Peñuelas, J., Reich, P.B., Rillig, M.C., Sack, L., Shipley, B., Tedersoo, L., Valladares, F., van Bodegom, P., Weigelt, P., Wright, J.P., Weigelt, A., 2021. Global root traits (GRooT) database. Global Ecology and Biogeography 30, 25–37. https://doi.org/10.1111/geb.13179

Hallmann, C.A., Sorg, M., Jongejans, E., Siepel, H., Hofland, N., Schwan, H., Stenmans, W., Müller, A., Sumser, H., Hörren, T., Goulson, D., Kroon, H. de, 2017. More than 75 percent decline over 27 years in total flying insect biomass in protected areas. PLOS ONE 12, e0185809. https://doi.org/10.1371/journal.pone.0185809

Hegland, S.J., Nielsen, A., Lázaro, A., Bjerknes, A.-L., Totland, Ø., 2009. How does climate warming affect plant-pollinator interactions? Ecology Letters 12, 184–195. https://doi.org/10.1111/j.1461-0248.2008.01269.x

Herben, T., Šerá, B., Klimešová, J., 2015. Clonal growth and sexual reproduction: tradeoffs and environmental constraints. Oikos 124, 469–476. https://doi.org/10.1111/oik.01692

Høye, T.T., Post, E., Schmidt, N.M., Trøjelsgaard, K., Forchhammer, M.C., 2013. Shorter flowering seasons and declining abundance of flower visitors in a warmer Arctic. Nature Clim Change 3, 759–763. https://doi.org/10.1038/nclimate1909

Huang, L., Koubek, T., Weiser, M., Herben, T., 2018. Environmental drivers and phylogenetic constraints of growth phenologies across a large set of herbaceous species. Journal of Ecology 106, 1621–1633. https://doi.org/10.1111/1365-2745.12927

Intergovernmental Panel on Climate Change (IPCC) (Ed.), 2023. Weather and Climate Extreme Events in a Changing Climate, in: Climate Change 2021 – The Physical Science Basis: Working Group I Contribution to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, pp. 1513–1766. https://doi.org/10.1017/9781009157896.013

Iversen, C.M., McCormack, M.L., Powell, A.S., Blackwood, C.B., Freschet, G.T., Kattge, J., Roumet, C., Stover, D.B., Soudzilovskaia, N.A., Valverde-Barrantes, O.J., van Bodegom, P.M., Violle, C., 2017. A global Fine-Root Ecology Database to address below-ground challenges in plant ecology. New Phytologist 215, 15–26. https://doi.org/10.1111/nph.14486

Jia, P., Bayaerta, T., Li, X., Du, G., 2011. Relationships between Flowering Phenology and Functional Traits in Eastern Tibet Alpine Meadow. Arctic, Antarctic, and Alpine Research 43, 585–592. https://doi.org/10.1657/1938-4246-43.4.585

Kattge, J., Bönisch, G., Díaz, S., Lavorel, S., Prentice, I.C., Leadley, P., Tautenhahn, S., Werner, G.D.A., Aakala, T., Abedi, M., Acosta, A.T.R., Adamidis, G.C., Adamson, K., Aiba, M., Albert, C.H., Alcántara, J.M., Alcázar C, C., Aleixo, I., Ali, H., Amiaud, B., Ammer, C., Amoroso, M.M., Anand, M., Anderson, C., Anten, N., Antos, J., Apgaua, D.M.G., Ashman, T.-L., Asmara, D.H., Asner, G.P., Aspinwall, M., Atkin, O., Aubin, I., Baastrup-Spohr, L., Bahalkeh, K., Bahn, M., Baker, T., Baker, W.J., Bakker, J.P., Baldocchi, D., Baltzer, J., Banerjee, A., Baranger, A., Barlow, J., Barneche, D.R., Baruch, Z., Bastianelli, D., Battles, J., Bauerle, W., Bauters, M., Bazzato, E., Beckmann, M., Beeckman, H., Beierkuhnlein, C., Bekker, R., Belfry, G., Belluau, M., Beloiu, M., Benavides, R., Benomar, L., Berdugo-Lattke, M.L., Berenguer, E., Bergamin, R., Bergmann, J., Bergmann Carlucci, M., Berner, L., Bernhardt-Römermann, M., Bigler, C., Bjorkman, A.D., Blackman, C., Blanco, C., Blonder, B., Blumenthal, D., Bocanegra-González, K.T., Boeckx, P., Bohlman, S., Böhning-Gaese, K., Boisvert-Marsh, L., Bond, W., Bond-Lamberty, B., Boom, A., Boonman, C.C.F., Bordin, K., Boughton, E.H., Boukili, V., Bowman, D.M.J.S., Bravo, S., Brendel, M.R., Broadley, M.R., Brown, K.A., Bruelheide, H., Brumnich, F., Bruun, H.H., Bruy, D., Buchanan, S.W., Bucher, S.F., Buchmann, N., Buitenwerf, R., Bunker, D.E., Bürger, J., Burrascano, S., Burslem, D.F.R.P., Butterfield, B.J., Byun, C., Marques, M., Scalon, M.C., Caccianiga, M., Cadotte, M., Cailleret, M., Camac, J., Camarero, J.J., Campany, C., Campetella, G., Campos, J.A., Cano-Arboleda, L., Canullo, R., Carbognani, M., Carvalho, F., Casanoves, F., Castagneyrol, B., Catford, J.A., Cavender-Bares, J., Cerabolini, B.E.L., Cervellini, M., Chacón-Madrigal, E., Chapin, K., Chapin, F.S., Chelli, S., Chen, S.-C., Chen, A., Cherubini, P., Chianucci, F., Choat, B., Chung, K.-S., Chytrý, M., Ciccarelli, D., Coll, L., Collins, C.G., Conti, L., Coomes, D., Cornelissen, J.H.C., Cornwell, W.K., Corona, P., Coyea, M., Craine, J., Craven, D., Cromsigt, J.P.G.M., Csecserits, A., Cufar, K., Cuntz, M., da Silva, A.C., Dahlin, K.M., Dainese, M., Dalke, I., Dalle Fratte, M., Dang-Le, A.T., Danihelka, J., Dannoura, M., Dawson, S., de Beer, A.J., De Frutos, A., De Long, J.R., Dechant, B., Delagrange, S., Delpierre, N., Derroire, G., Dias, A.S., Diaz-Toribio, M.H., Dimitrakopoulos, P.G., Dobrowolski, M., Doktor, D., Dřevojan, P., Dong, N., Dransfield, J., Dressler, S., Duarte, L., Ducouret, E., Dullinger, S., Durka, W., Duursma, R., Dymova, O., E-Vojtkó, A., Eckstein, R.L., Ejtehadi, H., Elser, J., Emilio, T., Engemann, K., Erfanian, M.B., Erfmeier, A., Esquivel-Muelbert, A., Esser, G., Estiarte, M., Domingues, T.F., Fagan, W.F., Fagúndez, J., Falster, D.S., Fan, Y., Fang, J., Farris, E., Fazlioglu, F., Feng, Y., Fernandez-Mendez, F., Ferrara, C., Ferreira, J., Fidelis, A., Finegan, B., Firn, J., Flowers, T.J., Flynn, D.F.B., Fontana, V., Forey, E., Forgiarini, C., François, L., Frangipani, M., Frank, D., Frenette-Dussault, C., Freschet, G.T., Fry, E.L., Fyllas, N.M., Mazzochini, G.G., Gachet, S., Gallagher, R., Ganade, G., Ganga, F., García-Palacios, P., Gargaglione, V., Garnier, E., Garrido, J.L., de Gasper, A.L., Gea-Izquierdo, G., Gibson, D., Gillison, A.N., Giroldo, A., Glasenhardt, M.-C., Gleason, S., Gliesch, M., Goldberg, E., Göldel, B., Gonzalez-Akre, E., Gonzalez-Andujar, J.L., González-Melo, A., González-Robles, A., Graae, B.J., Granda, E., Graves, S., Green, W.A., Gregor, T., Gross, N., Guerin, G.R., Günther, A., Gutiérrez, A.G., Haddock, L., Haines, A., Hall, J., Hambuckers, A., Han, W., Harrison, S.P., Hattingh, W., Hawes, J.E., He, T., He, P., Heberling, J.M., Helm, A., Hempel, S., Hentschel, J., Hérault, B., Hereş, A.-M., Herz, K., Heuertz, M., Hickler, T., Hietz, P., Higuchi, P., Hipp, A.L., Hirons, A., Hock, M., Hogan, J.A., Holl, K., Honnay, O., Hornstein, D., Hou, E., Hough-Snee, N., Hovstad, K.A., Ichie, T., Igić, B., Illa, E., Isaac, M., Ishihara, M., Ivanov, L., Ivanova, L., Iversen, C.M., Izquierdo, J., Jackson, R.B., Jackson, B., Jactel, H., Jagodzinski, A.M., Jandt, U., Jansen, S., Jenkins, T., Jentsch, A., Jespersen, J.R.P., Jiang, G.-F., Johansen, J.L., Johnson, D., Jokela, E.J., Joly, C.A., Jordan, G.J., Joseph, G.S., Junaedi, D., Junker, R.R., Justes, E., Kabzems, R., Kane, J., Kaplan, Z., Kattenborn, T., Kavelenova, L., Kearsley, E., Kempel, A., Kenzo, T., Kerkhoff, A., Khalil, M.I., Kinlock, N.L., Kissling, W.D., Kitajima, K., Kitzberger, T., Kjøller, R., Klein, T., Kleyer, M., Klimešová, J., Klipel, J., Kloeppel, B., Klotz, S., Knops, J.M.H., Kohyama, T., Koike, F., Kollmann, J., Komac, B., Komatsu, K., König, C., Kraft, N.J.B., Kramer, K., Kreft, H., Kühn, I., Kumarathunge, D., Kuppler, J., Kurokawa, H., Kurosawa, Y., Kuyah, S., Laclau, J.-P., Lafleur, B., Lallai, E., Lamb, E., Lamprecht, A., Larkin, D.J., Laughlin, D., Le Bagousse-Pinguet, Y., le Maire, G., le Roux, P.C., le Roux, E., Lee, T., Lens, F., Lewis, S.L., Lhotsky, B., Li, Y., Li, X., Lichstein, J.W., Liebergesell, M., Lim, J.Y., Lin, Y.-S., Linares, J.C., Liu, C., Liu, D., Liu, U., Livingstone, S., Llusià, J., Lohbeck, M., López-García, Á., Lopez-Gonzalez, G., Lososová, Z., Louault, F., Lukács, B.A., Lukeš, P., Luo, Y., Lussu, M., Ma, S., Maciel Rabelo Pereira, C., Mack, M., Maire, V., Mäkelä, A., Mäkinen, H., Malhado, A.C.M., Mallik, A., Manning, P., Manzoni, S., Marchetti, Z., Marchino, L., Marcilio-Silva, V., Marcon, E., Marignani, M., Markesteijn, L., Martin, A., Martínez-Garza, C., Martínez-Vilalta, J., Mašková, T., Mason, K., Mason, N., Massad, T.J., Masse, J., Mayrose, I., McCarthy, J., McCormack, M.L., McCulloh, K., McFadden, I.R., McGill, B.J., McPartland, M.Y., Medeiros, J.S., Medlyn, B., Meerts, P., Mehrabi, Z., Meir, P., Melo, F.P.L., Mencuccini, M., Meredieu, C., Messier, J., Mészáros, I., Metsaranta, J., Michaletz, S.T., Michelaki, C., Migalina, S., Milla, R., Miller, J.E.D., Minden, V., Ming, R., Mokany, K., Moles, A.T., Molnár V, A., Molofsky, J., Molz, M., Montgomery, R.A., Monty, A., Moravcová, L., Moreno-Martínez, A., Moretti, M., Mori, A.S., Mori, S., Morris, D., Morrison, J., Mucina, L., Mueller, S., Muir, C.D., Müller, S.C., Munoz, F., Myers-Smith, I.H., Myster, R.W., Nagano, M., Naidu, S., Narayanan, A., Natesan, B., Negoita, L., Nelson, A.S., Neuschulz, E.L., Ni, J., Niedrist, G., Nieto, J., Niinemets, Ü., Nolan, R., Nottebrock, H., Nouvellon, Y., Novakovskiy, A., Network, T.N., Nystuen, K.O., O'Grady, A., O'Hara, K., O'Reilly-Nugent, A., Oakley, S., Oberhuber, W., Ohtsuka, T., Oliveira, R., Öllerer, K., Olson, M.E., Onipchenko, V., Onoda, Y., Onstein, R.E., Ordonez, J.C., Osada, N., Ostonen, I., Ottaviani, G., Otto, S., Overbeck, G.E., Ozinga, W.A., Pahl, A.T., Paine, C.E.T., Pakeman, R.J., Papageorgiou, A.C., Parfionova, E., Pärtel, M., Patacca, M., Paula, S., Paule, J., Pauli, H., Pausas, J.G., Peco, B., Penuelas, J., Perea, A., Peri, P.L., Petisco-Souza, A.C., Petraglia, A., Petritan, A.M., Phillips, O.L., Pierce, S., Pillar, V.D., Pisek, J., Pomogaybin, A., Poorter, H., Portsmuth, A., Poschlod, P., Potvin, C., Pounds, D., Powell, A.S., Power, S.A., Prinzing, A., Puglielli, G., Pyšek, P., Raevel, V., Rammig, A., Ransijn, J., Ray, C.A., Reich, P.B., Reichstein, M., Reid, D.E.B., Réjou-Méchain, M., de Dios, V.R., Ribeiro, S., Richardson, S., Riibak, K., Rillig, M.C., Riviera, F., Robert, E.M.R., Roberts, S., Robroek, B., Roddy, A., Rodrigues, A.V., Rogers, A., Rollinson, E., Rolo, V., Römermann, C., Ronzhina, D., Roscher, C., Rosell, J.A., Rosenfield, M.F., Rossi, C., Roy, D.B., Royer-Tardif, S., Rüger, N., Ruiz-Peinado, R., Rumpf, S.B., Rusch, G.M., Ryo, M., Sack, L., Saldaña, A., Salgado-Negret, B., Salguero-Gomez, R., Santa-Regina, I., Santacruz-García, A.C., Santos, J., Sardans, J., Schamp, B., Scherer-Lorenzen, M., Schleuning, M., Schmid, B., Schmidt, M., Schmitt, S., Schneider, J.V., Schowanek, S.D., Schrader, J., Schrodt, F., Schuldt, B., Schurr, F., Selaya Garvizu, G., Semchenko, M., Seymour, C., Sfair, J.C., Sharpe, J.M., Sheppard, C.S., Sheremetiev, S., Shiodera, S., Shipley, B., Shovon, T.A., Siebenkäs, A., Sierra, C., Silva, V., Silva, M., Sitzia, T., Sjöman, H., Slot, M., Smith, N.G., Sodhi, D., Soltis, P., Soltis, D., Somers, B., Sonnier, G., Sørensen, M.V., Sosinski Jr, E.E., Soudzilovskaia, N.A., Souza, A.F., Spasojevic, M., Sperandii, M.G., Stan, A.B., Stegen, J., Steinbauer, K., Stephan, J.G., Sterck, F., Stojanovic, D.B., Strydom, T., Suarez, M.L., Svenning, J.-C., Svitková, I., Svitok, M., Svoboda, M., Swaine, E., Swenson, N., Tabarelli, M., Takagi, K., Tappeiner, U., Tarifa, R., Tauugourdeau, S., Tavsanoglu, C., te Beest, M., Tedersoo, L., Thiffault, N., Thom, D., Thomas, E., Thompson, K., Thornton, P.E., Thuiller, W., Tichý, L., Tissue, D., Tjoelker, M.G., Tng, D.Y.P., Tobias, J., Török, P., Tarin, T., Torres-Ruiz, J.M., Tóthmérész, B., Treurnicht, M., Trivellone, V., Trolliet, F., Trotsiuk, V., Tsakalos, J.L., Tsiripidis, I., Tysklind, N., Umehara, T., Usoltsev, V., Vadeboncoeur, M., Vaezi, J., Valladares, F., Vamosi, J., van Bodegom, P.M., van Breugel, M., Van Cleemput, E., van de Weg, M., van der Merwe, S., van der Plas, F., van der Sande, M.T., van Kleunen, M., Van Meerbeek, K., Vanderwel, M., Vanselow, K.A., Vårhammar, A., Varone, L., Vasquez Valderrama, M.Y., Vassilev, K., Vellend, M., Veneklaas, E.J., Verbeeck, H., Verheyen, K., Vibrans, A., Vieira, I., Villacís, J., Violle, C., Vivek, P., Wagner, K., Waldram, M., Waldron, A., Walker, A.P., Waller, M., Walther, G., Wang, H., Wang, F., Wang, W., Watkins, H., Watkins, J., Weber, U., Weedon, J.T., Wei, L., Weigelt, P., Weiher, E., Wells, A.W., Wellstein, C., Wenk, E., Westoby, M., Westwood, A., White, P.J., Whitten, M., Williams, M., Winkler, D.E., Winter, K., Womack, C., Wright, I.J., Wright, S.J., Wright, J., Pinho, B.X., Ximenes, F., Yamada, T., Yamaji, K., Yanai, R., Yankov, N., Yguel, B., Zanini, K.J., Zanne, A.E., Zelený, D., Zhao, Y.-P., Zheng, Jingming, Zheng, Ji, Ziemińska, K., Zirbel, C.R., Zizka, G., Zo-Bi, I.C., Zotz, G., Wirth, C., 2020. TRY plant trait database – enhanced coverage and open access. Global Change Biology 26, 119–188. https://doi.org/10.1111/gcb.14904

Kleyer, M., Bekker, R. m., Knevel, I. c., Bakker, J. p., Thompson, K., Sonnenschein, M., Poschlod, P., Van Groenendael, J. m., Klimeš, L., Klimešová, J., Klotz, S., Rusch, G. m., Hermy, M., Adriaens, D., Boedeltje, G., Bossuyt, B., Dannemann, A., Endels, P., Götzenberger, L., Hodgson, J. g., Jackel, A.-K., Kühn, I., Kunzmann, D., Ozinga, W. a., Römermann, C., Stadler, M., Schlegelmilch, J., Steendam, H. j., Tackenberg, O., Wilmann, B., Cornelissen, J. h. c., Eriksson, O., Garnier, E., Peco, B., 2008. The LEDA

Traitbase: a database of life-history traits of the Northwest European flora. Journal of Ecology 96, 1266–1274. https://doi.org/10.1111/j.1365-2745.2008.01430.x

Klotz, S., Kühn, I., Durka, W., 2002. BiolFlor: Eine Datenbank mit biologisch-ökologischen Merkmalen zur Flora von Deutschland. Schriftenreihe für Vegetationskunde, Bonn: Bundesamt für Naturschutz.

Knight, T.M., Steets, J.A., Vamosi, J.C., Mazer, S.J., Burd, M., Campbell, D.R., Dudash, M.R., Johnston, M.O., Mitchell, R.J., Ashman, T.-L., 2005. Pollen Limitation of Plant Reproduction: Pattern and Process. Annual Review of Ecology, Evolution, and Systematics 36, 467–497. https://doi.org/10.1146/annurev.ecolsys.36.102403.115320

König, P., Tautenhahn, S., Cornelissen, J.H.C., Kattge, J., Bönisch, G., Römermann, C., 2018. Advances in flowering phenology across the Northern Hemisphere are explained by functional traits. Global Ecology and Biogeography 27, 310–321. https://doi.org/10.1111/geb.12696

Korell, L., Andrzejak, M., Berger, S., Durka, W., Haider, S., Hensen, I., Herion, Y., Höfner, J., Kindermann, L., Klotz, S., Knight, T.M., Linstädter, A., Madaj, A.-M., Merbach, I., Michalski, S., Plos, C., Roscher, C., Schädler, M., Welk, E., Auge, H., 2024. Land use modulates resistance of grasslands against future climate and inter-annual climate variability in a large field experiment. Global Change Biology 30, e17418. https://doi.org/10.1111/gcb.17418

Kotilainen, A., Mattila, A.L.K., Møller, C., Koivusaari, S., Hyvärinen, M.-T., Hällfors, M.H., 2024. Higher thermal plasticity in flowering phenology increases flowering output. Ecology and Evolution 14, e11657. https://doi.org/10.1002/ece3.11657

Kuppler, J., Kotowska, M.M., 2021. A meta-analysis of responses in floral traits and flower–visitor interactions to water deficit. Global Change Biology 27, 3095–3108. https://doi.org/10.1111/gcb.15621

Kuppler, J., Wieland, J., Junker, R.R., Ayasse, M., 2021. Drought-induced reduction in flower size and abundance correlates with reduced flower visits by bumble bees. AoB PLANTS 13. https://doi.org/10.1093/aobpla/plab001

Lesica, P., Kittelson, P.M., 2010. Precipitation and temperature are associated with advanced flowering phenology in a semi-arid grassland. Journal of Arid Environments 74, 1013–1017. https://doi.org/10.1016/j.jaridenv.2010.02.002

Liu, H., Wang, H., Li, N., Shao, J., Zhou, X., van Groenigen, K.J., Thakur, M.P., 2022. Phenological mismatches between above- and belowground plant responses to climate warming. Nat. Clim. Chang. 12, 97–102. https://doi.org/10.1038/s41558-021-01244-x

Macgregor, C.J., Thomas, C.D., Roy, D.B., Beaumont, M.A., Bell, J.R., Brereton, T., Bridle, J.R., Dytham, C., Fox, R., Gotthard, K., Hoffmann, A.A., Martin, G., Middlebrook, I., Nylin, S., Platts, P.J., Rasteiro, R., Saccheri, I.J., Villoutreix, R., Wheat, C.W., Hill, J.K., 2019. Climate-induced phenology shifts linked to range expansions in species with multiple reproductive cycles per year. Nat Commun 10, 4455. https://doi.org/10.1038/s41467-019-12479-w

Menzel, A., Sparks, T.H., Estrella, N., Koch, E., Aasa, A., Ahas, R., Alm-Kübler, K., Bissolli, P., Braslavská, O., Briede, A., Chmielewski, F.M., Crepinsek, Z., Curnel, Y., Dahl, Å., Defila, C., Donnelly, A., Filella, Y., Jatczak, K., Måge, F., Mestre, A., Nordli, Ø., Peñuelas, J., Pirinen, P., Remišová, V., Scheifinger, H., Striz, M., Susnik, A., Van Vliet, A.J.H., Wielgolaski, F.-E., Zach, S., Zust, A., 2006. European phenological response to climate change matches the warming pattern. Global Change Biology 12, 1969–1976. https://doi.org/10.1111/j.1365-2486.2006.01193.x

Miller-Rushing, A.J., Primack, R.B., 2008. Global Warming and Flowering Times in Thoreau's Concord: A Community Perspective. Ecology 89, 332–341. https://doi.org/10.1890/07-0068.1

Murren, C.J., 2002. Phenotypic integration in plants. Plant Species Biology 17, 89–99. https://doi.org/10.1046/j.1442-1984.2002.00079.x

Nord, E.A., Lynch, J.P., 2009. Plant phenology: a critical controller of soil resource acquisition. Journal of Experimental Botany 60, 1927–1937. https://doi.org/10.1093/jxb/erp018

Nordt, B., Hensen, I., Bucher, S.F., Freiberg, M., Primack, R.B., Stevens, A.-D., Bonn, A., Wirth, C., Jakubka, D., Plos, C., Sporbert, M., Römermann, C., 2021. The PhenObs initiative: A standardised protocol for monitoring phenological responses to climate change using herbaceous plant species in botanical gardens. Functional Ecology 35, 821–834. https://doi.org/10.1111/1365-2435.13747

Ogilvie, J.E., Forrest, J.R., 2017. Interactions between bee foraging and floral resource phenology shape bee populations and communities. Current Opinion in Insect Science, Pests and resistance * Behavioural ecology 21, 75–82. https://doi.org/10.1016/j.cois.2017.05.015

Ogilvie, J.E., Griffin, S.R., Gezon, Z.J., Inouye, B.D., Underwood, N., Inouye, D.W., Irwin, R.E., 2017. Interannual bumble bee abundance is driven by indirect climate effects on floral resource phenology. Ecology Letters 20, 1507–1515. https://doi.org/10.1111/ele.12854

Opedal, Ø.H., 2019. The evolvability of animal-pollinated flowers: towards predicting adaptation to novel pollinator communities. New Phytologist 221, 1128–1135. https://doi.org/10.1111/nph.15403

Ovaskainen, O., Skorokhodova, S., Yakovleva, M., Sukhov, A., Kutenkov, A., Kutenkova, N., Shcherbakov, A., Meyke, E., Delgado, M. del M., 2013. Community-level phenological response to climate change. Proceedings of the National Academy of Sciences 110, 13434–13439. https://doi.org/10.1073/pnas.1305533110

Pacini, E., Franchi, G.G., 2020. Pollen biodiversity – why are pollen grains different despite having the same function? A review. Botanical Journal of the Linnean Society 193, 141–164. https://doi.org/10.1093/botlinnean/boaa014

Peitsch, D., Fietz, A., Hertel, H., de Souza, J., Ventura, D.F., Menzel, R., 1992. The spectral input systems of hymenopteran insects and their receptor-based colour vision. J Comp Physiol A 170, 23–40. https://doi.org/10.1007/BF00190398

Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., Bret-Harte, M.S., Cornwell, W.K., Craine, J.M., Gurvich, D.E., Urcelay, C., Veneklaas, E.J., Reich, P.B., Poorter, L., Wright, I.J., Ray, P., Enrico, L., Pausas, J.G., Vos, A.C. de, Buchmann, N., Funes, G., Quétier, F., Hodgson, J.G., Thompson, K., Morgan, H.D., Steege, H. ter, Sack, L., Blonder, B., Poschlod, P., Vaieretti, M.V., Conti, G., Staver, A.C., Aquino, S., Cornelissen, J.H.C., 2016. Corrigendum to: New handbook for standardised measurement of plant functional traits worldwide. Aust. J. Bot. 64, 715–716. https://doi.org/10.1071/bt12225_co

Potts, S.G., Biesmeijer, J.C., Kremen, C., Neumann, P., Schweiger, O., Kunin, W.E., 2010. Global pollinator declines: trends, impacts and drivers. Trends in Ecology & Evolution 25, 345–353. https://doi.org/10.1016/j.tree.2010.01.007

Reich, P.B., 2014. The world-wide 'fast–slow' plant economics spectrum: a traits manifesto. Journal of Ecology 102, 275–301. https://doi.org/10.1111/1365-2745.12211

Roddy, A.B., Martínez-Perez, C., Teixido, A.L., Cornelissen, T.G., Olson, M.E., Oliveira, R.S., Silveira, F.A.O., 2021. Towards the flower economics spectrum. New Phytologist 229, 665–672. https://doi.org/10.1111/nph.16823

Rosbakh, S., Hartig, F., Sandanov, D.V., Bukharova, E.V., Miller, T.K., Primack, R.B., 2021. Siberian plants shift their phenology in response to climate change. Global Change Biology 27, 4435–4448. https://doi.org/10.1111/gcb.15744

Rosbakh, S., Pacini, E., Nepi, M., Poschlod, P., 2018. An Unexplored Side of Regeneration Niche: Seed Quantity and Quality Are Determined by the Effect of Temperature on Pollen Performance. Front. Plant Sci. 9. https://doi.org/10.3389/fpls.2018.01036

Rudolf, V.H.W., 2019. The role of seasonal timing and phenological shifts for species coexistence. Ecology Letters 22, 1324–1338. https://doi.org/10.1111/ele.13277

Schädler, M., Buscot, F., Klotz, S., Reitz, T., Durka, W., Bumberger, J., Merbach, I., Michalski, S.G., Kirsch, K., Remmler, P., Schulz, E., Auge, H., 2019. Investigating the consequences of climate change under different land-use regimes: a novel experimental infrastructure. Ecosphere 10, e02635. https://doi.org/10.1002/ecs2.2635

Schleuning, M., Fründ, J., Schweiger, O., Welk, E., Albrecht, J., Albrecht, M., Beil, M., Benadi, G., Blüthgen, N., Bruelheide, H., Böhning-Gaese, K., Dehling, D.M., Dormann, C.F., Exeler, N., Farwig, N., Harpke, A., Hickler, T., Kratochwil, A., Kuhlmann, M., Kühn, I., Michez, D., Mudri-Stojnić, S., Plein, M., Rasmont, P., Schwabe, A., Settele, J., Vujić, A., Weiner, C.N., Wiemers, M., Hof, C., 2016. Ecological networks are more sensitive to plant than to animal extinction under climate change. Nat Commun 7, 13965. https://doi.org/10.1038/ncomms13965

Schnablová, R., Bartušková, A., Horčičková, E., Šmarda, P., Klimešová, J., Herben, T., 2024. Diversity and functional differentiation of renewal buds in temperate herbaceous plants. New Phytologist 244, 292–306. https://doi.org/10.1111/nph.20042

Schnablová, R., Huang, L., Klimešová, J., Šmarda, P., Herben, T., 2021. Inflorescence preformation prior to winter: a surprisingly widespread strategy that drives phenology of temperate perennial herbs. New Phytologist 229, 620–630. https://doi.org/10.1111/nph.16880

Schwieger, S., Blume-Werry, G., Peters, B., Smiljanić, M., Kreyling, J., 2019. Patterns and drivers in spring and autumn phenology differ above- and belowground in four ecosystems under the same macroclimatic conditions. Plant Soil 445, 217–229. https://doi.org/10.1007/s11104-019-04300-w

Segrestin, J., Bernard-Verdier, M., Violle, C., Richarte, J., Navas, M.-L., Garnier, E., 2018. When is the best time to flower and disperse? A comparative analysis of plant reproductive phenology in the Mediterranean. Functional Ecology 32, 1770–1783. https://doi.org/10.1111/1365-2435.13098

Segrestin, J., Navas, M.-L., Garnier, E., 2020. Reproductive phenology as a dimension of the phenotypic space in 139 plant species from the Mediterranean. New Phytologist 225, 740–753. https://doi.org/10.1111/nph.16165

Sheikh, F.R., Jose-Santhi, J., Kalia, D., Singh, K., Singh, R.K., 2022. Sugars as the regulators of dormancy and sprouting in geophytes. Industrial Crops and Products 189, 115817. https://doi.org/10.1016/j.indcrop.2022.115817

Sherry, R.A., Zhou, X., Gu, S., Arnone, J.A., Schimel, D.S., Verburg, P.S., Wallace, L.L., Luo, Y., 2007. Divergence of reproductive phenology under climate warming. Proceedings of the National Academy of Sciences 104, 198–202. https://doi.org/10.1073/pnas.0605642104

Sooraj, N.P., Jaishanker, R., Athira, K., Sajeev, C.R., Lijimol, D., Saroj, K.V., Ammini, J., Pillai, M.S., Dadhwal, V.K., 2019. Comparative study on the floral spectral reflectance of invasive and non-invasive plants. Ecological Informatics 53, 100990. https://doi.org/10.1016/j.ecoinf.2019.100990

Sporbert, M., Jakubka, D., Bucher, S.F., Hensen, I., Freiberg, M., Heubach, K., König, A., Nordt, B., Plos, C., Blinova, I., Bonn, A., Knickmann, B., Koubek, T., Linstädter, A., Mašková, T., Primack, R.B., Rosche, C., Shah, M.A., Stevens, A.-D., Tielbörger, K., Träger, S., Wirth, C., Römermann, C., 2022. Functional traits influence patterns in vegetative and reproductive plant phenology – a multi-botanical garden study. New Phytologist 235, 2199–2210. https://doi.org/10.1111/nph.18345

Stuble, K.L., Bennion, L.D., Kuebbing, S.E., 2021. Plant phenological responses to experimental warming—A synthesis. Global Change Biology 27, 4110–4124. https://doi.org/10.1111/gcb.15685

Sun, S., Frelich, L.E., 2011a. Flowering phenology and height growth pattern are associated with maximum plant height, relative growth rate and stem tissue mass density in herbaceous grassland species. Journal of Ecology 99, 991–1000. https://doi.org/10.1111/j.1365-2745.2011.01830.x

Sun, S., Frelich, L.E., 2011b. Flowering phenology and height growth pattern are associated with maximum plant height, relative growth rate and stem tissue mass density in herbaceous grassland species. Journal of Ecology 99, 991–1000. https://doi.org/10.1111/j.1365-2745.2011.01830.x

Valencia, E., Méndez, M., Saavedra, N., Maestre, F.T., 2016. Plant size and leaf area influence phenological and reproductive responses to warming in semiarid Mediterranean species. Perspectives in Plant Ecology, Evolution and Systematics 21, 31–40. https://doi.org/10.1016/j.ppees.2016.05.003

Vanbergen, A.J., the Insect Pollinators Initiative, 2013. Threats to an ecosystem service: pressures on pollinators. Frontiers in Ecology and the Environment 11, 251–259. https://doi.org/10.1890/120126

Wang, Y., Yang, X.-D., Ali, A., Lv, G.-H., Long, Y.-X., Wang, Y.-Y., Ma, Y.-G., Xu, C.-C., 2020. Flowering Phenology Shifts in Response to Functional Traits, Growth Form, and Phylogeny of Woody Species in a Desert Area. Front. Plant Sci. 11. https://doi.org/10.3389/fpls.2020.00536

Weigelt, A., Mommer, L., Andraczek, K., Iversen, C.M., Bergmann, J., Bruelheide, H., Fan, Y., Freschet, G.T., Guerrero-Ramírez, N.R., Kattge, J., Kuyper, T.W., Laughlin, D.C., Meier, I.C., van der Plas, F., Poorter, H., Roumet, C., van Ruijven, J., Sabatini, F.M., Semchenko, M., Sweeney, C.J., Valverde-Barrantes, O.J., York, L.M., McCormack, M.L., 2021. An integrated framework of plant form and function: the belowground perspective. New Phytologist 232, 42–59. https://doi.org/10.1111/nph.17590

Weigelt, A., Mommer, L., Andraczek, K., Iversen, C.M., Bergmann, J., Bruelheide, H., Freschet, G.T., Guerrero-Ramírez, N.R., Kattge, J., Kuyper, T.W., Laughlin, D.C., Meier, I.C., van der Plas, F., Poorter, H., Roumet, C., van Ruijven, J., Sabatini, F.M., Semchenko, M., Sweeney, C.J., Valverde-Barrantes, O.J., York, L.M., McCormack, M.L., 2023. The importance of trait selection in ecology. Nature 618, E29–E30. https://doi.org/10.1038/s41586-023-06148-8

Westoby, M., Falster, D.S., Moles, A.T., Vesk, P.A., Wright, I.J., 2002. Plant Ecological Strategies: Some Leading Dimensions of Variation Between Species. Annual Review of Ecology and Systematics 33, 125–159. https://doi.org/10.1146/annurev.ecolsys.33.010802.150452

Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J.H.C., Diemer, M., Flexas, J., Garnier, E., Groom, P.K., Gulias, J., Hikosaka, K., Lamont, B.B., Lee, T., Lee, W., Lusk, C., Midgley, J.J., Navas, M.-L., Niinemets, Ü., Oleksyn, J., Osada, N., Poorter, H., Poot, P., Prior, L., Pyankov, V.I., Roumet, C., Thomas, S.C., Tjoelker, M.G., Veneklaas, E.J., Villar, R., 2004. The worldwide leaf economics spectrum. Nature 428, 821–827. https://doi.org/10.1038/nature02403

Xin-Yi, C., Chen, W.U., Jin-Xue, H., De-Cheng, X., 2023. Effects of warming on fine root phenology of forests: a review. Chinese Journal of Plant Ecology 47, 1471. https://doi.org/10.17521/cjpe.2022.0326

Ye, Z., Mu, Y., Van Duzen, S., Ryser, P., 2024. Root and shoot phenology, architecture, and organ properties: an integrated trait network among 44 herbaceous wetland species. New Phytologist 244, 436–450. https://doi.org/10.1111/nph.19747

Zhang, F.-P., Yang, Y.-J., Yang, Q.-Y., Zhang, W., Brodribb, T.J., Hao, G.-Y., Hu, H., Zhang, S.-B., 2017. Floral Mass per Area and Water Maintenance Traits Are Correlated with Floral Longevity in Paphiopedilum (Orchidaceae). Front. Plant Sci. 8. https://doi.org/10.3389/fpls.2017.00501

Zhang, X., Li, B., Peñuelas, J., Sardans, J., Cheng, D., Yu, H., Zhong, Q., 2023. Resource-acquisitive species have greater plasticity in leaf functional traits than resource-conservative species in response to nitrogen addition in subtropical China. Science of The Total Environment 903, 166177. https://doi.org/10.1016/j.scitotenv.2023.166177

Appendices

Author contributions

Deklaration der Beiträge von Autoren zur kumulativen Arbeit (entsprechend §7 (5) der Promotionsordnung der Naturwissenschaftlichen Fakultäten I, II und III der MLU).

Chapter II

Plos, C., Hornick, T., Dunker, S., Sporbert, M., Jakubka, D., Nordt, B., Lenk, A., Walther, F., Hensen, I., Römermann, C. Interspecific phenological variation in herbaceous species is more strongly reflected in vegetative traits than in floral traits

	Carolin Plos [75%]	Thomas Hornick [2%]	Susanne Dunker [2%]	Maria Sporbert [3%]	Desiree Jakubka [1%]	Birgit Nordt [1%]	Annalena Lenk [1%]	Franziska Walther [1%]	Isabell Hensen [6%]	Christine Römermann [12%]
Entwurf (Design)	40%	0 %	1 %	0 %	0 %	0 %	0 %	0 %	20 %	40 %
Umsetzung (Implementation)	80 %	6 %	6 %	2 %	2 %	2 %	1 %	1 %	0 %	0 %
Auswertung (Analysis)	85 %	1 %	0 %	9 %	0 %	0 %	0 %	0 %	0 %	5 %
Schreiben (Writing)	85 %	1 %	1 %	1 %	1 %	1 %	1 %	1 %	4 %	4 %

Chapter III

Plos, C., Hensen, I., Korell, L., Auge, H., Römermann, C., 2024. Plant species phenology differs between climate and land-use scenarios and relates to plant functional traits. *Ecology and Evolution* 14, e11441. https://doi.org/10.1002/ece3.11441

	Carolin Plos [85%]	Isabell Hensen [3%]	Lotte Korell [1%]	Harald Auge [4%]	Christine Römermann [15%]
Entwurf (Design)	50 %	6 %	1 %	3 %	40 %
Umsetzung (Implementation)	100 %	0 %	0 %	0 %	0 %
Auswertung (Analysis)	80 %	0 %	1 %	10 %	10 %
Schreiben (Writing)	90 %	5 %	1 %	2 %	5 %

Chapter IV

Plos, C., Stelbrink, N., Römermann, C., Knight, T.M., Hensen, I., 2023. Abiotic conditions affect nectar properties and flower visitation in four herbaceous plant species. *Flora* 303, 152279. https://doi.org/10.1016/j.flora.2023.152279

	Carolin Plos [70%]	Niklas Stelbrink [16%]	Christine Römermann [5%]	Tiffany Knight [3%]	Isabell Hensen [6%]
Entwurf (Design)	70 %	0 %	5 %	5 %	20 %
Umsetzung (Implementation)	30 %	70 %	0 %	0 %	0 %
Auswertung (Analysis)	90 %	0 %	10 %	0 %	0 %
Schreiben (Writing)	90 %	0 %	5 %	5 %	5%

Datum:

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Carolin Plos *Prof. Dr. Isabell Hensen*

Acknowledgment/ Danksagung

I am very grateful to all the people who have supported me throughout the course of this thesis. First of all, I would like to thank my main supervisors Isabell Hensen and Christine Römermann. I truly appreciate your support and kindness throughout this process, as well as the opportunity to develop my very own project. Isabell, I would like to thank you especially for your always open-hearted guidance and mentorship, as well as for giving me the freedom to follow my own research ideas. Thank you, Christine, for all the fruitful discussions about my work, your always valuable feedback, statistical advice and for encouraging me to give so many presentations, all of which have taught me a lot.

Many thanks to my PAC team members Harald Auge, Lotte Korell and Tiffany Knight for always supporting me when needed, providing statistical support and the fruitful discussions about my manuscripts.

I am grateful for the opportunity to be involved in the PhenObs project from the almost very beginning and to experience the growth and development of this great network. I want to thank all PhenObs members—particularly Albert-Dieter Stevens, Birgit Nordt, Martin Freiberg, and Richard Primack—for the valuable exchange and inspiring discussions, especially during the early stages of my project. Special thanks go to the PhenObs coordinators, Emma Jardine, Desiree Jakubka, Maria Sporbert, and Robert Rauschkolb. Many thanks also go to everyone involved in the phenological monitoring in the Botanical Gardens, whose efforts have helped this network thrive. I am especially grateful to Birgit Müller, Katrin Kittlaus, Janin Naumann and Birgit Nordt. Many thanks as well to all the gardeners who care for and maintain the diverse plants in the Botanical Gardens.

A huge thank you to Susanne Dunker and Thomas Hornick for introducing me to the world of pollen traits and multispectral imaging flow cytometry, enabling me to explore this exciting new field of research. Thank you for great exchange, your always valuable feedback and the nice time in your lab. Many thanks to Konstantin Albrecht for your invaluable support with the pollen preparations and Franziska Walther for valuable exchange on pollen traits.

I would like to thank Martin Schädler for the great opportunity to work at the Global Change Experimental Facility. My thanks also go to Konrad Kirsch for his support and enjoyable conversations that made work fun, even through the extremes of summer and winter weather, as well as to him and the entire Bad Lauchstädt team for maintaining the GCEF. Thanks also to Martin Andrzejak for the nice exchange during the field work and for sharing your experiences with the specifics at the GCEF.

Many thanks to the student helpers Laura Moro, Marie Schramm, Jenny Friedrichs, Konrad Adler, Julia Zelychenko, Julian Selke, Lara Escherich, Annalena Lenk, Nahid Rasouli, Angela

Diederen and Karla Barfuss for supporting the phenological monitoring, trait measurements or pollen annotations. Special thanks go to Niklas Stelbrink who did his Bachelor thesis with me. Thank you for your great work and nice collaboration.

It was a particular pleasure for me to be part not only of the Plant Ecology group in Halle but also of the Biodiversity of Plants group in Jena, even if this sometimes led to scheduling difficulties. A heartfelt thanks to all my colleagues from the Plant Ecology and Geobotany working group in Halle for this very nice, supportive and welcoming working atmosphere. Special thanks to Maria Sporbert, Julia Dieskau, Sabrina Träger, Kevin Kožić, Yolanda Cáceres, Adrian Schaar, Tobias Proß, Michael Köhler, Lina Lüttgert, Mariem Saadani, Amanda Ratier Backes and Andrea Davrinche for becoming friends and sharing both the highs and lows of this PhD journey. It was always a pleasure working with you and spending time together, whether in the office or in the bars of Halle. Thank you also to the Biodiversity of Plants group for giving me such a warm welcome in Jena, for the enjoyable exchanges on both work-related and non-work-related topics, the incredibly supportive atmosphere, and for exploring the best lunch spots in Jena together. Special thanks to Franziska Bucher for your kindness and support, sharing your expertise and being a great office mate. Many thanks also to Gabriel Walther, Desiree Jakubka and Josephine Ulrich for sharing part of this PhD journey with me. I always enjoyed our time together.

My PhD studies were supported by the graduate scholarship of the federal state of Saxony-Anhalt. I am grateful for the opportunity to be part of yDiv, graduate school of iDiv. I always enjoyed the excellent and inspiring courses, the yDiv retreat and the scientific and non-scientific exchange with my fellow PhD students. A special thank you to Nicole Sachmerda-Schulz and the whole yDiv team for all your dedication and support.

Ein besonderer Dank gilt meiner Familie, insbesondere meinen Eltern und Großeltern, für all eure Unterstützung seit Beginn meines Studiums. Insbesondere danken möchte ich meiner Oma Inge Knecht, die schon früh meine Begeisterung für die Natur geweckt und gefördert hat und mit der ich meine Leidenschaft für Pflanzen und Phänologie teile. Danken möchte ich auch meinen engsten Freunden, insbesondere Marie, Anna, Jule, Sarah, Lisa und Theresa, für eure Unterstützung und die vielen schönen gemeinsamen Momente während dieser Zeit. Und zu guter Letzt – Danke, Lukas, für deine unermüdliche Unterstützung, Geduld und Liebe, und dass du immer an meiner Seite bist. Ohne dich wäre diese Reise nicht dasselbe gewesen.

Curriculum vitae

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Scientific Employment

2023 - present	**Scientific Employee, Coordination of the International Master's program 'Biodiversity Sciences'**, Geobotany and Botanical Garden, Martin-Luther University, Halle-Wittenberg PI: Prof. Dr. Helge Bruelheide
2022	**Scientific Employee**, Geobotany and Botanical Garden, Martin-Luther University, Halle-Wittenberg PI: Prof. Dr. Isabell Hensen
2021 – 2022	**Scientific Employee**, Institute of Ecology and Evolution with Herbarium Haussknecht and Botanical Garden, Friedrich Schiller University Jena PI: Prof. Dr. Christine Römermann

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Education

2018 - 2025	**Doctoral Researcher**, Institute of Biology, Geobotany und Botanical Garden, Martin-Luther University, Halle-Wittenberg Research topic: "The relationship between phenology and functional traits in herbaceous plants in the face of climate change and implications for pollinators" Supervisor: Prof. Dr. Isabell Hensen, Co-Supervisor: Prof. Dr. Christine Römermann (Friedrich Schiller University Jena)
2013 – 2017	**Master of Science Biology**, Martin-Luther University, Halle-Wittenberg Master thesis: „Comparing co-occurrence networks of floodplain meadow communities between the local and regional scale" Supervisor: Dr. Erik Welk
2009 – 2013	**Bachelor of Science Biology**, Martin-Luther University, Halle-Wittenberg Bachelor thesis: „Combined effects of UV-B and drought stress on native and invasive ancestries of *Verbascum thapsus* L." Supervisor: Prof. Dr. Alexandra Erfmeier; Dr. Maria Hock

Teaching expertise

2022 – 2024	Practical course Müritz National park, (Module: Evolution and Biodiversity, teacher training students Biology)
2023 – 2024	Excursions for Biodiversity Sciences Master students
2022	Practical course Pennickental, (Module Geobotany, B.Sc.), Friedrich Schiller University Jena
2019	Practical course (Module Field Ecology, M.Sc. Biology)
2014	Practical course (Module Plant Ecology, B.Sc. Biology)

Graduation candidates (Co-Supervision)

2022	M.Sc. graduation candidate Nahid Rasouli Paeenroudposhti Title: “Linking flowering phenology with seasonal variation in flower traits with pollinator diversity and density”
2020	B.Sc. graduation candidate Niklas Stelbrink, Title: „Influence of temperature and soil moisture on plant-pollinator interactions and sucrose content in nectar“

Scientific activities and memberships

since 2019	yDiv Graduate school of the German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig
since 2019	International Association of Vegetation Science (IAVS)
since 2023	Reviewer for *Alpine Botany*
since 2024	Reviewer for *Scientific Reports*; *Functional Ecology*; *Ecology and Evolution*
since 2025	Reviewer for *Journal of Ecology*

Scholarship

2018 -2021	Graduate scholarship of the federal state of Saxony-Anhalt (Landesgraduiertenstipendium)

Publications and conference contributions

Publications

Plos, C., Hensen, I., Korell, L., Auge, H., Römermann, C., 2024. Plant species phenology differs between climate and land-use scenarios and relates to plant functional traits. Ecology and Evolution 14, e11441. https://doi.org/10.1002/ece3.11441

Plos, C., Stelbrink, N., Römermann, C., Knight, T.M., Hensen, I., 2023. Abiotic conditions affect nectar properties and flower visitation in four herbaceous plant species. Flora 303, 152279. https://doi.org/10.1016/j.flora.2023.152279

Walther, F., Hofmann, M., Rakosy, D., ***Plos, C.***, Deilmann, T.J., Lenk, A., Römermann, C., Harpole, W.S., Hornick, T., Dunker, S., 2025. Multispectral Imaging Flow Cytometry for Spatio-Temporal Pollen Trait Variation Measurements of Insect-Pollinated Plants. Cytometry Part A 107, 293–308. https://doi.org/10.1002/cyto.a.24932

Andrzejak, M., Knight, T.M., ***Plos, C.***, Korell, L., 2025. Changes in reproduction mediate the effects of climate change and grassland management on plant population dynamics. Ecological Applications 35, e3063. https://doi.org/10.1002/eap.3063

Korell, L., Andrzejak, M., Berger, S., Durka, W., Haider, S., Hensen, I., Herion, Y., Höfner, J., Kindermann, L., Klotz, S., Knight, T.M., Linstädter, A., Madaj, A.-M., Merbach, I., Michalski, S., ***Plos, C.***, Roscher, C., Schädler, M., Welk, E., Auge, H., 2024. Land use modulates resistance of grasslands against future climate and inter-annual climate variability in a large field experiment. Global Change Biology 30, e17418. https://doi.org/10.1111/gcb.17418

Rauschkolb, R., Bucher, S.F., Hensen, I., Ahrends, A., Fernández-Pascual, E., Heubach, K., Jakubka, D., Jiménez-Alfaro, B., König, A., Koubek, T., Kehl, A., Khuroo, A.A., Lindstädter, A., Shafee, F., Mašková, T., Platonova, E., Panico, P., ***Plos, C.***, Primack, R., Rosche, C., Shah, M.A., Sporbert, M., Stevens, A.-D., Tarquini, F., Tielbörger, K., Träger, S., Vange, V., Weigelt, P., Bonn, A., Freiberg, M., Knickmann, B., Nordt, B., Wirth, C., Römermann, C., 2024. Spatial variability in herbaceous plant phenology is mostly explained by variability in temperature but also by photoperiod and functional traits. Int J Biometeorol. https://doi.org/10.1007/s00484-024-02621-9

Sporbert, M., Jakubka, D., Bucher, S.F., Hensen, I., Freiberg, M., Heubach, K., König, A., Nordt, B., ***Plos, C.***, Blinova, I., Bonn, A., Knickmann, B., Koubek, T., Linstädter, A., Mašková, T., Primack, R.B., Rosche, C., Shah, M.A., Stevens, A.-D., Tielbörger, K., Träger, S., Wirth, C., Römermann, C., 2022. Functional traits influence patterns in vegetative and reproductive plant phenology – a multi-botanical garden study. New Phytologist 235, 2199–2210. https://doi.org/10.1111/nph.18345

Nordt, B., Hensen, I., Bucher, S.F., Freiberg, M., Primack, R.B., Stevens, A.-D., Bonn, A., Wirth, C., Jakubka, D., ***Plos, C.***, Sporbert, M., Römermann, C., 2021. The PhenObs initiative: A standardised protocol for monitoring phenological responses to climate change using herbaceous plant species in botanical gardens. Functional Ecology 35, 821–834. https://doi.org/10.1111/1365-2435.13747

Hock, M., ***Plos, C.***, Sporbert, M., Erfmeier, A., 2020. Combined Effects of UV-B and Drought on Native and Exotic Populations of Verbascum thapsus L. Plants 9, 269. https://doi.org/10.3390/plants9020269

Submitted paper

Plos, C., Hornick, T., Dunker, S., Sporbert, M., Jakubka, D., Nordt, B., Lenk, A., Walther, F., Hensen, I., Römermann, C., Interspecific phenological variation in herbaceous species is more strongly reflected in vegetative traits than in floral traits. Under consideration in *Journal of Ecology*

Conference contributions

Plos, C., Hensen, I., Korell, L., Auge, H. ,Römermann, C (2025): Plant species phenology differs between climate and land-use scenarios and relates to plant functional traits. Workshop “10 years of GCEF”, Helmholtz Centre for Environmental Research (UFZ), Halle, Germany, 13. -14.01.2025 (Talk)

Plos, C., Hensen, I., Korell, L., Auge, H. ,Römermann, C (2023): Climate and land-use interactively affect the flowering phenology of grassland species. 52nd Annual Conference of the German Ecological Society (GfÖ), Leipzig, Germany, 11.-15.09.2023 (Talk)

Plos, C., Hensen, I., Sporbert, M., Jakubka, D., Dunker, S., Hornick, T., Nordt, B., Lenk, A., Walther, F., Römermann, C (2023): Do floral traits explain phenological patterns in herbaceous plants? 52nd Annual Conference of the German Ecological Society (GfÖ), Leipzig, Germany, 11.-15.09.2023 (Poster)

Plos, C., Römermann, C., Hensen, I. (2022): Varying responses of flowering phenology to future climate on meadows versus pastures. Frontiers in Experimental Research on Changing Environments, Helmholtz Centre for Environmental Research (UFZ), Leipzig, Germany, 07.-09.06.2022 (Talk)

Plos, C., Stelbrink, N., Rosche, C., Knight, T., Hensen, I. & Römermann, C. (2020): The effect of temperature on nectar production and pollinator visitation rates in four herbaceous species. 34th Annual Meeting of the Scandinavian Association for Pollination (SCAPE), Virtual Conference University of Northampton. 6.-8.11.2020 (Poster)

Plos, C., Rosche, C., Hensen, I. & Römermann, C. (2019): Species-specific responses of nectar quantity and pollinator frequency to temperature. 62nd IAVS Symposium of the International Association for Vegetation Science (IAVS), Bremen, Germany. 14.-19.07.2019 (Poster)

Plos, C., Römermann, C. & Hensen, I. (2019): Plant species responses to changing climate – the relationship between phenology, functional diversity and genetic diversity. PopBio - 32nd Conference of the Specialist Group Plant Population Biology of the Ecological Society of Germany, Austria and Switzerland (GfÖ), Warsaw, Poland. 23.-25.05. 2019 (Poster)

Plos, C., Römermann, C. & Hensen, I. (2018): Plant species responses to changing climate – the relationship between phenology, functional diversity and genetic diversity. 4th iDiv Annual Conference, Leipzig, Germany. 11.-12.12.2018. (Poster)

Plos, C., Jandt, U. & Welk, E. (2018): Cross-scale transferability of co-occurrence relationships in Central German floodplain meadows. 17th workshop of the German working group on vegetation databases, Jena, Germany 14.-16.03.2018. (Poster)

Hock, M., *Plos, C.*, Sporbert, M. & Erfmeier, A. (2014): UV-B radiation and drought – Combined stress effects on native and exotic origins of *Verbascum thapsus* L. 44th Annual Meeting of the Ecological Society of Germany, Austria and Switzerland, Hildesheim, Germany, 08.-12.09.2014. (Poster)

Eigenständigkeitserklärung

Hiermit erkläre ich, dass ich die vorliegende Doktorarbeit mit dem Titel „The relationship between phenology and functional traits in herbaceous plants in the face of climate change and implications for pollinators“ eigenständig und ohne fremde Hilfe verfasst sowie keine anderen als die im Text angegebenen Quellen und Hilfsmittel verwendet habe. Textstellen, welche aus verwendeten Werken wörtlich oder inhaltlich übernommen wurden, wurden von mir als solche kenntlich gemacht. Ich erkläre weiterhin, dass ich mich bisher noch nie um einen Doktorgrad beworben habe. Die vorliegende Doktorarbeit wurde bis zu diesem Zeitpunkt weder bei der Naturwissenschaftlichen Fakultät I – Biowissenschaften der Martin-Luther-Universität Halle-Wittenberg noch einer anderen wissenschaftlichen Einrichtung zum Zweck der Promotion vorgelegt.

Carolin Plos, Halle (Saale), 26.03.2025

“As it is important to consider nature from the point of view of science remembering nomenclature and system of humankind, and so, if possible, go a step further in that direction, so it is equally important often to ignore or forget all that people presume they know, and take an original and unprejudiced view of nature, letting her make what impression she will on you, as the first people, and all children and natural people still do.

Henry David Thoreau (*Journal*, 28 February 1860)