Interactions among herbivory, nutrient enrichment and climate change as drivers of plant traits, performance and community diversity

Dissertation

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Frau Maria-Theresa Jessen

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GutachterInnen
1. Prof. Dr. Isabell Hensen
2. Assoc. Prof. Dr. Anu Eskelinen
3. Prof. Dr. Stan Harpole

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To future generations:

May you still enjoy and explore the biodiversity of our planet!

Saxifraga aizoides

To understand the whole it is necessary to understand the parts. To understand the parts, it is necessary to understand the whole. Such is the circle of understanding. We move from part to whole and back again, and in that dance of comprehension, in that amazing circle of understanding, we come alive to meaning, to value, and to vision.

Ken Wilber, The Eye of Spirit, 2001

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Maria-Theresa Jessen, Elina Kaarlejärvi, Johan Olofsson, Anu Eskelinen (2020) Global Change Biology, Volume 26, issue 12, pages 6742-6752 https://doi.org/10.1111/gcb.15378

Chapter III

Litter accumulation, but not light limitation drives early plant recruitment

Maria-Theresa Jessen, Harald Auge, W. Stan Harpole, Anu Eskelinen

(Manuscript submitted to Journal of Ecology)

Chapter IV

Silene latifolia responses to light and nutrients depend on grazing and future climate

Maria-Theresa Jessen, Harald Auge, W. Stan Harpole, Yann Hautier, Anu Eskelinen

(Manuscript)

AUTHOR CONTRIBUTIONS

Chapter II

MTJ collected and analysed the data and wrote the manuscript with substantial contributions from AE. EK and JO contributed editing the manuscript. AE and EK developed and established the experiment with contributions from JO.

Chapter III

MTJ collected and analysed the data and wrote the manuscript with substantial contributions from AE. HA and WSH contributed editing the manuscript. AE developed and established the experiment with contributions from WSH and HA.

Chapter IV

MTJ collected and analysed the data and wrote the manuscript with substantial contributions from AE. HA, WSH and YH contributed editing the manuscript. AE developed and established the experiment with contributions from WSH and HA.

Author abbreviations:

AE: Anu Eskelinen, **EK**: Elina Kaarlejärvi, **HA**: Harald Auge, **JO**: Johan Olofsson, **MTJ**: Maria-Theresa Jessen, **WSH**: W Stan Harpole, **YH**: Yann Hautier

Summary

Nutrient enrichment, changing grazer management, and climate change are three important factors affecting grassland ecosystems worldwide that have discernible effects on individual plants (i.e. growth and recruitment) and thus also on plant community composition and diversity. However, their combined effects have rarely been studied, particularly from a mechanistic perspective that can explain why plant community composition changes and diversity declines.

In this work, I investigated the role of intraspecific trait responses (i.e., variation in traits within a species) as a mechanism for plants growing in tundra to cope with multiple, interacting and long-term (> 9 years) changes in their growing environment. Specifically, I exposed plants to combinations of fertilization, herbivory exclusion and climate warming to understand how the combined relaxation of nutrient and temperature limitations influences intraspecific trait manifestation and its interaction an manipulation of grazing. In addition, I examined seedling diversity in a Central European grassland in response to fertilization and herbivory exclusion with the goal of determining the mechanism that can cause declining diversity during the early stages of recruitment. As nutrient enrichment and abandonment of grazing can affect seedling recruitment via light limitation (e.g. by increased aboveground biomass) or increased litter accumulation (e.g. after-life effects of increased plant biomass), I experimentally decoupled these two processes. As a novel extension of previous studies that addressed the long-standing debate about fertilizer-induced light limitation and subsequent decline in plant community diversity, I added light in the field via LED lamps to test directly the role of light limitation. In the same experimental setup, I also examined the performance and trait response of a phytometer to interacting and short-term (< 1 year) manipulations of fertilization, herbivory exclusion, light addition and future climate. The aim here was to understand the role of light limitation for individuals in the community based on the performance and trait responses of a single species. Using an experimental combination of relaxed light and nutrient limitation, herbivory exclusion and climate change simulations I also wanted to understand how these factors interactively influence plant individual performance and trait responses with consequences on species competitive ability and community composition and diversity.

I found that grazing animals were a key factor shaping plant intraspecific trait responses, but also modulating these trait manifestations in response to nutrient enrichment and climate warming. Fertilization and climate warming also modified trait responses, but to a much lesser extent than herbivory. In addition, herbivores determined the relationship between trait change and change in species abundance at the community level. This emphasizes both the importance of intraspecific trait plasticity as a mechanism to cope with concurrent abiotic and biotic changes as well as the key role of herbivores in modulating the trait-environment relationship. With regard to seedling diversity I found that litter accumulation, but not light availability, strongly influenced early seedling recruitment. The detrimental effect of litter was independent of fertilization or herbivory exclusion, but fertilization itself had a negative effect on seedling emergence which was, however, marginal compared to the strong effect of litter. In the phytometer experiment, future climate and fertilization interacted to cause the phytometer to increase in height particularly in plots without light addition, suggesting that competition for light is an important mechanism driving plant height under densely vegetated conditions. Furthermore, future climate increased the phytometer biomass when protected from herbivores. Additionally, herbivores strongly controlled performance and trait values regardless of resource availability.

Overall, these results highlight that active grazer management can be an important tool to influence plant competitive abilities and thus community composition and diversity under nutrient enrichment and climate change in both northern and central European grasslands. In addition, my results highlight the detrimental effects of litter accumulation on seedling-level diversity and show for the first time that light availability is not the main driver reducing diversity in early recruitment.

ZUSAMMENFASSUNG

Nährstoffanreicherung, verändertes Weidemanagement und Klimawandel sind drei wichtige Faktoren, die sich weltweit auf Grünlandökosysteme auswirken und erkennbare Auswirkungen auf einzelne Pflanzen (d. h. Wachstum und Rekrutierung) und somit auch auf die Zusammensetzung und Vielfalt von Pflanzengemeinschaften haben. Ihre kombinierten Auswirkungen sind jedoch nur selten untersucht worden, insbesondere aus einer mechanistischen Perspektive, die erklären kann, warum sich die Zusammensetzung von Pflanzengemeinschaften verändert und die Vielfalt abnimmt.

In dieser Arbeit untersuchte ich die Rolle intraspezifischer Merkmalsreaktionen (d. h. die Variation von Merkmalen innerhalb einer Art) als Mechanismus für Pflanzen, die in der Tundra wachsen, um mit multiplen, interagierenden und langfristigen (> 9 Jahre) Veränderungen in ihrer Wachstumsumgebung fertig zu werden. Konkret setzte ich Pflanzen Kombinationen aus Düngung, Ausschluss von Herbivoren und Klimaerwärmung aus, um zu verstehen, wie die kombinierte Lockerung von Nährstoff- und Temperaturbeschränkungen die Manifestation intraspezifischer Merkmale und deren Wechselwirkung mit der Manipulation der Beweidung beeinflusst. Außerdem untersuchte ich die Keimlingsvielfalt in einem mitteleuropäischen Grünland als Reaktion auf Düngung und Ausschluss von Herbivorie mit dem Ziel, den Mechanismus zu ermitteln, der zu einem Rückgang der Vielfalt in den frühen Phasen der Rekrutierung führen kann. Da die Anreicherung mit Nährstoffen und die Einstellung der Beweidung die Rekrutierung von Keimlingen über Lichtlimitierung (z. B. durch erhöhte oberirdische Biomasse) oder erhöhte Streuakkumulation (z. B. Nachwirkungen der erhöhten Pflanzenbiomasse) beeinflussen können, habe ich diese beiden Prozesse experimentell entkoppelt. Als neuartige Erweiterung früherer Studien, die sich mit der seit langem geführten Debatte über die durch Düngemittel verursachte Lichtlimitierung und den anschließenden Rückgang der Vielfalt der Pflanzengemeinschaften befassten, fügte ich im Feld über LED-Lampen Licht hinzu, um die Rolle der Lichtlimitierung direkt zu testen. Im gleichen Versuchsaufbau untersuchte ich auch die Leistung und die Merkmalsreaktion eines Phytometers auf interaktive und kurzfristige (< 1 Jahr) Manipulationen der Düngung, des Herbivorenausschlusses, der Lichtzufuhr und des zukünftigen Klimas. Ziel war es, die Rolle der Lichtbegrenzung für die Individuen der Gemeinschaft anhand der Leistung

und der Merkmalsreaktionen einer einzelnen Art zu verstehen. Mithilfe einer experimentellen Kombination aus Aufhebung von Licht- und Nährstoffbegrenzung, Ausschluss von Herbivoren und Simulationen des Klimawandels wollte ich auch verstehen, wie diese Faktoren die individuelle Leistung und die Merkmalsreaktionen von Pflanzen beeinflussen, was sich auf die Konkurrenzfähigkeit der Arten sowie die Zusammensetzung und Vielfalt der Gemeinschaft auswirkt.

Ich fand heraus, dass Weidetiere ein Schlüsselfaktor sind, der die Reaktion der Pflanzen auf intraspezifische Merkmale beeinflusst, aber auch die Manifestation dieser Merkmale als Reaktion auf Nährstoffanreicherung und Klimaerwärmung moduliert. Auch die Düngung und die Klimaerwärmung veränderten die Merkmalsausprägungen, jedoch in weitaus geringerem Maße als die Pflanzenfresser. Darüber hinaus bestimmten Herbivoren die Beziehung zwischen Merkmalsänderungen und Änderungen der Artenvielfalt auf Gemeinschaftsebene. Dies unterstreicht sowohl die Bedeutung intraspezifischer Merkmalsplastizität als Mechanismus zur Bewältigung gleichzeitiger abiotischer und biotischer Veränderungen als auch die Schlüsselrolle von Pflanzenfressern bei der Modulation der Merkmals-Umwelt-Beziehung. In Bezug auf die Keimlingsvielfalt stellte ich fest, dass die Anhäufung von Streu, nicht aber die Lichtverfügbarkeit, die frühe Rekrutierung von Keimlingen stark beeinflusst. Die nachteilige Wirkung der Streu war unabhängig von der Düngung oder dem Ausschluss von Herbivoren, aber die Düngung selbst hatte einen negativen Effekt auf den Keimlingsaufwuchs, der jedoch im Vergleich zu der starken Wirkung der Streu marginal war. Im Phytometerexperiment bewirkten das künftige Klima und die Düngung in Wechselwirkung, dass der Phytometer vor allem in Parzellen ohne Lichtzufuhr an Höhe zunahm, was darauf hindeutet, dass die Konkurrenz um Licht ein wichtiger Mechanismus ist, der die Pflanzenhöhe unter dicht bewachsenen Bedingungen bestimmt. Außerdem erhöhte das künftige Klima die Biomasse des Phytometers, wenn es vor Herbivoren geschützt war. Darüber hinaus kontrollierten Herbivoren die Leistung und die Merkmalswerte stark, unabhängig von der Verfügbarkeit von Ressourcen.

Insgesamt zeigen diese Ergebnisse, dass ein aktives Weidemanagement ein wichtiges Instrument zur Beeinflussung der Konkurrenzfähigkeit von Pflanzen und damit der Zusammensetzung und Vielfalt von Lebensgemeinschaften bei

Nährstoffanreicherung und Klimawandel in nord- und mitteleuropäischen Grünlandgebieten sein kann. Darüber hinaus unterstreichen meine Ergebnisse die nachteiligen Auswirkungen der Streuakkumulation auf die Diversität auf Sämlingsebene und zeigen zum ersten Mal, dass die Lichtverfügbarkeit nicht der Hauptfaktor ist, der die Diversität bei der frühen Rekrutierung reduziert.

CHAPTER I – GENERAL INTRODUCTION

Nutrient enrichment, changes in land use and climate change are major drivers of a global decline in biodiversity (Sala *et al.* 2000). Changes in land use include overgrazing of semi natural grasslands in Central Europe and traditionally used rangelands in Northern Europe (Turunen & Vuojala-Magga 2014; Kuemmerle *et al.* 2016; Axelsson-Linkowski *et al.* 2020). At the same time, areas which were formerly grazed, including species-rich grasslands in Central Europe, are increasingly being abandoned (Poschlod & WallisDeVries 2002; Kuemmerle *et al.* 2016). This can lead to secondary succession and consequently to changes in community composition and diversity (Kapfer & Popova 2020). In this thesis, I investigate how these changes in grazing management and concurrent nutrient enrichment and climate change are altering plant traits, performance, recruitment, and thus grassland community composition and diversity, and what mechanisms underlie these changes.

RESOURCE AVAILABILITY AND PLANT AND COMMUNITY RESPONSES

Generally, plant communities are characterized by the current species pool in a spatially defined area (Ricklefs 2008; Vellend 2010) and, according to the work of Hutchinson (1961), the community's diversity relates to the species which can coexist in the community (note that there are other theories about community diversity e.g. in Eriksson 1993 but these are outside the scope of this thesis). Both community composition and diversity are transient, only representing a momentary snapshot of the community and are determined by interacting abiotic and biotic factors (Watts 1947; Vellend 2010; Schulze *et al.* 2019).

Resource availability (i.e. nutrients, water and light), as an abiotic factor, is key to plant nutrition and growth, but can have contrasting effects on overall community dynamics when considered at the level of not only at single plant but the whole community (Kimmel *et al.* 2020). Natural and anthropogenic nutrient enrichment is considered a major global change driver because it alters plant species composition and diversity, soil features and trophic interactions in ecosystems worldwide (Galloway *et al.* 2008; Gruner *et al.* 2008; Bobbink *et al.* 2010; Burkle & Irwin 2010; Hautier *et al.* 2014; Stevens 2019). One community response to increased availability of nutrients

is an increase in overall community productivity, leading to high amounts of live and dead biomass (Harpole *et al.* 2011; Stevens *et al.* 2015). As a result, many studies have observed a reduction in plant diversity (e.g. Baer *et al.* 2003; Clark & Tilman 2008; Harpole *et al.* 2016; Seabloom *et al.* 2021). The negative productivity-diversity relationship prevalent at high levels of productivity (Grime 1973) can be explained by an increase in overall biomass and promotion of fast-growing and tall-statured species (Reich 2014). These increase competition for light (Hautier, Niklaus & Hector 2009; DeMalach, Zaady & Kadmon 2017b) at the expense of short-statured species (Goldberg *et al.* 2017). Plants suffering from greater light limitation therefore have a higher probability of disappearing from the community (Kaarlejärvi, Eskelinen & Olofsson 2017). These dynamics are based on the long-standing debate around the 'resource-ratio-hypothesis,' according to which competition shifts towards the most limiting resource, which, when there is high productivity, should be light (Tilman 1985). Even though this mechanism is widely acknowledged, experimental results indirectly manipulating light supply with fertilization partly show contrasting results (Rajaniemi 2002; Dickson & Foster 2011). Therefore, Harpole *et al.* (2017) have called for an experiment to examine directly the role of light competition with respect to diversity combined with nutrient additions in the field.

HERBIVORES AND PLANT AND COMMUNITY RESPONSES

Mammalian herbivores are an essential component in many natural systems and shape plant community composition and diversity. Due to their important role, herbivores are sometimes referred to as ecosystem engineers (Jones, Lawton & Shachak 1997). However, land use change, climate change and socio-economic reasons have led**,** globally, to changes in the abundance and management of both domesticated and wild herbivores (Estes *et al.* 2011; Ripple *et al.* 2015; Uboni *et al.* 2016; Harrison *et al.* 2018). If grazing is discontinued, there may be significant impacts on ecosystems: for example, grassland without grazing (or equivalent management) could follow secondary successional trajectories and eventually transform into forests in areas suitable for tree growth (Milchunas, Sala & Lauenroth 1988). On the other hand, if grazing is intensified, overgrazing can cause, for example, a substantial reduction in diversity (Ihse, Allard & Nordberg 1998; Török *et al.* 2018).

At the community level, herbivores can influence plant community composition and diversity through consumption and trampling (Olff & Ritchie 1998; Eskelinen & Oksanen 2006; Gordon & Prins 2019). Both the removal of biomass and trampling are disturbances which can reduce competition for light by reducing dominant species or creating open patches in vegetation (Eichberg & Donath 2018). In concert with either natural or experimentally increased productivity, herbivores can therefore counteract a loss of diversity (Hillebrand *et al.* 2007; Borer *et al.* 2014b; Eskelinen, Kaarlejärvi & Olofsson 2017). However, the ability of herbivores to consume the additional biomass produced under higher productivity is limited. A recent global-scale study by Borer *et al.* (2020) showed that fertilization-induced biomass accumulation can outstrip the consumption capacity of herbivores. This aligns to the 'exploitation ecosystems' hypothesis of Oksanen *et al.* (1981), predicting that the importance of herbivory decreases with increasing productivity.

Next to the biomass removal effect of herbivores, there is also evidence that grazing can stimulate plant growth (Hawkes & Sullivan 2001; Ramula *et al.* 2019). This has been termed the 'compensatory growth hypothesis' (McNaughton 1983; Strauss & Agrawal 1999) and can be seen as a tolerance strategy towards herbivory as plants can regrow lost tissue or increase seed production and thus maintain their net performance (e.g. Lennartsson, Ramula & Tuomi 2018). In consequence, plants which are able to tolerate repeated grazing can gain dominance in the plant community as a whole (Chase, Leibold & Simms 2000; Fornoni 2011).There is no clear evidence that the ability to compensate for grazing damage via compensatory growth is promoted under higher nutrient availability (Fornoni 2011), and a previous meta-analysis suggests that this ability is plant group specific rather than dependent on nutrients (Hawkes & Sullivan 2001).

Besides the direct effects of grazing, herbivores can also indirectly influence plant communities via changes in soil nutrient mineralization (Risch *et al.* 2020) or soil nitrogen (N) and carbon (C) pools (Sitters *et al.* 2020), dependent on site productivity and climate (Risch *et al.* 2020). Such changes in soil nutrient conditions can, in turn, shift plant community composition (Sitters *et al.* 2017). These examples illustrate that the effects of nutrient enrichment and changes in grazing patterns on plant individuals and communities should be assessed interactively as partially already done on a global level (Borer *et al.* 2014a).

CLIMATE CHANGE AND PLANT AND COMMUNITY RESPONSES

Temperatures on land rose by 1.59 °C globally from 1850–1900 to 2011–2020 (IPCC 2021). Precipitation patterns are projected to change on a more regional scale and show more variability than temperatures (Murphy 2000; IPCC 2021). Warmer temperatures are expected to increase biomass of individual plants and communities (Kardol *et al.* 2010; Lin, Xia & Wan 2010), alter plant species' ranges (Kelly & Goulden 2008), impact phenology (Cleland *et al.* 2006), and change both plant community composition and diversity (Parmesan & Yohe 2003; Post & Pedersen 2008). However, community biomass responses to warming vary from positive (Post & Pedersen 2008) to none at all (Little *et al.* 2017). Net effects of warming probably depend on the duration and intensity of warmer temperatures (Elmendorf *et al.* 2012; Cantarel *et al.* 2013; Quan *et al.* 2021) and therefore lead to different short-term versus long-term plant and community responses. Furthermore, the effects of climate warming can, both on the plant individual (i.e. as responses in growth or performance) as well as on the community level (i.e. as responses in biomass or diversity), be modified by site productivity (Jonsdottir *et al.* 2005; Klanderud & Totland 2005). In addition, warmer temperatures can also increase productivity by promoting nutrient mineralization (Luo 2007; Salazar *et al.* 2020), therefore indirectly affecting plant communities via a temperature-dependent fertilizing effect (De Long *et al.* 2015). Such observations are prevalent in high latitude or high-altitude systems where plant responses are both more temperature- and nutrient-limited compared to temperate systems. In these systems, water availability and thus changes in precipitation might be a more important driver of plant and community responses in general (Korell *et al.* 2021). In addition, the effect of precipitation change on community diversity can depend on nutrients (Eskelinen & Harrison 2015) and can also vary for different plant functional groups (DeMalach, Zaady & Kadmon 2017a). In summary, how climate change affects community responses may depend on site location, productivity, local plant identities and the within-community biotic interactions which can be themselves modified by changing climate (Vandvik *et al.* 2020).

Herbivores can also markedly drive community responses to climate change, and climate can, in turn, alter plant-herbivore interactions (Hamann *et al.* 2021) and trait responses to herbivores (Lang *et al.* 2020). In high latitude and altitude systems

in particular, herbivores have been found to counteract warming-induced biomass accumulation (Post & Pedersen 2008), species loss (Klein, Harte & Zhao 2004) and shrub encroachment (Olofsson *et al.* 2009). In addition, they have been shown to counteract the combined effects of nutrient increases and warming by preventing the immigration of warm-adapted species (Kaarlejärvi, Eskelinen & Olofsson 2013), thereby maintaining community diversity (Eskelinen, Kaarlejärvi & Olofsson 2017). Based on this, herbivores can be an important factor modulating community responses to both climate change and nutrient enrichment. However, temperate regions are, in this sense, not well studied, even though grazer management has historically been important and is also being re-discovered as a conservation tool (Poschlod & WallisDeVries 2002; Chen *et al.* 2021). In addition, processes influencing plant communities in nature are complex, requiring experiments which try to mimic the complexity to allow robust insights into natural processes (Komatsu *et al.* 2019; Manning 2019).

TRAIT VARIATION AS A RESPONSE TO RESOURCE AVAILABILITY, HERBIVORY AND CLIMATE

Plant functional traits (i.e. morphological and physiological traits that are indirectly linked to plant fitness (sensu Violle *et al.* 2007)) have widely been studied in attempts to explain community composition and plant performance across and within ecosystems and plant functional groups (McGill *et al.* 2006; Diaz *et al.* 2016). In times of global change, where the abiotic and biotic environment is being modified and consequently so are intra- and inter-specific interactions, trait-environment relationships can help to predict future community composition (Suding *et al.* 2008). Generally, plant traits can be differentiated along the fast/slow axes based on their ability to utilize readily available resources (Reich 2014). According to this framework, taller species thrive under resource-rich conditions, while smaller species are associated with resource-limitation (Reich 2014; Diaz *et al.* 2016). This pattern is also reflected in leaf traits such that leaves with high nutrient concentrations and high photosynthetic rates invest less in dry mass per leaf area, while low leaf nutrient concentration and photosynthetic rates are coupled with high investment in dry mass per leaf area (Wright *et al.* 2004). Comparable generalities exist in response to grazing, where low stature, small leaves and low foliar N content reduce grazing risk (Diaz, Noy-Meyr & Cabido 2001; Diaz *et al.* 2007; Evju *et al.* 2009). General trait

responses to changing climate are more difficult to identify and depend on the traits measured and the type of climate change (i.e*.* for example increase in temperatures, drought or cold spells) considered (Guittar *et al.* 2016). Under competition for light, which is an important mechanism driving plant community responses under the combined influence of nutrient enrichment, changes in grazing patterns and climate change, plant traits can reflect strategies either to avoid or tolerate light limited conditions (Valladares & Niinemets 2008; Poorter *et al.* 2019). The most characteristic trait for shade avoidance is tall growth (Valladares *et al.* 2016), which brings a competitive advantage in the exploitation of light as a resource, especially in nutrient-rich conditions (Goldberg *et al.* 2017).

The relationships between traits, abiotic and biotic changes and community responses have traditionally been assessed using community-weighted means, which average trait values for individual species and weight them according to species abundance in the community (Garnier *et al.* 2004). However, more recently it has been emphasized that trait responses to environmental changes can vary within species (Siefert *et al.* 2015; Moran, Hartig & Bell 2016). It is not always clear to what extent these variations are genetically or phenotypically driven (Violle *et al.* 2012). However, plasticity or intraspecific trait variation adds a new dimension to the trait-environment relationships, potentially allowing species to be less vulnerable to changing conditions than previously thought (Nicotra *et al.* 2010; Liancourt *et al.* 2015). This has important implications at the community level, for example by reducing the likelihood of species turnover (Jung *et al.* 2014) or magnifying community trait change over time (Bjorkman *et al.* 2018). Considering the global change and biotic factors studied in this thesis, intraspecific trait change has been found in response to altered productivity (Siefert & Ritchie 2016; Firn *et al.* 2019a; Mudrák *et al.* 2019), grazing (Firn *et al.* 2017; Firn *et al.* 2019b) and climate change (Nicotra *et al.* 2010; Liancourt *et al.* 2015). The ability to plastically respond to environmental changes can allow species to persist in the community because plasticity increases their competitive ability relative to other species and thus their performance (Goldberg 1996; Turcotte & Levine 2016). Even though the importance of intraspecific trait variation is recognized throughout taxa and ecosystems (Des Roches *et al.* 2018), the combination of multiple global changes on intraspecific trait responses is, as yet, little explored.

PLANT RECRUITMENT IN RESPONSE TO RESOURCE AVAILABILITY AND HERBIVORY

Recruitment can occur from external seed sources as immigration and from local seed reservoirs in the form of local plant reproduction or the soil seed bank. In general, recruitment is an essential part of plant community dynamics, as species which successfully establish form the resulting community and can determine community diversity. Constraints limiting recruitment are widely discussed since the seedling stage is one of the most vulnerable phases in plant life (Clark *et al.* 2007). The success of recruitment can, for instance, be related to productivity (Stevens *et al.* 2004b; Gross, Mittelbach & Reynolds 2005; Clark & Tilman 2010). According to the 'shifting-limitation-hypothesis' the regional species pool constrains diversity at intermediate productivity via limited seed availability or dispersal, while at high productivity competitive exclusion gains in importance (Foster *et al.* 2004). This means that less competitive plants, including seedlings, are potentially lost for reasons including asymmetry in light availability (DeMalach, Zaady & Kadmon 2017b). Therefore, diversity of successfully recruiting species could be directly linked to light availability, especially under fertilized conditions; however, this has never been tested directly in the field, only in the greenhouse (Hautier, Niklaus & Hector 2009). This could lead to results that deviate from natural conditions (Poorter *et al.* 2016), because field conditions are more variable, less controlled and more multilayered than *ex situ* conditions.

High productivity is also associated with both live and dead biomass build-up, which can impose filters other than light limitation on recruitment (Facelli & Pickett 1991; Foster & Gross 1998; Lamb 2008; Loydi *et al.* 2013). These can be abiotic (e.g. changes in temperature and water availability, physical barriers) and biotic (e.g. competition for space and resources other than light) and consequently are critical drivers for recruitment as seedlings are more vulnerable to competition and abiotic conditions than adult plants (Fenner 1987). For example, seeds and seedlings can get trapped in the litter, may be unable to penetrate through the litter layer after germination and die (Ruprecht, Szabó & Collins 2012). Seedlings can also suffer from limited access to water or light imposed by the litter layer (Facelli & Pickett 1991). Disturbances such as grazing by mammalian herbivores, which remove litter and live biomass via consumption and trampling, can facilitate recruitment by creating suitable

microsites (Eskelinen *et al.* 2016). Abandonment of formerly grazed areas can, therefore, lead to higher litter accumulation and thus a reduction in seedling recruitment and consequently in community diversity (Wilsey & Polley 2003; Wilsey & Martin 2015). Despite much research directly manipulating litter and live biomass and indirectly manipulating light conditions these two mechanism have never been decoupled experimentally. Information from such studies can potentially provide important knowledge to feed into, for example, restoration measures (Facelli & Springbett 2009).

NORTHERN AND CENTRAL EUROPEAN GRASSLANDS IN THE ANTHROPOCENE

Grasslands represent more than 25% of the terrestrial area of the planet (Török *et al.* 2021). They range from high latitude tundra to equatorial savannas and are present on all continents except Antarctica (Dixon *et al.* 2014). Grasslands provide many important ecosystem services, including food and forage, pollinator support, biodiversity, erosion control, and carbon sequestration (Bengtsson *et al.* 2019).

High latitude grassland systems are naturally nutrient-limited because of low external nutrient input (but see Dentener *et al.* 2006) and cold-limited mineralization rates (Shaver & Chapin 1980; LeBauer & Treseder 2008). However, climate warming − which is predicted to progress more rapidly in high latitudes (Serreze & Barry 2011) − can accelerate nutrient turnover (Aerts 2006; Luo 2007; Salazar *et al.* 2020). This would relax former nutrient- but also cold-limitations, leading to changes in plant performance and community composition (Aerts, Cornelissen & Dorrepaal 2006; Van der Wal & Stien 2014). These systems are also periodically grazed by free ranging semi-domesticated reindeer (*Rangifer tarandus tarandus*), which can influence the growth and performance of single plant species but also entire communities by grazing, trampling and feces deposition (Eskelinen 2008; Barthelemy, Stark & Olofsson 2015; Sundqvist *et al.* 2019). In addition, they can modify both plant and community responses not only to warming, but also to nutrient enrichment (Olofsson *et al.* 2009; Kaarlejärvi, Eskelinen & Olofsson 2013; Eskelinen, Kaarlejärvi & Olofsson 2017). Overall, reindeer abundance is increasing in Northern Europe (Uboni *et al.* 2016), despite the increasingly challenging requirements for the herders (Axelsson-Linkowski *et al.* 2020). These current challenges include increased uncertainties with

regard to forage availability in terms of climate change, decline in herding areas due to competing land use interests and consequently overgrazing in the remaining areas (Turunen & Vuojala-Magga 2014; Axelsson-Linkowski *et al.* 2020).

In Central European grassland systems, traditional pastoralism has long been replaced by industrialized (i.e. intense) pasture use (Hejcman *et al.* 2013). This has led to a conversion of species-rich semi-natural grasslands to rather species-poor grasslands (Isselstein *et al.* 2007; Straubinger, Reisch & Poschlod 2021). In addition, nutrient enrichment caused by extensive agriculture (Wesche *et al.* 2012) and climate change including a trend towards greater risk of drought (Christidis, Jones & Stott 2014; King & Karoly 2017; Spinoni *et al.* 2018) impose further interacting pressures on Central European grassland communities. A recent study investigating the impact of the different climate change scenarios on different land use sectors as well as biodiversity, predicts a strong decline in grasslands grazed by sheep as well as a severe decline in biodiversity in response to high end climate change projections (Harrison *et al.* 2018).

High latitude and Central European grasslands are located in geographically different regions, which may affect the importance or interactions of global change factors that the resident plant communities are exposed to. However, nutrient enrichment, changes in grazing patterns and climate change are of global relevance. They also act in concert on plant communities, thus justifying the need for their effects to be studied in combination in many places worldwide (Fraser *et al.* 2013). Insights from such studies will not only reveal information about the mechanisms by which these three factors change plant communities, but will also reveal whether current abiotic and biotic change drivers work synergistically and thus become even more pressing for the environment (e.g. Manning 2019).

AIMS OF THE THESIS

In this thesis, I investigate the interactive effect of nutrient enrichment, grazing by mammalian herbivores and climate change on plant trait and biomass responses to understand how these factors interactively drive plant performance and consequent community composition. Furthermore, I elucidate and untangle the roles of light limitation versus litter accumulation under conditions of fertilization and herbivory

exclusion to uncover the mechanism driving diversity during the early recruitment phase. The thesis consists of three scientific articles (Figure 1) for which I have analyzed data collected from two different experimental setups in the field and these results are summarized and set into a broader context and perspective in the final synthesis chapter.

In **chapter II** I assess the interactive influence of nutrient enrichment, herbivory exclusion and climate warming on the intraspecific trait manifestation of eight common tundra species. At the time of the study, the species had been exposed to the experimentally manipulated factors for nine years and should thus display longer-term trait responses. In addition, I address the relationship between the change in individual plant trait responses and plant abundance in the community. I did this to test whether intraspecific trait variation can be a valid mechanism for plants to persist and perform well under multiple and interacting changes in their growing environment.

In **chapter III** I present the role of light limitation versus litter accumulation for diversity during early seedling recruitment. This is particularly important because theory and previous studies have highlighted fertilization-induced light limitation as one major explanation for diversity loss in adult plant communities. Furthermore, it has been shown that herbivores can counteract this pattern. Therefore, I examine seedling recruitment under the combined influence of nutrient enrichment, herbivore exclusion, litter removal and light addition in a full factorial combination to unravel the dominant mechanism driving recruitment success and diversity.

In **chapter IV** I investigate phytometer performance and trait responses to the short-term impact of resource addition (i.e. nutrients and light) in combination with herbivory exclusion and future climate manipulations (i.e. increased temperatures and seasonal variation in precipitation patterns). I aim to examine plants' short-term responses to these interacting factors and thus understand consequences for species coexistence and diversity. In addition, I actively test whether competition for light is a mechanism explaining plant trait manifestations in this interactive setting.
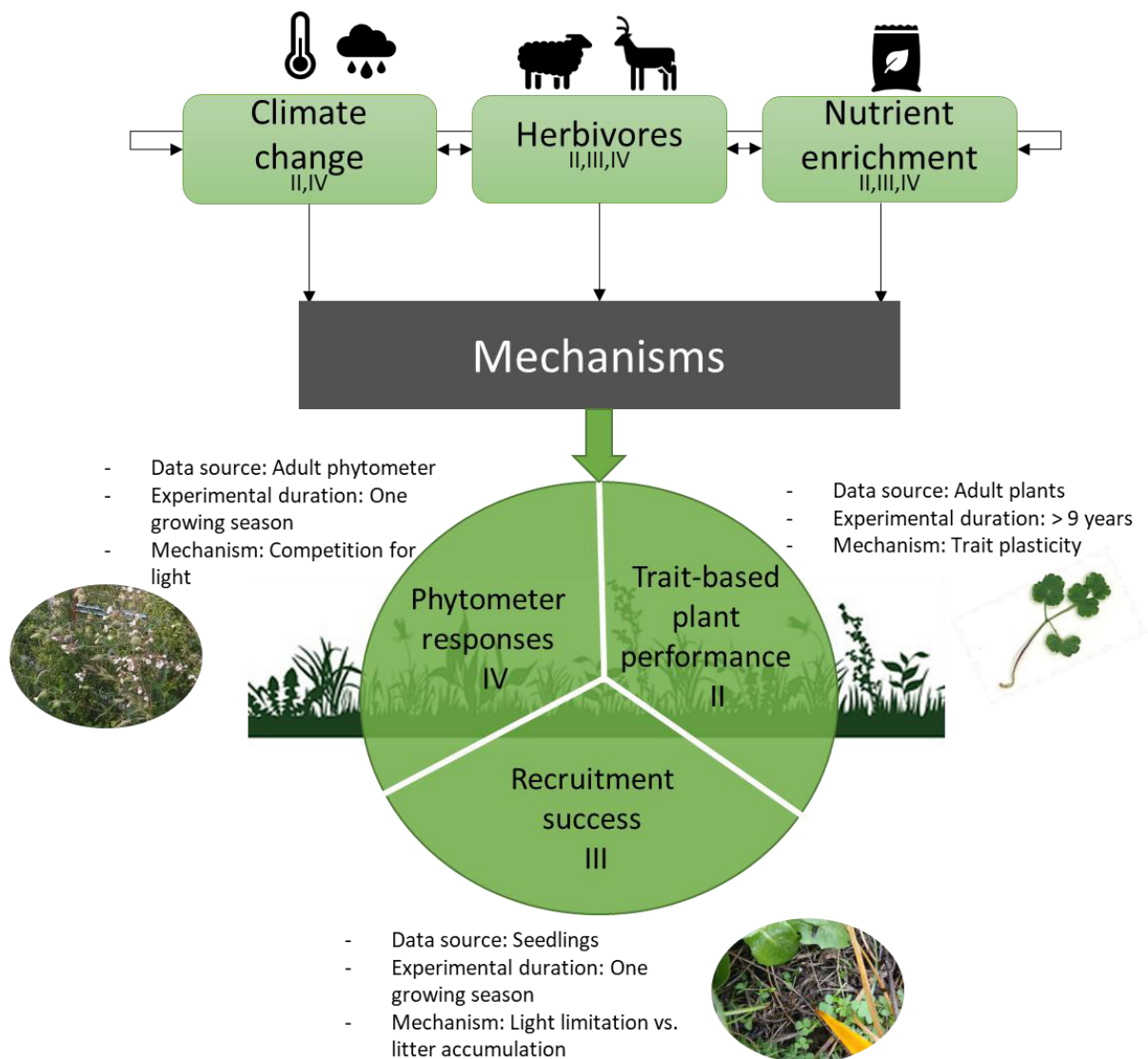
Figure 1. *Schematic outline of the focus of the three experimental chapters.*

MATERIALS AND METHODS

This section is intended to give a broad overview of the experimental set-ups I used and the measurements I have taken to acquire the data for this thesis. For a detailed description of the experiments, the treatments, the measurements taken and the data analyses please see the material and methods section in the respective chapters themselves.

CHAPTER II: WARMING AND GRAZING EXPERIMENT IN KILPISJÄRVI

Study site

The study area of **chapter II** is situated in north-western Finnish Lapland, in Kilpisjärivi (69.055°N, 20.887°E) on the south-western slope of Mt. Iso-Jehkats, 750 m above sea level (Figure 2). Climatically, this region is assigned to the maritime and continental climate north of the Arctic Circle (Järvinen 1987). The long-term (1971-2000) annual temperature is – 4°C, although more recent records and simulations predict an increase in temperature to - 2°C or even -0.9°C (Kivinen *et al.* 2012). The long-term (1971-2000) annual precipitation average is around 800 mm with an equal amount of snow and rainfall, although the amount of rainfall is predicted to increase over time (Kivinen *et al.* 2012). The vegetation comprises herbs and forbs of species-rich tundra meadows (Kaarlejärvi, Eskelinen & Olofsson 2013; Eskelinen, Kaarlejärvi & Olofsson 2017; Kaarlejärvi, Eskelinen & Olofsson 2017). Typical species include *Deschampsia flexuosa*, *Festuca ovina*, *Potentilla crantzii*, *Viola biflora*, *Thalictrum alpinum* and *Astragalus alpinus* (Eskelinen, Kaarlejärvi & Olofsson 2017). In summer (June to August), the research site is grazed by various sized herds of semi-domestic reindeer (*Rangifer tarandus tarandus*) (Heikkinen *et al.* 2005; Eskelinen & Oksanen 2006).

Experimental design

The study for **chapter II** utilized a long-term experiment (i.e. nine years) consisting of 56 plots in a full-factorial combination of mammalian herbivore exclusion, manual NPK fertilization and passive warming with Open Top Chambers (OTCs). In addition to the physical temperature increase, the warming treatment extended the overall growing season at both the beginning and end**,** as predicted for this area (Kivinen *et al.* 2012). The fertilization treatment simulated increased anthropogenic and natural nutrient input (Galloway *et al.* 2004; Dentener *et al.* 2006), and also tested the role of nutrient limitation for plants (Borer *et al.* 2014a).

Set-up of treatments

The herbivory exclusion treatment consisted of permanent fences, which were installed around the exclosure plots to exclude ranging reindeer and naturally occurring rodents such as mountain hare, voles and lemmings (Figure 3a). The climate

manipulations in **chapter II** were achieved using OTCs (Figure 3a), which are widely used to increase air and soil temperature in circumboreal systems to study the effect of climate warming on vegetation (Marion *et al.* 1997). The OTCs increased air temperature by about 2°C compared to the control (Kaarlejärvi, Eskelinen & Olofsson 2013). For the fertilization treatment, NPK fertilizer was applied annually to the plots assigned to the fertilization treatment, following the protocol for grassland systems worldwide (Borer *et al.* 2014a).

Measurements and data analysis

To assess intraspecific trait manifestation in response to the treatment combinations, I measured plant vegetative height (cm), SLA (mm^2/mg), foliar C:N and leaf greenness according to the standard protocol (Cornelissen *et al.* 2003; Perez-Harguindeguy *et al.* 2013). The traits were chosen as surrogates for species' competitive ability in terms of resource acquisition and palatability for herbivores (Evans & Poorter 2001; Keddy *et al.* 2002; Westoby *et al.* 2002; Diaz *et al.* 2004; Evju *et al.* 2009; Reich 2014). For the measurements, I selected eight tundra species that were common in the experimental area. The species were *Anthoxanthum odoratum* L., *Bistorta vivipara* (L.) Delarbre, *Ranunculus acris* L., *Sibbaldia procumbens* L., *Solidago virgaurea* L., *Thalictrum alpinum* L., *Vaccinium vitis-idaea* L. and *Viola biflora* L. As a measure of plant performance, I used relative species abundance and determined this with a modified point intercept method (Jonasson 1988; Kaarlejärvi, Eskelinen & Olofsson 2013).

I analyzed the data with R statistical software (R Core Team 2020). For information about the detailed statistical approaches please see the data analysis section in **chapter II**.

CHAPTERS **III** & **IV**: LIGHT ADDITION EXPERIMENT IN **B**AD **L**AUCHSTÄDT

Study site

The study area of **chapters III** and **IV** is located in Central Germany, close to the research station Bad Lauchstädt (51°22060 N, 11°50060 E) (Figure 2). The prevailing climate in this region is characterized as subcontinental and has a mean annual air temperature of 8.9 °C and a mean annual rainfall amount of 489 mm (Schädler *et al.*

2019). The experiment was within the Global Change Experimental Facility (GCEF). This is a long-term experimental site used to study ecological questions related to plants and soil in different land use types under ambient and future climate change conditions (Schädler *et al.* 2019). For this thesis, I only examined the extensively used pastures of the GCEF which involve short-term (24 h) high-intensity grazing (rotational or mob grazing) by about 20 sheep two to three times during each growing season (Schädler *et al.* 2019). The vegetation in these pastures comprises grasses, legumes and herbs typical of the dryland meadows of Central Germany, such as *Bromus hordaceus*, *Dactylis glomerata*, *Festuca pratensis*, *Lotus corniculatus*, *Medicago falcata*, *Securigera varia, Achillea millefolium*, *Centaurea jacea*, *Daucus carota*, *Galium album*, *Scabiosa ochroleuca* and *Silene latifolia.*

Experimental design

For **chapters III** and **IV** I used an experiment which was initiated in 2017 and designed to investigate the role of light limitation under fertilization, exclusion of herbivory and changing climate at the plant and community level. To test this, the experiment is equipped with recently developed and modern LED lamps (C65, Valoya, Finland) which add light within the vegetation understory. The experiment is fully-factorial with all possible treatment combinations of fertilization, herbivory exclusion and light addition. In total there are 80 experimental subplots, half of which are subject to the ambient climate and the other half to future climate (i.e. increased temperature and increased spring and autumn precipitation, but decreased summer precipitation). For **chapter III** I added an additional treatment of litter removal to the overall experimental set-up, resulting in 160 experimental units to which I added a seed mixture of 15 common and locally occurring species. For **chapter IV** one individual of *Silene latifolia* was planted into each experimental subplot.

Set-up of treatments

In the research described in chapters III and IV, mobile fence units were used which excluded the sheep, but not voles and mice which frequently occur in the plots. The climate manipulation was implemented using automated roof structures with foldable tarps, which increased night temperatures and blocked precipitation (Figure 3b). In general, future precipitation amounts were achieved by adding collected rainwater

during spring and autumn and by shielding the plots from rain during summer. The amount of water addition or retention was based on previous weeks' rainfall in the ambient climate conditions (Schädler *et al.* 2019). For the fertilization treatment, NPK fertilizer was applied to the plots annually and followed the protocol for grassland systems worldwide (Borer *et al.* 2014a). For the light addition treatment, I used the previously mentioned modern LED lamps (C65, Valoya, Finland) (Figure 3c) which mimic the spectrum of natural sunlight without increasing the soil surface temperature (see Supplementary Information of **chapter III**, Table S2). The lamps were installed in intact vegetation to mimic a gap in vegetation which could aid seedling recruitment (**chapter III**) or benefit plant growth (**chapter IV**) by removing the shading of surrounding vegetation

Measurements and data analyses

In **chapter III** I counted the number and richness of seedlings germinating from seed in each experimental unit in one growing season. In **chapter IV** I measured the total aboveground biomass of the harvested phytometers as an indicator of their performance, as in Liancourt *et al.* (2015). In addition, I collected data on vegetative height (cm), SLA (mm^2/mg) and foliar C:N to determine whether any of these traits reflected signs of light limitation or otherwise responded to the short-term influences of the experimental treatments.

In **chapter III** I only used data from the ambient climate conditions in the statistical analysis (i.e. data from 80 experimental units). In **chapter IV** I used the full data set. I analyzed the data with R statistical software (R Core Team 2020). For information

about the detailed statistical approaches, please see the data analysis section in **chapter III** and **chapter IV**.
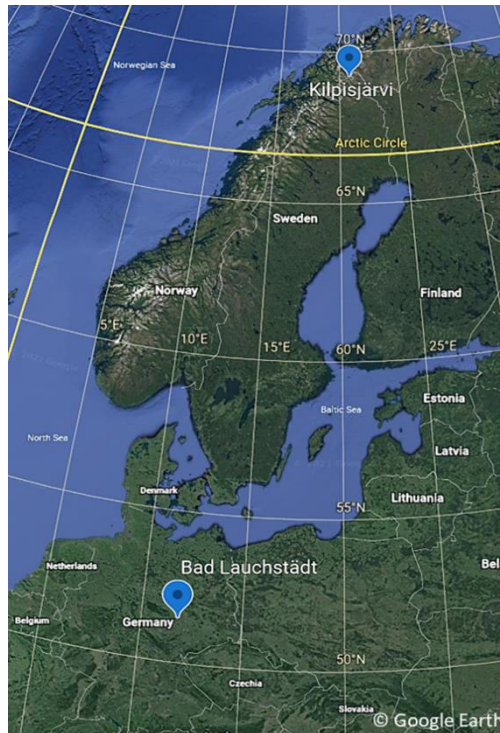
Figure 2. *Map showing the location of the study areas. Field work for chapter II was conducted in Kilpisjärvi, and field work for chapter III-IV was conducted in Bad Lauchstädt.*
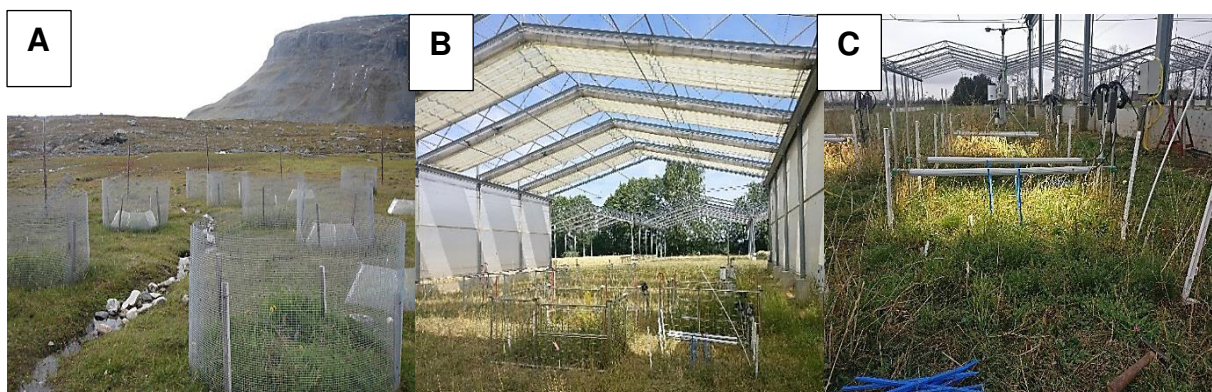
Figure 3. *A Climate manipulations (OTCs) and reindeer exclosures used at the experimental site in Kilpisjärvi (photo credit Anu Eskelinen). B Climate manipulations (roofs with foldable tarps and rain sprinklers) and sheep exclosures at the experimental site in Bad Lauchstädt. C Light addition in the field using recently developed LED lamps which mimic the spectrum of the natural sunlight and in particular add light to the community understory.*

CHAPTER II

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Mammalian herbivory shapes intraspecific trait responses to warmer climate and nutrient enrichment

Maria-Theresa Jessen[1,2,3] | Elina Kaarlejärvi[4] | Johan Olofsson[5] | Anu Eskelinen[2,3,6]

[1]Department of Community Ecology, Helmholtz Centre for Environmental Research – UFZ, Halle, Germany

[2]Department of Physiological Diversity, Helmholtz Centre for Environmental Research – UFZ, Leipzig, Germany

[3]German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany

[4]Research Centre for Ecological Change, University of Helsinki, Helsinki, Finland

[5]Department of Ecology and Environmental Sciences, Umea University, Umea, Sweden

[6]Department of Ecology and Genetics, University of Oulu, Oulu, Finland

Correspondence
Maria-Theresa Jessen, German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher Platz 5a, D-04103 Leipzig, Germany.
Email: maria-theresa.jessen@idiv.de

Abstract

Variation in intraspecific traits is one important mechanism that can allow plant species to respond to global changes. Understanding plant trait responses to environmental changes such as grazing patterns, nutrient enrichment and climate warming is, thus, essential for predicting the composition of future plant communities. We measured traits of eight common tundra species in a fully factorial field experiment with mammalian herbivore exclusion, fertilization, and passive warming, and assessed how trait responsiveness to the treatments was associated with abundance changes in those treatments. Herbivory exhibited the strongest impact on traits. Exclusion of herbivores increased vegetative plant height by 50% and specific leaf area (SLA) by 19%, and decreased foliar C:N by 11%; fertilization and warming also increased height and SLA but to a smaller extent. Herbivory also modulated intraspecific height, SLA and foliar C:N responses to fertilization and warming, and these interactions were species-specific. Furthermore, herbivory affected how trait change translated into relative abundance change: increased height under warming and fertilization was more positively related to abundance change inside fences than in grazed plots. Our findings highlight the key role of mammalian herbivory when assessing intraspecific trait change in tundra and its consequences for plant performance under global changes.

KEYWORDS
anthropogenic change, climate warming, grazing, herbivory, intraspecific trait plasticity, nutrient addition, open-top chamber, plant performance, reindeer, trait–environment relationship

1 | INTRODUCTION

Around the globe, high latitude and altitude systems face shifts in grazing regimes concurrently with increasing temperatures and accelerated nutrient cycling (Aerts, 2006; Uboni et al., 2016; Wookey et al., 2009). Recent studies have successfully predicted community responses to these anthropogenic changes using species' functional traits (i.e. interspecific traits; Bjorkman et al., 2018; Eskelinen et al., 2012; Kaarlejärvi et al., 2017; Soudzilovskaia et al., 2013). These are often traits related to size (e.g. height) or resource-use strategy, for example, slow–fast traits such as foliar C:N and SLA (Reich, 2014; Westoby et al., 2002; Wright

et al., 2004). In addition, plant species can respond to environmental changes via intraspecific trait plasticity, that is, within-species trait changes (Liancourt et al., 2015; Moran et al., 2016; Nicotra et al., 2010; Siefert et al., 2015), which can be equal or greater than interspecific variation (Des Roches et al., 2018). Intraspecific trait plasticity can allow communities to respond rapidly to global changes without turnover of species (Jung et al., 2014) or magnify community-level trait change over time (Bjorkman et al., 2018). Therefore, intraspecific traits need to be considered if we are to make accurate predictions about community responses to global changes.

Human-induced alterations in land use and introductions and extirpations of grazers and/or their predators can have huge consequences for the composition, diversity and trait distribution of plant communities (Bakker & Svenning, 2018; Estes et al., 2011; Kaarlejärvi et al., 2017; Post et al., 2019). Herbivores can change community trait composition by targeting and consuming species with tall stature, high SLA and low foliar C:N (Diaz et al., 2007; Evju et al., 2009). Recent studies imply that grazing by mammalian herbivores can also markedly affect intraspecific traits (Firn, Nguyen, et al., 2019; Firn et al., 2017).

Anthropogenic nutrient enrichment, either via airborne deposition or climate warming inducing the release of nutrients from soil organic matter, is a major cause of biodiversity loss and shifts in plant community composition worldwide (Boutin et al., 2017; Stevens, 2019; Tilman et al., 2001). In experimental studies, nutrient addition has also been shown to modify intraspecific traits, for example, to enhance plant height, SLA, foliar N content and leaf greenness (Mudrák et al., 2019; Tatarko & Knops, 2018). These are traits related to rapid growth in resource-rich conditions (Reich, 2014; Wright et al., 2004) and they are therefore likely to confer greater performance and competitive ability under nutrient-rich conditions (Carmona et al., 2019; Suding et al., 2005). Similar intraspecific trait expressions occur in height and SLA (but not foliar C:N or leaf greenness) in response to warming (Bjorkman et al., 2018; Hudson et al., 2011). Moreover, accelerated nutrient turnover in warmer temperatures (Aerts, 2006) should increase above-ground biomass and in turn promote taller plants with a greater competitive ability for light (Elmendorf et al., 2012).

However, not much is known about how mammalian herbivory, increased nutrients and warming interact to affect intraspecific traits, although in nature they occur simultaneously and can either magnify or mitigate each other's impacts on plant communities (Eskelinen et al., 2017; Gough et al., 2007; Kaarlejärvi et al., 2017; Olsen et al., 2014). For example, the absence of grazers can lead to increased biomass and decreased light availability under the canopy (Borer, Seabloom, et al., 2014; Olofsson et al., 2009), and even more so under conditions that are warmer and nutrient-enriched (Kaarlejärvi et al., 2017; Post & Pedersen, 2008), which favour species with traits that are advantageous in light-limited conditions (e.g. tall stems and high SLA; Kaarlejärvi et al., 2017). However, in the presence of grazers, plants experience increased grazing risk, which should promote species and plant individuals with traits associated

with low visibility to, and palatability for, herbivores (e.g. short stems, small SLA, high foliar C:N; Evju et al., 2009).

Intraspecific trait change (i.e. plasticity) in response to contemporary global changes will probably affect population performance (Des Roches et al., 2018; Liancourt et al., 2015) as plants that are able to respond to altered resource availability could also be better competitors under novel conditions (Ashton et al., 2010; Bret-Harte et al., 2001). In consequence, plasticity in traits related to rapid resource-use under warmer and more nutrient-rich conditions could increase competitive ability and population fitness (Firn et al., 2012; Liancourt et al., 2015; but see Siefert & Ritchie, 2016). However, those same trait responses to nutrient enrichment and warming could increase palatability and grazing risk (Evju et al., 2009), translating into decreased abundance and population fitness in grazed conditions (Firn et al., 2012). Whether intraspecific trait change under nutrient-enriched and warmer conditions is manifested in greater species' success may therefore critically depend on grazing.

We experimentally investigated intraspecific trait responses of eight common tundra plant species to mammalian herbivory, fertilization and climate warming. We measured four commonly used traits (vegetative height, SLA, foliar C:N and leaf greenness) linked to resource uptake strategies and competitive ability for light (Evans & Poorter, 2001; Reich, 2014; Wright et al., 2004). We further examined how trait responsiveness to the treatments was linked to species' performance in relation to other species in a community (i.e. its competitive advantage; Goldberg, 1996), measured as change in relative abundance (i.e. the proportion of total community biomass belonging to each species). Our relative abundance measure was based on biomass estimates obtained using the point intercept method (Jonasson, 1988); hereafter called 'abundance' for simplicity. We predicted: (a) Herbivory would decrease intraspecific height and SLA (but not leaf greenness), and increase foliar C:N. (b) Fertilization and warming would increase intraspecific height, SLA and leaf greenness and decrease foliar C:N. (c) These shifts, induced by warming and fertilization, would be more pronounced in the absence of herbivores and smaller in the presence of herbivores. (d) Intraspecific trait change in response to fertilization and warming measured at the individual level would correlate with increased abundance at the community level in the absence of herbivores, but with smaller or decreased abundance in the presence of herbivores.

2 | MATERIALS AND METHODS

2.1 | Study site and experimental design

This experiment was carried out in NW Finnish Lapland, in Kilpisjärvi (69.055°N, 20.887°E). The experimental site was located on the south-western slope of Mt. Iso-Jehkats 750 m above sea level (Kaarlejärvi et al., 2013). The study site is characterized as species-rich tundra meadow dominated by grasses and forbs (Eskelinen et al., 2017; Kaarlejärvi et al., 2013, 2017). The area is seasonally (June–August) grazed by semidomesticated reindeer

(*Rangifer tarandus tarandus*) of fluctuating herd sizes (Eskelinen & Oksanen, 2006; Heikkinen et al., 2005); recent observations report 9–17 reindeer per km² (Kaarlejärvi et al., 2017). Other important mammalian herbivores, which can markedly affect vegetation, are Norwegian lemmings (*Lemmus lemmus* L.) and grey-sided voles (*Myodes rufocanus* Sund.; Moen, 1990; Virtanen et al., 1997). The mean annual air temperature in the area is −2.0°C (Kaarlejärvi et al., 2017).

We established the experiment in 2009, with a full factorial combination of passive warming, mammalian herbivore exclusion and fertilization, resulting in seven different treatment combinations plus the control. Each treatment combination and control were replicated seven times resulting in a total of 56 experimental plots of 0.8 × 0.7 m (Eskelinen et al., 2017; Kaarlejärvi et al., 2013, 2017). We implemented warming by using hexagonal open top chambers (OTC), a widely used method to investigate effects of warming in tundra areas (Henry & Molau, 1997; Marion et al., 1997). The OTCs were 146 cm wide at the bottom. In this experiment OTCs were used for spring and autumn warming (May–June and August–October). We removed the OTCs for July, the time when the reindeer are present in the area. This allowed equal grazing in all unfenced plots, including the joint treatment of warming and grazing, as OTCs can be a potential grazing barrier for larger herbivores (Moise & Henry, 2010). The other major herbivores, voles and lemmings, could enter the OTCs year around. Our warming treatment therefore extends the growing season at both ends, that is, in April–June and August–September, which matches with predictions for this region (Kivinen et al., 2012). OTCs increased air temperature in June by 1.92°C and in August by 1.23°C compared to the control (Kaarlejärvi et al., 2013). We implemented the herbivore exclusion treatment by establishing circular fences (160 cm in diameter, 100 cm in height, mesh size 10 × 10 mm) embedded 15 cm deep into the soil around each fenced plot (Kaarlejärvi et al., 2013). Additionally, we fenced the entire experimental area with a temporary reindeer fence from the beginning of August to the end of June in the following year. This was done to protect the experiment from straying reindeer outside the normal grazing season, and ensured that grazing pressure was similar in all plots (Kaarlejärvi et al., 2013). We fertilized manually with fast-dissolving NPK fertilizer mixed with 1 L of water to every fertilized plot twice per growing season (mid-June and end of July), resulting in an addition of 9.6 g N, 5.4 g P and 13.2 g K per m² annually. We watered plots not receiving the fertilization treatment with the same amount of water. Mammalian herbivory and ongoing climate warming may accelerate nutrient cycling and increase plant available nutrients (Aerts, 2006; Barthelemy et al., 2018), though to a lesser extent than the fertilization treatment applied in this experiment (Barthelemy et al., 2015; Rustad et al., 2001). The fertilization treatment tested the general role of nutrient limitation for plant growth, following levels used in other experiments in a variety of ecosystems (Borer, Harpole, et al., 2014; Eskelinen et al., 2012; Sitters et al., 2019; Sundqvist et al., 2014). Our treatment also mimicked between-habitat variation in soil

nutrient concentrations in tundra (Eskelinen et al., 2009) and nutrient enrichment effects in some heavily impacted regions (e.g. heavily impacted alpine tundra; Dentener et al., 2006; Galloway et al., 2004).

2.2 | Trait sampling

To investigate intraspecific trait manifestation, we chose eight abundant species in the area and experimental plots based on earlier surveys: *Anthoxanthum odoratum* L., *Bistorta vivipara* (L.) Delarbre, *Ranunculus acris* L., *Sibbaldia procumbens* L., *Solidago virgaurea* L., *Thalictrum alpinum* L., *Vaccinium vitis-idaea* L. and *Viola biflora* L. We selected species encompassing a broad range of sizes (heights) and traits related to rapid resource acquisition (SLA, foliar C:N). We collected the trait data from the eight chosen species from the experimental plots at the end of July to mid-August, in 2018, following a standard sampling protocol (Cornelissen et al., 2003; Perez-Harguindeguy et al., 2013). We collected data on vegetative height (cm) as an indicator for competitive ability under different light conditions (Evans & Poorter, 2001; Westoby et al., 2002). We also collected information on leaf greenness as a surrogate for leaf chlorophyll content which can change in relation to light conditions (Valladares & Niinemets, 2008). Furthermore, we collected data on SLA (mm² per mg dry mass) and foliar C:N; traits associated with slow/fast resource uptake strategy and palatability for herbivores (Diaz et al., 2001, 2004; Evju et al., 2009). Plant height and leaf greenness were measured directly in the field on three vital, fully developed and undamaged individuals per species and plot. The sampled individuals had not been damaged by grazers in the year of sampling (i.e. height in the grazed plots was not a result of plant tissue loss at the time of sampling). This resulted in three replicates per plot. Leaf greenness was measured with a SPAD-502 Plus Chlorophyll Meter (Konica Minolta, Japan). *Thalictrum alpinum* was excluded from leaf greenness measurements, because its leaves were too small for the cuvette of the chlorophyll meter. We sampled leaves for SLA and foliar CN measurements from the same individuals for which we measured height and leaf greenness. In addition, we collected seven more leaves, each from a different individual, for foliar C:N analysis in order to have sufficient plant material. All leaves originating from one plot were pooled. This resulted in one replicate per plot for foliar C:N.

2.3 | Abundance measurements

We used a modified point-intercept method (Jonasson, 1988) with 108 systematically distributed points in 25 × 50 cm² quadrats for measuring species abundance (Kaarlejärvi et al., 2013). In this method, a pin is lowered from each point to the ground and all hits with vegetation are recorded. The number of hits correlates well with biomass (Jonasson, 1988). We used relative species abundance (i.e. the proportion of total community biomass

belonging to each species) as an indicator of species competitive performance in a community. In other studies, biomass has been used as a measure of individual species performance (Liancourt et al., 2015).

2.4 | Data analysis

To assess the interactive effects of herbivore exclusion, fertilization and warming on intraspecific plant height, SLA, foliar C:N and leaf greenness (predictions a, b, c), we applied linear mixed effect models with treatments and species as fixed factors for each measured trait separately. Traits were analysed separately because they were correlated. Plot was used as a random factor to account for the nested sampling design (i.e. that species were collected from the same plots). As treatment effects strongly varied between species, we also ran separate models for each species. For *S. procumbens*, the three-way exclosure × fertilization × warming interaction was omitted from the models as it was absent from this treatment combination. We assessed the significance of the treatment effects using *F* tests. We used model diagnostic plots to check the homogeneity of variances and the normality of errors (Crawley, 2007) and the data were log- or square-root transformed whenever necessary (see Table 1; Table S1 for more information of transformed variables).

Furthermore, we calculated trait change according to Equation (1):

$$\text{Trait change}_{i,j,k} = \text{mean}(\text{trait value}_{i,j,k}) - \text{mean}(\text{trait value}_{i,j=C,k}), \quad (1)$$

where *i* refers to one of the eight species, *j* is one of the seven different treatments and *k* is one of the four measured traits. *C* refers to all control plots.

For the species abundance data, we calculated change in the same manner (Equation 2) based on abundance data collected in 2018.

$$\text{Change of relative abundance}_{i,j} = \text{mean}(\text{relative abundance}_{i,j}) \quad (2)$$
$$- \text{mean}(\text{relative abundance}_{i,j=C}),$$

where *i* refers to one of the eight species and *j* is one of the seven different treatments, *C* refers to all control plots.

To assess whether a change in intraspecific trait values (i.e. plasticity) was linked to a change in relative abundance and to assess how this relationship depended on herbivory (prediction d), we fitted linear mixed effects models with change in relative abundance as the response variable and herbivore exclusion, trait value change and their interaction as fixed explanatory factors. We ran separate models for each measured trait, but not for each species because there were too few data points (i.e. one replicate per species and treatment combination); however, we added species as a random effect.

We used the 'lme4' package (Bates et al., 2015) to run linear mixed effect models, the 'car' package for assessing the significance of the treatments effects (Fox & Weisberg, 2019), the 'dplyr' package for data manipulation (Wickham et al., 2018) and the 'ggplot2' package for plotting (Wickham, 2016) in R statistical software (version 3.6.1; R Core Team, 2019).

TABLE 1 Results of mixed effects models testing the effects of exclosure, fertilization, warming and their interactions on intraspecific trait values of height, SLA, foliar C:N and leaf greenness across eight studied species

Source of variation	Height[a]		SLA[a]		Foliar C:N[b]		Leaf greenness	
	F	p	F	p	F	p	F	p
Exclosure	111.9	**<.001**	36.8	**<.001**	41.5	**<.001**	0.7	.399
Fertilization	31.1	**<.001**	5.8	**.02**	20.5	**<.001**	19.2	**<.001**
Warming	16.6	**<.001**	3.3	*.08*	40.4	**<.001**	0.3	.565
Species	519.6	**<.001**	474.3	**<.001**	1,359.2	**<.001**	208.3	**<.001**
E × F	<0.1	.806	3.9	*.053*	3.6	*.063*	0.2	.628
E × W	3.0	*.09*	<0.1	.814	4.9	**.032**	0.7	.398
E × S	4.9	**<.001**	3.1	**.003**	12.5	**<.001**	3.8	**<.001**
F × W	0.3	.577	0.3	.958	2.8	.103	2.4	.128
F × S	8.6	**<.001**	2.3	**.026**	4.1	**<.001**	3.1	**.005**
W × S	7.8	**<.001**	11.7	**<.001**	29.2	**<.001**	18.2	**<.001**
E × F × W	0.8	.385	0.2	.678	<0.1	.89	<0.1	.826
E × F × S	9.9	**<.001**	6.9	**<.001**	2.5	**.016**	0.9	.487
E × W × S	2.7	**.009**	0.8	.562	4.0	**<.001**	0.8	.533
F × W × S	2.6	**.013**	1.2	.31	5.7	**<.001**	0.7	.679
E × F × W × S	1.0	.441	2.5	**.019**	4.9	**<.001**	1.3	.261

Note: Significant results (*p* < .05) are in bold and marginally significant results (*p* < .1) are in italics.
Abbreviations: E, exclosure; F, fertilization; S, species; SLA, specific leaf area; W, warming.
[a]Log-transformed.
[b]Square-root transformed.

3 | RESULTS

3.1 | Interactive effects of herbivore exclusion, fertilization and warming on plant intraspecific trait responses

Herbivore exclusion, fertilization and warming all exhibited significant positive main effects on height across all species (Figure 1a; Table 1). Plants were, on average, 50% taller inside fences than in grazed plots, while fertilization increased height by 28% and warming increased height by 11%. These general patterns were also valid at the species level (Figure S2; Table S1). Herbivore exclusion interacted with fertilization and this interaction also depended on species (Table 1, three-way E × F × S interaction). Overall, across the species, fertilization tended to have greater positive impact when herbivores were excluded (Figure 1a, but there was no significant two-way interaction); at the individual species level this was the case especially with some

tall-statured species (e.g. *S. virgaurea*), while with some smaller species (*V. biflora*) the positive impact of fertilization was greater when herbivores were present (Figure S2e,h). Across the species, the effect of herbivore exclusion on height significantly interacted with warming such that when grazers were present, warming increased height compared to ambient conditions; however, when grazers were absent warmed and ambient plots did not differ from each other (E × W interaction, Figure 1a; Figure S1; Table 1). However, herbivore exclusion was still the strongest overall predictor of height (Figure 1a).

Across all species, herbivore exclusion increased SLA by 19% and fertilization by 10%, while warming had no effect on SLA (Figure 1b; Table 1). The positive effect of fertilization on SLA was stronger inside fences than in grazed plots (E × F interaction, Figure 1b; Figure S3; Table 1; Table S1).

Herbivore exclusion reduced foliar C:N by 11% and fertilization reduced it by 7.5%. Warming, however, increased foliar C:N by 12% across all species (Figure 1c; Table 1). The same pattern was valid at
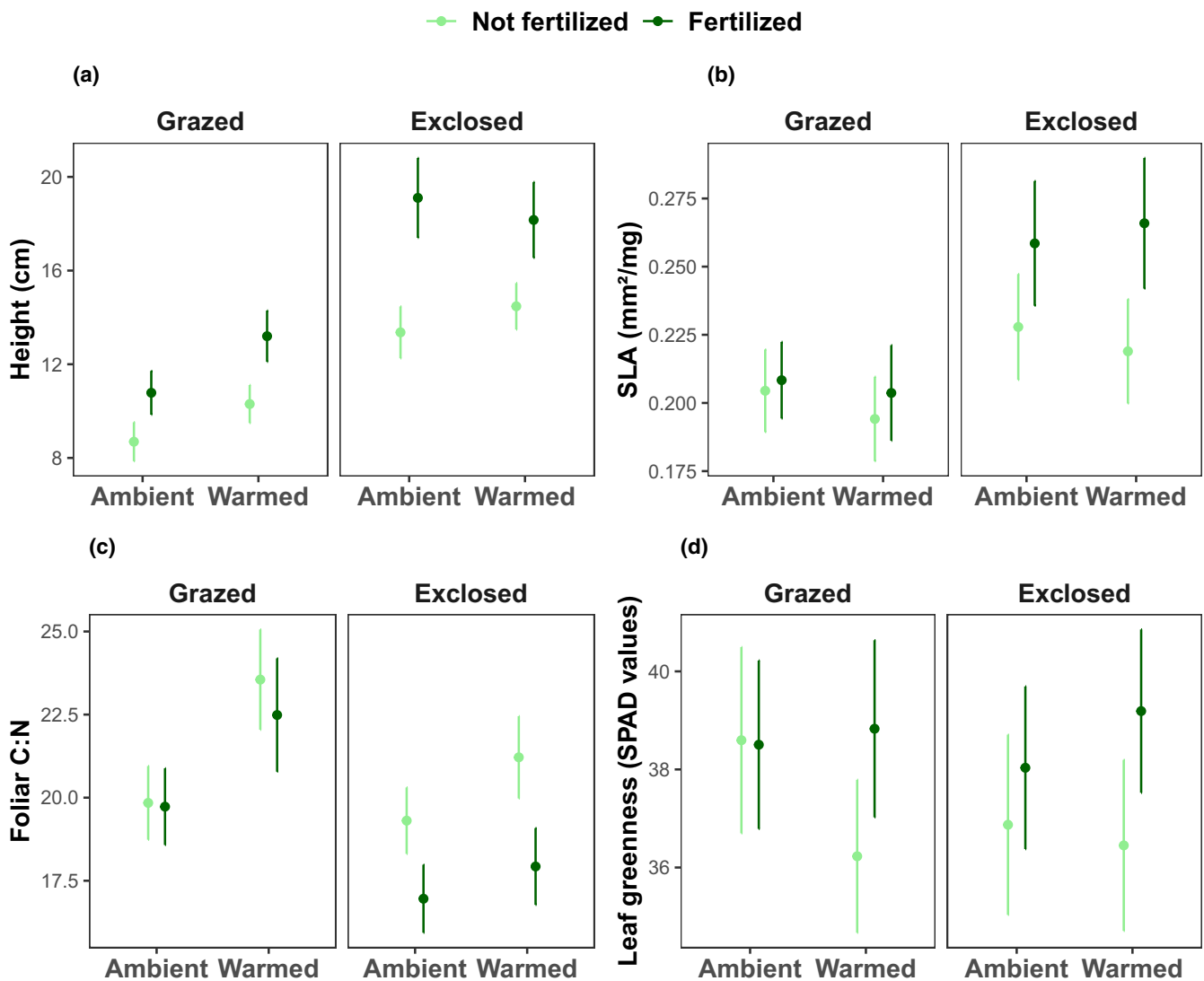
FIGURE 1 Trait values (mean ± *SE*) of (a) height, (b) specific leaf area (SLA), (c) foliar C:N and (d) leaf greenness (SPAD) across eight tundra species in all treatment combinations of exclosure, fertilization and warming (*n* = 56). Leaf greenness values were measured for three individuals per plot with the exception of *Thalictrum alpinum*, where the leaves were too small for the chlorophyll meter cuvette

FIGURE 2 Relationship between relative abundance change and changes in (a) height, (b) specific leaf area (SLA), (c) foliar C:N or (d) leaf greenness. The fitted line is a linear regression. Each data point represents the mean per species and treatment combination, resulting in eight (species) times seven (treatment combinations) points. Based on the calculations in Equations (1) and (2), there are fewer data points in the grazed panels because grazed only plots were used as controls
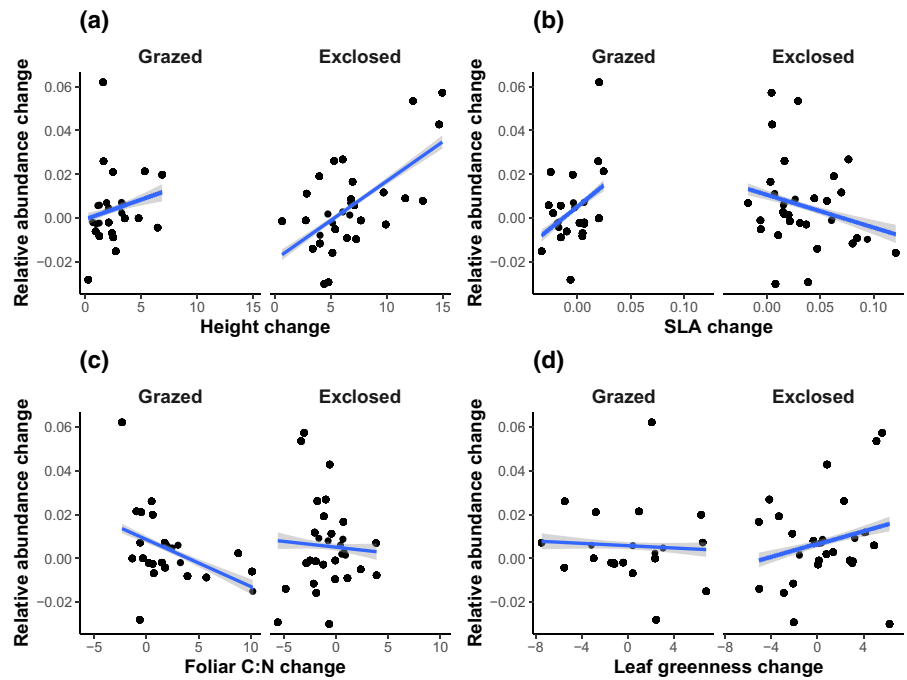
the species level (Figure S4). Herbivory also tended to mediate the effect of fertilization on foliar C:N such that fertilization reduced C:N more inside fences than outside fences (marginally significant E × F interaction, Figure S4; Table S1). In addition, warming increased foliar C:N more strongly in grazed than in fenced plots (E × W interaction, Figure 1c; Figure S4; Table 1; Table S1).

Fertilization increased leaf greenness, but neither warming nor grazing showed any effects on greenness across the species (Figure 1d; Table 1). Leaf greenness of individual species showed mixed responses to herbivore exclusion, fertilization and warming (Figure S5; Table S1).

3.2 | Intraspecific trait changes and change in relative abundance

We found evidence that trait changes were associated with changes in relative abundance. The direction of this relationship (positive or negative) depended on the trait and on herbivory (Figure 2a–d). Height change (i.e. height plasticity) was associated with increases in relative abundance, indicating that height plasticity in response to warming and fertilization translates to abundance gain. However, herbivores modified this relationship so that height plasticity increased relative abundance more strongly under fenced than under grazed conditions (trait change × E interaction, Figure 2a; Table 2). For SLA we observed the opposite; SLA change in response to warming and fertilizing was related to decreased relative abundance under fenced conditions, and increased relative abundance under grazed conditions (trait change × E interaction, Figure 2b; Table 2). In other words, plants that were more plastic with respect to SLA increased their relative abundance only when grazers were present. Herbivores did not affect the relationship between either foliar C:N or leaf greenness and relative abundance. However, plasticity in greenness was associated with an increase in relative abundance (Table 2).

TABLE 2 Results of four mixed effects models testing the effect of trait change (height, SLA, foliar C:N and leaf greenness) and its interaction with grazing on relative abundance change across species. In the models, species was treated as a random effect

Source of variation	Relative abundance change		R^2 marginal	R^2 conditional
	F	*p*		
Height change	334.47	**<.001**	.17	.48
Exclosure (E)	103.97	**<.001**		
E × Height change	36.54	**<.001**		
SLA change	89.20	**<.001**	.06	.54
Exclosure (E)	74.49	**<.001**		
E × SLA change	46.42	**<.001**		
Foliar C:N change	3.18	.074	.007	.50
Exclosure (E)	13.82	**<.001**		
E × Foliar C:N change	3.41	*.065*		
Leaf greenness change	18.93	**<.001**	.02	.48
Exclosure (E)	9.97	**.002**		
E × Leaf greenness change	<0.1	.785		

Note: Significant results (*p* < .05) are in bold and marginally significant results (*p* < .1) are in italics.

4 | DISCUSSION

Recent studies suggest that climate warming and nutrient enrichment can lead to pronounced intraspecific trait shifts (Bjorkman et al., 2018; Firn, McGree, et al., 2019) and highlight the need to assess trait responses to multiple global changes that mimic future novel conditions (Donelson et al., 2018; Matesanz et al., 2010). We

found that while increased temperature and nutrients modified intraspecific traits, grazing was a key factor affecting intraspecific trait change in a tundra plant community. Importantly, we also demonstrate that these trait responses to environmental changes can link to abundance changes at the community level; however, these relationships are contingent on mammalian herbivory.

Our finding that fertilization and, to a lesser extent warming, increased intraspecific height and SLA and reduced foliar C:N supports our prediction and is consistent with earlier studies about the effects of warming and fertilization separately (Baruah et al., 2017; Bjorkman et al., 2018; Henn et al., 2018; Hudson et al., 2011; Siefert & Ritchie, 2016) or in combination (Campioli et al., 2012). These findings emphasize the fact that species are able to exhibit plasticity in their responses to higher nutrient levels and warmer temperatures: becoming taller, and altering traits related to resource use (SLA, foliar C:N). These traits can improve species competitive ability in resource-rich and light-limited conditions (Suding et al., 2005) and consequently influence species' coexistence (Callaway et al., 2003; Turcotte & Levine, 2016). Importantly, plasticity in these traits can make species less vulnerable to climate warming and nutrient eutrophication as plasticity can allow species to cope with novel conditions (Nicotra et al., 2010).

However, we also found that grazing had a stronger effect on intraspecific traits than either warming or fertilization. Our finding that, in the absence of grazers, plants greatly increased height and SLA and reduced foliar C:N supports our prediction and is in line with results from previous studies (Firn, Nguyen, et al., 2019; Whitworth-Hulse et al., 2016). When grazed repeatedly, plant individuals should invest less resources in stems and leaves (Milchunas et al., 1988), reducing visibility and palatability to grazers, and favouring shorter stature and smaller SLA (Diaz et al., 2007). Avoiding grazing is likely to come at the expense of optimizing resource uptake, while in ungrazed, highly competitive conditions optimization of resource uptake (e.g. light) is essential (Diaz et al., 2001).

In addition, fertilization increased SLA and for some species also had a positive impact on height, and reduced foliar C:N more in the absence of grazers. This corroborates our prediction and highlights that herbivores need to be accounted for when assessing the effect of nutrients on intraspecific traits. These results somewhat contradict findings by Firn et al. (2012) and Firn, McGree, et al. (2019) that the effect of herbivores on leaf traits either did not interact with fertilization or that the impact of fertilization was greater when herbivores were present. The long grazing history (Heikkinen et al., 2005) and relatively intense grazing at our site (Kaarlejärvi et al., 2017) may explain these disparate results. Earlier studies from the same system have shown that the presence of grazers mitigates the positive fertilization effect on lowland species' invasion and performance (Eskelinen et al., 2017; Kaarlejärvi et al., 2013) and reduces the loss likelihood of short-statured, low SLA species (Kaarlejärvi et al., 2017). The results from the present study show that, even under nutrient-rich conditions, herbivory promotes smaller stature and SLA and higher foliar C:N, and these effects extend to within-species variation.

Earlier studies have shown that tall-statured species are more likely to benefit from nutrient addition and warming, emphasizing

the importance of interspecific trait differences driving shifts in competitive dominance under global changes (Bjorkman et al., 2018; DeMarco et al., 2014; Eskelinen & Harrison, 2015; Kaarlejärvi et al., 2017; Klanderud, 2008). We found that plants exhibiting greater height increase in response to nutrient addition and warming also showed greater abundance increases, suggesting that height plasticity contributes to community trait change. Not only between-species differences, but also within-species trait variability can drive community and ecosystem responses to global changes (Liancourt et al., 2015; Nicotra et al., 2010).

Furthermore, we found that the relationship between trait change in height and SLA and relative abundance change was contingent on herbivory. Greater height plasticity was more beneficial for relative abundance in the absence of herbivores, as we predicted. In contrast to our prediction we found the opposite for SLA, as higher SLA plasticity lead to an increase in relative abundance in the presence of herbivores. Greater height plasticity in ungrazed plots is probably linked to better competitive ability for light in high-biomass and light-limited conditions, promoting greater abundance in a community (Turcotte & Levine, 2016). However, higher SLA plasticity in the presence of herbivores might rather be linked to plants' capacity to compensate for grazing damage (Brathen & Odasz-Albrigtsen, 2000). The combination of fertilization and warming, that is, resource-rich and otherwise favourable conditions for growth, can favour traits that support compensatory growth (e.g. high SLA, low foliar C:N; Augustine & McNaughton, 1998; Coley et al., 1985). This aligns with the overcompensation theory (McNaughton, 1983), stating that grazing can stimulate plant growth and enhance persistence especially under nutrient-rich and warmer conditions (Coley et al., 1985; Ramula et al., 2019). Overall, our results highlight that herbivory is a major factor influencing how much intraspecific trait plasticity facilitates performance and needs to be taken into account when assessing plant traits under warmer and more nutrient-rich conditions.

Overall, we observed strong general patterns despite the variation caused by species-specific differences. However, individual species still differed in their responses. For example, *V. biflora*, a small-statured species, increased height under nutrient-rich conditions more in grazed than in fenced conditions, whereas *S. virgaurea*, a tall-statured species, grew taller in nutrient-rich and fenced conditions. It is possible that repeated biomass loss to herbivores reduces any long-term benefit from nutrients especially in inherently tall species, possibly because of smaller root: shoot ratio in high nutrient availability and consequently less tolerance to repeated herbivory (Olff et al., 1990; Strauss & Agrawal, 1999). In contrast, inherently small-statured species, that can avoid being grazed may benefit from nutrients and competition-free environment in grazed systems. Our results, therefore, emphasize that intraspecific trait plasticity is also controlled by different factors for different species (Albert et al., 2010; Lang et al., 2020; Liancourt et al., 2015) and more research is needed to disentangle which inherent properties of species dictate these responses.

To conclude, our findings highlight the importance of intraspecific trait plasticity as a mechanism to cope with climate warming,

nutrient enrichment and changing grazing regimes. Our results also highlight the need to consider interdependencies among these global change drivers when assessing intraspecific trait change. While earlier studies have identified mammalian herbivory as a key factor modulating the impacts of nutrient enrichment and climate warming on plant community composition, productivity and diversity (Borer, Seabloom, et al., 2014; Kaarlejärvi et al., 2017; Post & Pedersen, 2008), we identified mammalian herbivory as a key factor mediating their impacts on intraspecific traits. Furthermore, herbivory also affected how intraspecific trait plasticity translates to changes in relative abundance in a community. These results suggest that decisions on management and regulation of grazer and predator populations play critical roles in altering trait change in tundra and its consequences on ecosystem functioning in the Anthropocene (Bakker & Svenning, 2018; Estes et al., 2011; Lundgren et al., 2020).

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in figshare at https://doi.org/10.6084/m9.figshare.13019738.v1.

ORCID

Maria-Theresa Jessen [iD] https://orcid.org/0000-0002-5238-7118
Elina Kaarlejärvi [iD] https://orcid.org/0000-0003-0014-0073
Anu Eskelinen [iD] https://orcid.org/0000-0003-1707-5263

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

SUPPLEMENTARY INFORMATION CHAPTER II
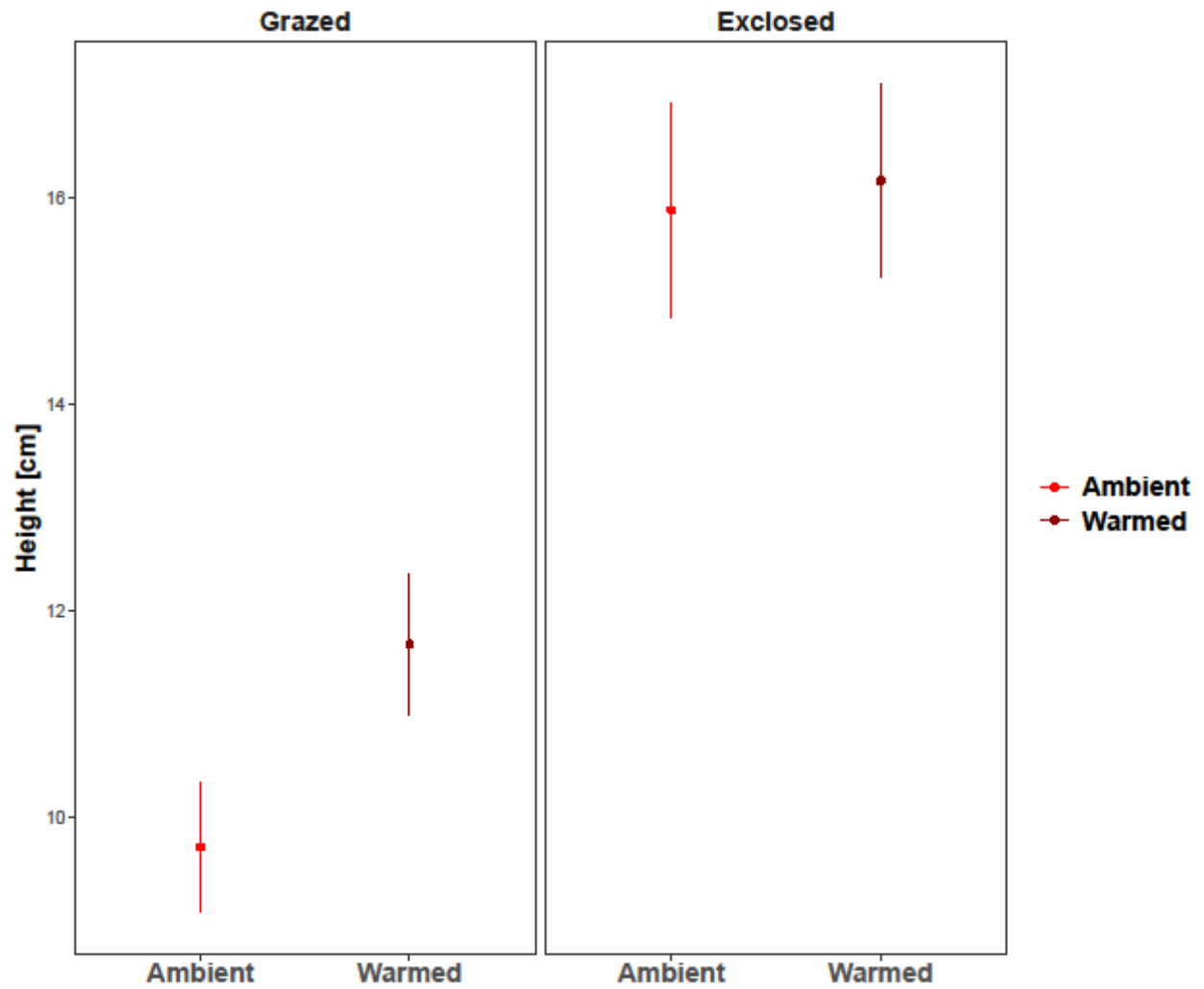

Figure S1. Trait values of height (mean ± SE) across eight sampled species in the treatment combinations of exclosure and warming.

Table S1. Results of mixed effects models testing the effects of exclosure, fertilization, warming and their interactions on trait values of height, SLA, foliar C:N and leaf greenness (LG) separately for the eight studied species. E = exclosure, F = fertilization, W = warming, n.a. = not available. Significant results (P < 0.05) are in bold and marginally significant results (P < 0.1) are in italics. † Log-transformed, ‡ square-root-transformed.

Species	Source of variation	Height † F	Height † P	SLA † F	SLA † P	Foliar C:N ‡ F	Foliar C:N ‡ P	LG † F	LG † P
Anthoxantum odoratum	Exclosure	64.8	**<0.001**	2.9	*0.097*	30.2	**<0.001**	7.4	**0.009**
	Fertilization	28.4	**<0.001**	4.0	*0.051*	74.6	**<0.001**	13.5	**0.006**
	Warming	4.9	**0.031**	1.4	0.238	26.1	**<0.001**	1.7	0.199
	E x F	3.0	*0.09*	6.9	**0.011**	0.4	0.552	0.3	0.619
	E x W	0.5	0.464	<0.1	0.876	1.4	0.244	0.2	0.631
	F x W	0.7	0.405	<0.1	0.954	7.2	**0.008**	0.9	0.345
	E x F x W	0.2	0.657	2.5	0.12	0.2	0.635	<0.1	0.898
Bistorta vivipara	Exclosure	20.8	**<0.001**	21.9	**<0.001**	62.8	**<0.001**	0.6	0.438
	Fertilization	9.8	**0.003**	4.2	**0.047**	15.9	**<0.001**	2.0	0.163
	Warming	14.1	**<0.001**	4.0	*0.053*	46.5	**<0.001**	6.7	**0.014**
	E x F	<0.1	0.905	14.6	**<0.001**	25.8	**<0.001**	1.2	0.283
	E x W	<0.1	0.803	<0.1	0.887	0.9	0.352	1.1	0.292
	F x W	<0.1	0.828	2.0	0.166	<0.1	0.990	1.2	0.277
	E x F x W	2.2	0.148	<0.1	0.822	0.3	0.565	<0.1	0.909
Ranunculus acris	Exclosure	46.8	**<0.001**	17.7	**<0.001**	38.2	**<0.001**	0.2	0.665
	Fertilization	25.0	**<0.001**	4.0	*0.054*	60.9	**<0.001**	3.4	*0.075*
	Warming	2.5	0.124	<0.1	0.917	14.8	**<0.001**	0.2	0.645
	E x F	0.6	0.443	3.8	*0.06*	7.1	**0.009**	0.8	0.373
	E x W	8.2	**0.007**	0.9	0.336	14.6	**<0.001**	0.5	0.477
	F x W	<0.1	0.981	0.1	0.721	4.3	**0.04**	<0.1	0.82
	E x F x W	<0.1	0.809	0.4	0.523	0.1	0.718	1.5	0.229
Sibbaldia procumbens	Exclosure	4.6	**0.049**	2.2	0.16	19.2	**<0.001**	1.3	0.272
	Fertilization	5.8	**0.03**	3.7	*0.075*	4.3	**0.043**	<0.1	0.838
	Warming	7.0	**0.019**	1.5	0.247	2.1	0.149	0.3	0.605
	E x F	<0.1	0.855	<0.1	0.81	<0.1	0.761	<0.1	0.775
	E x W	0.2	0.702	0.3	0.598	<0.1	0.980	<0.1	0.896
	F x W	0.4	0.563	5.6	**0.032**	23.1	**<0.001**	0.2	0.658
	E x F x W	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.

| Species	Factor								
Solidago virgaurea	Exclosure	73.3	**<0.001**	3.1	*0.088*	0.1	0.737	<0.1	0.876
	Fertilization	25.1	**<0.001**	0.6	0.461	3.9	**0.049**	0.4	0.524
	Warming	0.5	0.488	2.8	0.104	4.0	**0.048**	1.7	0.198
	E x F	5.4	**0.024**	0.2	0.649	<0.1	0.769	<0.1	0.964
	E x W	<0.1	0.897	1.0	0.322	3.6	*0.059*	0.2	0.638
	F x W	2.9	*0.093*	0.7	0.399	1.9	0.167	<0.1	0.789
	E x F x W	0.4	0.528	1.4	0.235	2.8	*0.097*	<0.1	0.825
Thalictrum alpinum	Exclosure	59.4	**<0.001**	6.0	**0.019**	30.0	**<0.001**	n.a.	n.a.
	Fertilization	8.9	**0.005**	4.7	**0.036**	7.6	**0.007**	n.a.	n.a.
	Warming	0.4	0.546	0.2	0.674	44.3	**<0.001**	n.a.	n.a.
	E x F	<0.1	0.890	5.4	**0.025**	6.2	**0.014**	n.a.	n.a.
	E x W	3.7	*0.061*	0.3	0.560	19.1	**<0.001**	n.a.	n.a.
	F x W	0.1	0.713	0.3	0.608	15.2	**<0.001**	n.a.	n.a.
	E x F x W	<0.1	0.863	<0.1	0.849	11.3	**<0.001**	n.a.	n.a.
Vaccinium vitis-idaea	Exclosure	28.9	**<0.001**	19.0	**<0.001**	58.0	**<0.001**	4.9	**0.033**
	Fertilization	0.3	0.578	<0.1	0.947	2.2	0.143	8.0	**0.007**
	Warming	21.3	**<0.001**	25.4	**<0.001**	114.4	**<0.001**	11.0	**0.002**
	E x F	0.2	0.748	2.6	0.114	3.3	*0.072*	0.2	0.648
	E x W	3.0	*0.092*	0.7	0.402	0.2	0.650	1.2	0.289
	F x W	2.5	0.118	0.2	0.647	0.1	0.745	0.38	0.539
	E x F x W	1.8	0.182	1.8	0.192	2.4	0.127	<0.1	0.824
Viola biflora	Exclosure	38.9	**<0.001**	24.1	**<0.001**	67.3	**<0.001**	0.1	0.738
	Fertilization	11.7	**0.001**	0.4	0.547	20.9	**<0.001**	0.7	0.42
	Warming	16.7	**<0.001**	3.9	*0.053*	2.3	0.129	6.0	**0.018**
	E x F	15.5	**<0.001**	2.2	0.149	0.9	0.344	0.8	0.377
	E x W	1.1	0.302	<0.1	0.779	<0.1	0.811	1.7	0.203
	F x W	0.3	0.564	0.6	0.44	0.2	0.679	2.9	*0.093*
	E x F x W	<0.1	0.812	<0.1	0.965	0.4	0.549	3.2	*0.082*
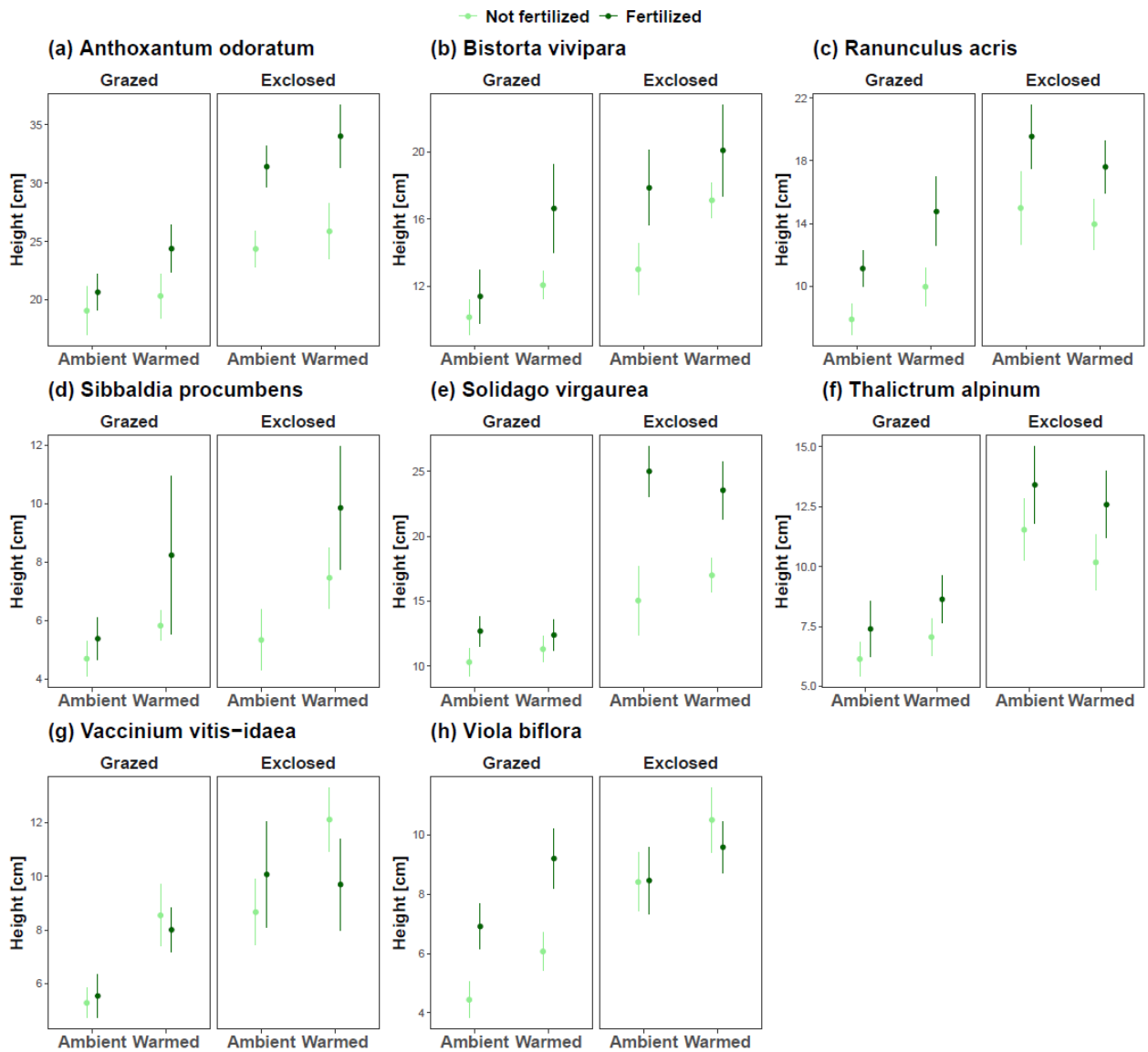
Figure S2. Vegetative height (mean ± SE) for eight tundra species ((a) – (h)) in all treatment combinations of exclosure, fertilization and warming (n = 56). Vegetative height was measured from three healthy and undamaged individuals per plot.
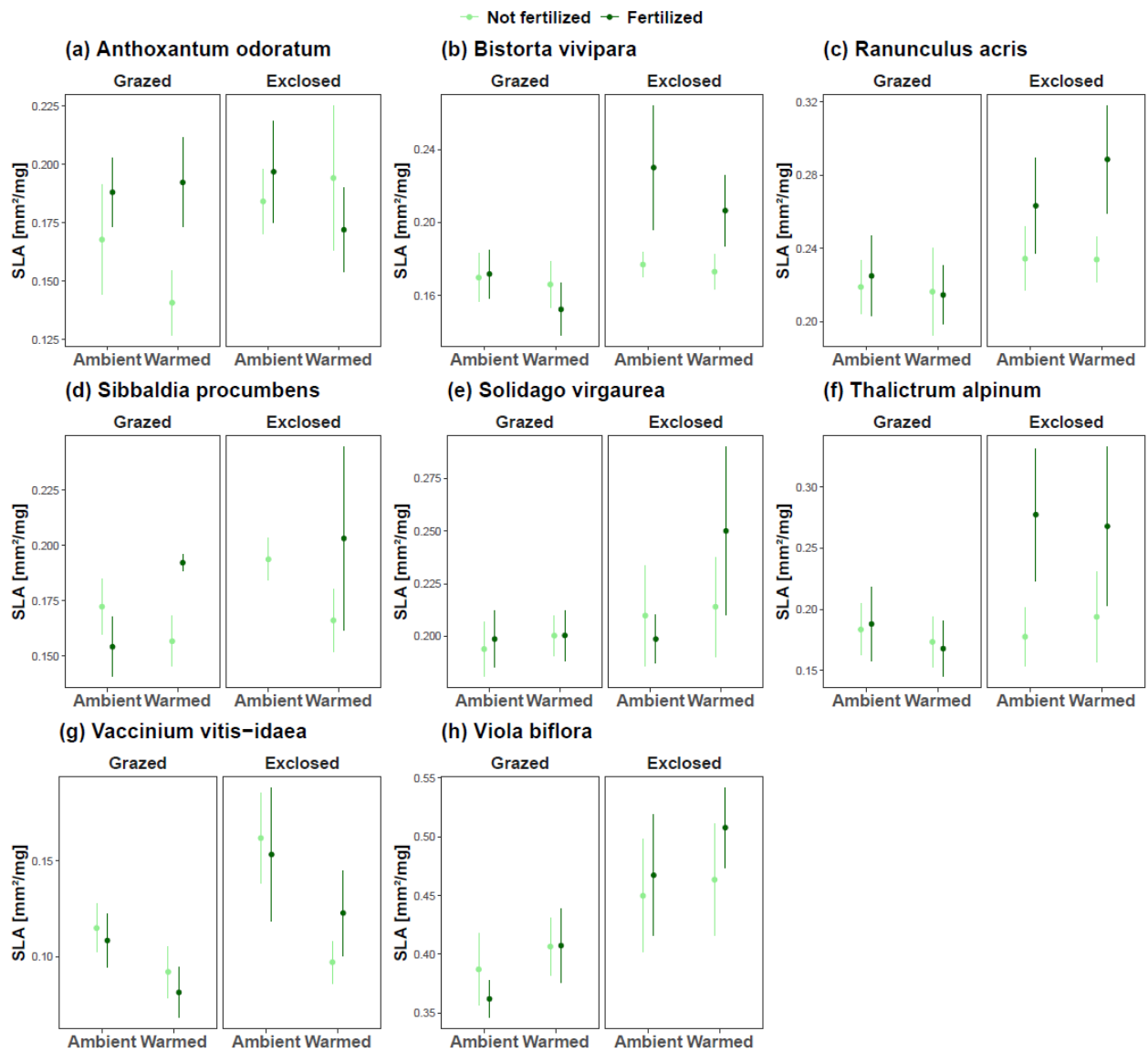
Figure S3. SLA (mean ± SE) for eight tundra species ((a) – (h)) in all treatment combinations of exclosure, fertilization and warming (n = 56). For SLA measurements, leaves of three healthy and undamaged individuals were sampled per plot.
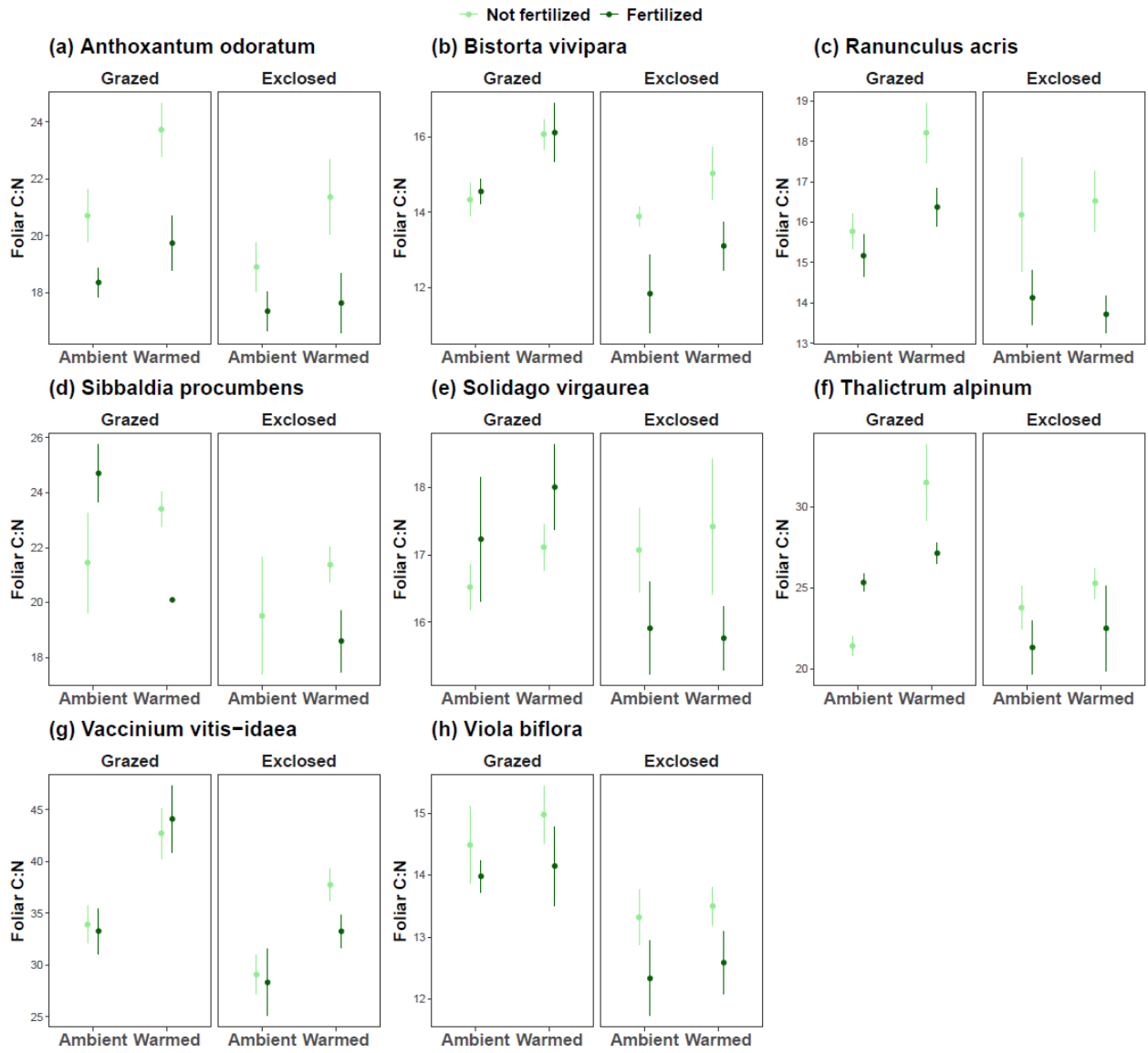
Figure S4. Foliar C:N (mean ± SE) for eight tundra species ((a) – (h)) in all treatment combinations of exclosure, fertilization and warming (n = 56). For foliar C:N, five to ten healthy and undamaged leaves were sampled per plot.
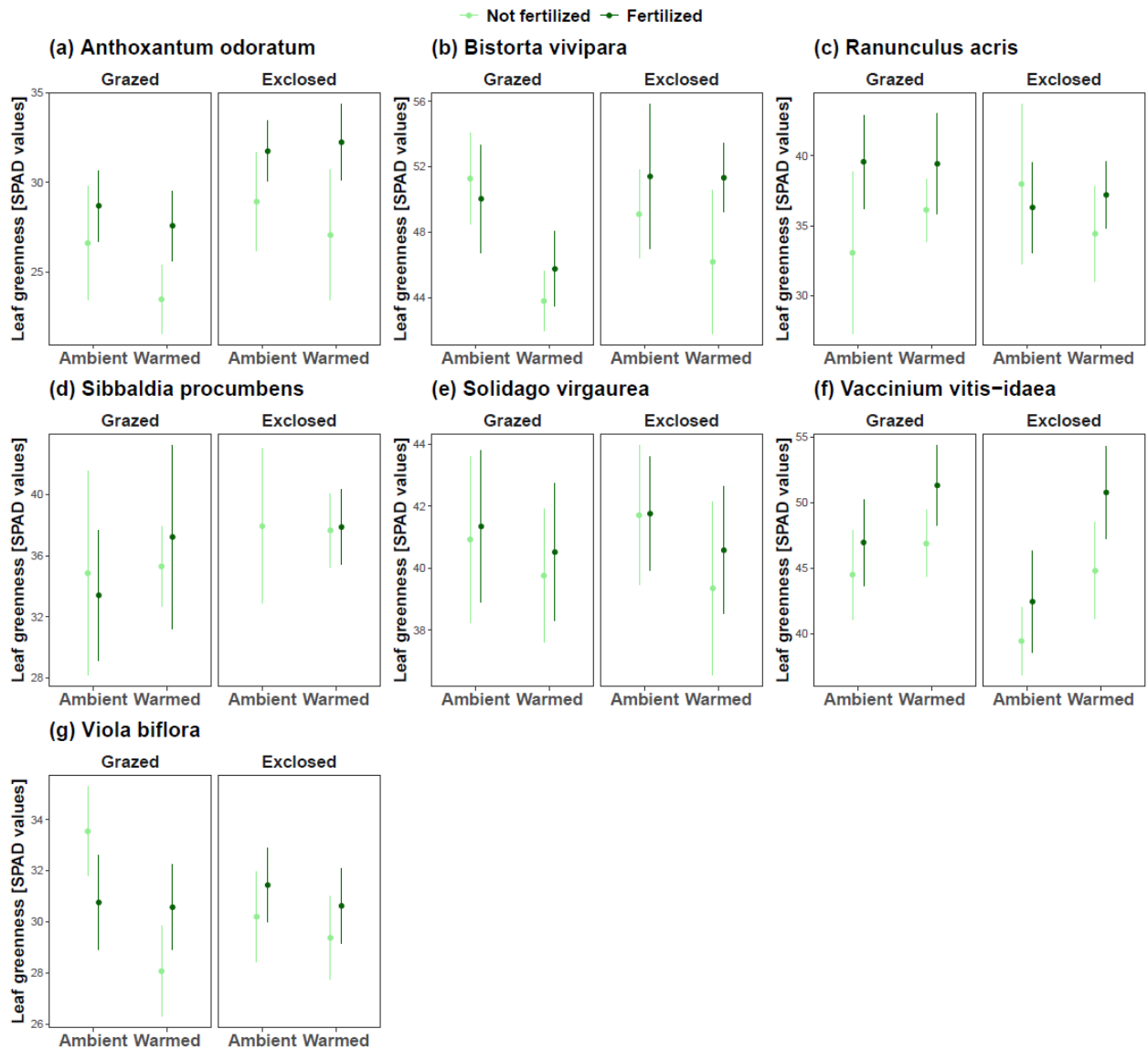
Figure S5. Leaf greenness (SPAD values) (mean ± SE) for seven tundra species ((a) – (g)) in all treatment combinations of exclosure, fertilization and warming (n = 56). SPAD values were measured from three healthy and undamaged individuals per plot with the exception of *T. alpinum*, which was too small to fit the chlorophyll meter cuvette.

CHAPTER III

Litter accumulation, but not light limitation drives early plant recruitment

Maria-Theresa Jessen[1,2,3,4], Harald Auge[1,2], W. Stanley Harpole[1,3,4], Anu Eskelinen[1,3,5]

[1]*German Centre for Integrative Biodiversity Research – iDiv Halle-Jena-Leipzig, Puschstraße 4, D-04103 Leipzig, Germany*

[2]*Department of Community Ecology, Helmholtz Centre for Environmental Research - UFZ, Theodor-Lieser- Straße 4, D-06120 Halle, Germany*

[3]*Department of Physiological Diversity, Helmholtz Centre for Environmental Research – UFZ, Permoserstr. 15, D-04318 Leipzig, Germany*

[4]*Martin Luther University Halle-Wittenberg, Am Kirchtor 1, 06108 Halle (Saale), Germany.*

[5]*Department of Ecology and Genetics, University of Oulu, FI-90014, Oulu, Finland*

Abstract:

1. Theory predicts a decline in grassland diversity under nutrient enrichment and exclusion of herbivory, and one possible cause is hampered seedling recruitment. Two potential drivers for reduced diversity at the seedling level can be diminished light availability and accumulation of dead biomass.

2. To test the importance of these two mechanisms on early recruitment, we added seeds of 15 herbaceous grassland plant species and monitored sown and natural seedling emergence during one growing season in a full factorial field experiment with light addition and litter removal under fertilization and exclusion of mammalian herbivores in an experimental grassland in Central Germany. We used modern LED lamps, mimicking the spectrum of natural sun light, to provide light to small-statured understory plants. This novel experimental set-up allowed us to specifically disentangle the roles of light limitation and litter accumulation independently and in combination.

3. In general, herbivore exclusion, but not fertilization increased the amount of litter biomass and decreased light intensity close to the ground. Litter removal increased seedling number and richness by 83% and 33%, respectively, while light addition had no significant main effect on seedling recruitment, nor did it interact with any other factors, and did not affect recruitment even when litter was removed. In addition, fertilization had a negative and herbivore exclusion a negligible impact on recruitment, and these effects were independent of litter removal. Furthermore, seedling number and richness were unrelated to light intensity and quality, litter depth, soil moisture, temperature and C:N.

4. Synthesis: These results provide novel insights into the role of light limitation vs. litter accumulation driving early recruitment and help understanding the mechanisms that affect diversity in grassland communities via recruitment. Our results highlight the detrimental role of litter accumulation as opposed to light deficiency driving early recruitment from seeds and call for management actions that reduce the amount of litter when maintaining or restoring diversity.

Keywords: diversity decline, nutrient enrichment, germination, LED lamps, litter removal, recruitment, seed addition, sheep grazing

Introduction

Anthropogenic and experimental nutrient enrichment can substantially reduce plant diversity (Stevens *et al.* 2004a; Clark & Tilman 2008; Bobbink *et al.* 2010; Borer *et al.* 2014b). Nutrient enrichment induced species loss can be explained by a shift in limiting resources from nutrients to light (Rajaniemi 2002; Hautier, Niklaus & Hector 2009; Dickson & Foster 2011) and diminished number of resource niches (Harpole & Tilman 2007), that lead to extinctions depending on species' initial abundance and traits (Suding *et al.* 2005). Besides causing extinctions, nutrient enrichment can affect species gains, and has been shown to be an important impediment for colonization by seed (Tilman 1993; Foster & Gross 1998; Stevens *et al.* 2004b; Lamb 2008; Fayolle, Violle & Navas 2009; Myers & Harms 2009).

One mechanism explaining diversity loss under nutrient enrichment is unequal light availability between adult plants and seedlings, i.e., diminished amount of light in dense vegetation, which can lead to reduced species gains by interfering colonization and recruitment dynamics (Goldberg & Miller 1990; Tilman 1993; Renne, Tracy & Colonna 2006; Hautier, Niklaus & Hector 2009). Light can be an important cue for breaking seed dormancy (Smith 1982; Seo *et al.* 2009) and for seedling development such as de-etiolation and cotyledon unfolding (Chen, Chory & Fankhauser 2004). Seedlings that emerge and develop early, i.e., before vegetation becomes dense, have better access to light and thus a competitive advantage over those that emerge later (Miller 1987). On the other hand, light can also be a stress factor for seedlings if, for example, irradiation is too high (Demmig-Adams & Adams 2006).

Colonization and plant recruitment could also be negatively affected by a physical barrier of dead biomass that can prevent seeds from reaching the soil surface and germinating (Facelli & Pickett 1991; Ruprecht, Szabó & Collins 2012). Dead biomass can also impair germination and seedling establishment via reduction in light availability (Foster & Gross 1998; Zhang, Wang & Wan 2019) or leachates that inhibit seedling growth (Bonanomi *et al.* 2011). Such negative effects of litter accumulation on species colonization and recruitment should be especially strong in nutrient-enriched conditions where more litter should accumulate due to greater productivity (Foster & Gross 1998; Stevens *et al.* 2004b; Loydi *et al.* 2013). To date, many studies have manipulated litter and/or biomass to test their roles for plant recruitment and colonization under nutrient enrichment but no attempts have been made to separate the effects of litter accumulation and light availability.

Mammalian herbivory can relax light limitation via consumption of plant biomass (Olff & Ritchie 1998; Borer *et al.* 2014b), often selectively consuming nutrient-rich and tall-statured species (Diaz *et al.* 2007; Evju *et al.* 2009). Herbivores can thus maintain diversity by preventing species extinctions and these positive effects on diversity can be especially pronounced in nutrient-enriched conditions (Bakker *et al.* 2006; Kaarlejärvi, Eskelinen & Olofsson 2017). Herbivores can also facilitate colonization and recruitment from seed via reducing the amount of litter by trampling, and increasing litter decomposition rates (Olofsson & Oksanen 2002; Wang *et al.* 2018), which can create favorable recruitment gaps for seedlings (Vandvik & Goldberg 2006). In the absence of herbivores, especially in nutrient-enriched conditions, both increased light limitation and increased amount of litter could therefore hamper species recruitment, and lead to reduced diversity.

We added seeds of 15 grassland species and investigated the roles of light limitation and litter accumulation, independently and in combination, on seed germination and early seedling establishment under nutrient enrichment and mammalian herbivory. Our experiment was carried out in an experimental grassland in Central Germany that was grazed by sheep. To reduce light limitation, we provided light to the small-statured understory plants using modern LED-lamps that mimicked the spectrum of natural sun light (Fig. 1). To manipulate litter, we removed undecomposed dead plant material from previous years, in a full-factorial combination with light addition. These two treatments were further performed in a full-factorial combination of fertilization and exclusion of sheep. We specifically asked (1) what are the roles of light availability and litter for recruitment of grassland plants from seed? (2) Does the relative importance of light availability and litter for recruitment change under nutrient enrichment, herbivory and their interaction? We predicted that both 1) litter removal and 2) light addition would increase recruitment, and that 3) litter removal and light addition would enhance recruitment more under fertilized and fenced conditions compared to unfertilized and grazed conditions. Furthermore, we examined treatment effects on light quantity (measured as light intensity close to the ground and under the litter) and quality (red to far red ratio (R:FR)), soil moisture, temperature and C:N and litter depth, and analyzed how these were associated with recruitment.

Material and Methods

Study site

The experiment was located in Germany, at Bad Lauchstädt Field Research Station (51°22060 N, 11°50060 E). The long-term mean annual precipitation in this area is 489 mm and the mean annual temperature is 8.9 °C (Schädler *et al.* 2019). The soils are fertile Haplic Chernozems (Altermann *et al.* 2005; Schädler *et al.* 2019). The experiment was conducted within the Global Change Experimental Facility (GCEF) which combines land use type and climate change research (Schädler *et al.* 2019). We used the five extensively used pastures under ambient climatic conditions of the GCEF in our experiment. These five pastures are exposed to sheep grazing by a herd of about 20 individuals of German black-headed mutton sheep two to three times year, depending on how much vegetation biomass is present. Each pasture (16 × 24 m) is grazed for a short period of high intensity for 24 hours at a time (Schädler *et al.* 2019). Both 2018 and 2019 were significant drought years in Central Europe (Hari *et al.* 2020) that were

characterized by severe water deficit during the summers and a strong decline in green vegetation in Central European pastures (Buras, Rammig & Zang 2020); during these years the pastures were grazed twice. The vegetation in the extensively used pastures resembles species-rich grassland vegetation in dryer regions of Central Germany (Schädler *et al.* 2019). The entire experimental area is fenced to keep out naturally occurring deer, while smaller herbivores like European hare (*Lepus europaeus*) can pass the fences.

Basic experimental design

In 2017, we established a full factorial experiment of fertilization and herbivore exclusion; 4 plots sized 1.4 × 1.4 m, separated by a 1-m buffer zone, were established in each of the five pastures resulting in a total of 20 plots. The four plots within each pasture were randomly assigned to one of the treatment combinations (grazed, fertilized + grazed, exclosed, fertilized + exclosed). The five pastures were thus considered as the block factor.

To fertilize, we applied slow-release granular NPK fertilizer mixture (Haifa Multicote 2 M 40-0-0 (40% N, Super Triple Phosphate TPS (45% P203), potassium sulfate fertilizer (50% K2O, 45% SO3) to fertilizer addition plots twice per growing season (later March -May and June), resulting in a yearly addition of 10 g N, 10 g P and 10 g K per m² (see the protocol of Borer *et al.* 2014a for grasslands around the globe). The fertilization treatment was started at the end of May 2017 when we applied the first fertilizer round. However, the herbivore exclusion treatment was started at the end of August 2017, i.e., three months later.

To implement the herbivore exclusion treatment, we fenced plots receiving exclosure treatment with 1.8 m x 1.8 m, 82 cm high, 10 cm mesh rectangular portable metal fences. The fences did not exclude mice and voles (mainly *Apodemus sylvaticus* and *Microtus arvalis*) which frequently occur in the plots (Jessen & Eskelinen, personal observation). In 2019, one plot originally intended for herbivore exclusion only was accidentally fertilized and one plot originally intended for herbivore exclusion and fertilization treatment was not fertilized. We therefore treated both as fertilized in data analyses. However, excluding these plots from the analyses did not change the results qualitatively.

For the light addition treatment, the 1.4 × 1.4 m plots were further divided into two smaller subplots, 0.7 m × 1.4 m each, one of which was randomly assigned to light addition, resulting in a total of 40 subplots according to a split-plot design. To add light, we installed two 120 cm long and 3.5 cm wide, high-intensity LED lamps (C65, Valoya, Finland) designed for growing plants in growth chambers, vertical farming applications, etc. (https://www.valoya.com/c-series-led-grow-lights/). The light addition treatment started at the same time as the fertilization treatment, i.e., at the end of May 2017. Our light addition treatment mimicked adding natural sunlight to a gap in vegetation in a real grassland; the spectrum was therefore designed to include all wave lengths of sunlight, including small amounts of UV and IF. The lamps did not alter the soil surface temperature (Fig. S1).

The lamps were installed horizontally to the ground and parallel to each other at a distance of 28 cm in an area of 0.7 × 1.4 m. Each year we placed the lamps on the subplots in early spring when temperatures were above zero and there was low risk of frost damage (February-April)

and took them down in the fall (October-November) when temperatures dropped close to zero, thus adding light during the active growing season. In 2019, we switched on the lamps on April 4, and not earlier, because temperatures still dropped below zero. By the time of our seedling survey, the lamps had been on for 46 days. The lamps in grazed subplots were removed for the period of grazing due to security reasons and switched off in the ungrazed subplots for the same time period to make sure all lighted subplots received similar light conditions. We intended to provide light for small-statured understory plants and seedlings that were likeliest to suffer from competition for light. Therefore, the lamps were installed 10 cm above the smallest plants on top of litter that lay on the ground, except for in litter removal plots where lamps provided light to the bare ground. Our treatment increased light intensity in the vegetation understory, i.e. removed shading by the surrounding vegetation. However, our design was not intended to study the mechanisms by which litter affects seedlings and therefore we did not provide light under litter (Fig.S2). When the plants grew during the course of the summer, the lamps were gradually raised to maintain 10 cm distance to the smallest plants. All lamps were set to the same height in all experimental plots to ensure equal conditions. We set the lamps to switch on two hours after sunrise and switch off two hours before sunset, and they automatically switched off when the air temperature exceeded 28°C to prevent overheating.

Litter removal experiment

In January 2019, we established two 20×20 cm litter removal units, separated by 10 cm, within each of the 40 subplots, resulting in 80 litter removal units and representing the sub-subplot level according to a split-split-plot design. One of these units was randomly assigned to litter removal, and the other was left intact. The purpose of our litter removal treatment was to target dead biomass that had accumulated during the previous years. We implemented the treatment in January when most of the biomass was from previous years and dead, either lying on the ground as litter or standing dead and about to soon fall down. However, there was little green biomass mixed with the live biomass, mostly short grass leaves which were not possible to disentangle from the dead biomass, and were therefore removed with the dead biomass. On average we removed about 400 g m^2 in control plots, 550 g m^2 in fertilized plots, 700 g m^2 in exclosed plots and 775 g m^2 in exclosed and fertilized plots (Fig. 1). These are medium to high litter amounts (Loydi *et al.* 2013). As no live biomass was removed when the growing season and growth of most biomass started, our treatment can functionally be called "litter removal".
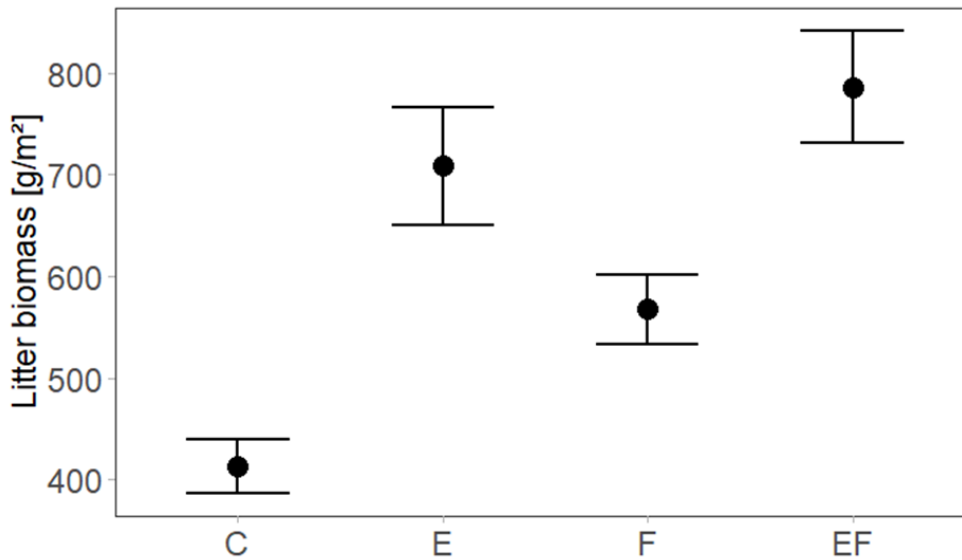
Figure 1. *Litter biomass weight (mean ± SE) in control (C), herbivory exclosure (E), fertilized (F) and herbivory exclosure and fertilization (EF) plots. The dead biomass was cut for establishing the litter removal treatment from 20 x 20 cm units in January 2019, oven dried and weighed. The values on the y-axis are scaled up to 1 m^2 starting from the size of the litter sampling units. Herbivory exclusion increased litter biomass ($F_{1,12}$ = 22.91, P < 0.001) and there is a trend that this effect was pronounced by fertilization (E x F interaction, $F_{1,12}$ = 3.22, P = 0.098).*

Seed addition

To study seedling recruitment response to the treatments, we selected 15 common Central-European grassland species (Table S1), abundant in the experimental plots, and added 50 seeds per species to all 80 litter removal units. Based on pre-seed addition seedling survey, seedling number was low under grazed conditions, possibly because grazers also affected flower and seed production (data not shown). Therefore, by adding a fixed amount of seeds independent of the species we ensured that there was a sufficient amount of seeds in each unit, all species had the same opportunity to respond to the treatments, and seed availability would not prevent examining treatment effects on recruitment for any species (for a similar approach see Zobel *et al.* 2000; Aicher, Larios & Suding 2011; Eskelinen *et al.* 2016). Species were chosen to encompass a broad range of size (e.g. seed size and adult plant stature) as indicators of germination success and relative competitive ability (Keddy *et al.* 2002). The seeds originated from a local wild collection from 2018 (Saale-Saaten Stolle, Germany) but represented the same accessions used for the initial establishment of the GCEF in 2014. Before sowing the seeds in the field, we tested their germination rate, ensuring the viability of the seed material (Table S1), and to make sure we were able to identify all species even from their first true leaves. Seeds of all 15 species were mixed together and manually sprinkled over the units. We used a cardboard frame to prevent seeds from spreading outside the experimental units. Vegetation was gently shaken to ensure that seeds settled to the ground. Sowing was done in January to make sure that all seeds experienced natural cold stratification.

Seedling survey

In spring 2019 the units were monitored frequently beginning in February to capture all emerging seedlings. However, due to the exceptionally cold late winter and early spring of 2019, with often freezing temperatures and ground frost in February and March, no seedlings were detected before April, and the first identifiable seedlings appeared in late April. Seedlings were counted and marked at the end of April and May. We identified all fully germinated seedlings (cotyledons and at least one true leaf out) into species and recorded their number. We counted seeded and naturally occurring species. Since we did not mark the seeds, it was not possible to distinguish naturally occurring seedlings from sown seedlings. Plants were counted as seedlings as long as their cotyledons were present. In this study we report data from the second sampling occasion (May 21 - 23), since this represents the peak number of seedlings. We also checked the plots in June and July for seeds germinating later; however, most seedlings had matured (i.e., no longer had cotyledons) and could no longer be counted as seedlings. Furthermore, as both 2018 and 2019 were extreme drought years with high temperatures and very little rain in June and July i.e. about 50% reduction of precipitation compared long-term observations from 1961 -1990 (Ionita *et al.* 2020), conditions were not favorable for any further germination. Although the drought may have changed the composition of naturally occurring seedlings through shifts in abundance in adult plant communities, it should not have affected the treatment effects observed on early recruitment in spring 2019.

Abiotic measurements

We recorded litter depth (cm) at the center of each unit from which litter was not removed (n=40). We measured volumetric water content (VWC) and soil temperature at the center of each unit (n= 80) at a depth of 3.81 cm with a soil moisture probe (TDR 100, Spectrum Technologies, USA). The measurements were taken at the end of May all on the same day one week after the latest rain event (7.5 mm). We collected two composite soil samples from each unit that were later pooled, dried in room temperature, and analyzed for C:N (VarioEL CNHS analyzer, Elemental Analyse Systeme GmbH, Hanau, Germany). We measured light intensity at each unit using a light meter (LI-250A, LI-190R, LI-COR, USA). Light measurements were taken on a cloudless day around noon at ground-level. The measurements were taken under live vegetation and litter layer when present, to quantify light conditions at the bottom layer at the time of seedling sampling. Light quality was measured at the same time with a handheld spectrometer (GL Spectis 1.0 touch, GL Optic, Poland). We focused on red to far red ratio (R:FR), an important indicator of vegetation density and composition (Skalova *et al.* 1999). The live and dead biomass collected at the time of implementing the litter removal treatment was oven-dried at 60°C for 48 hours and weighed.

Statistical analysis

We used linear mixed effects models to assess the interactive effects of herbivore exclusion, fertilization, light addition and litter removal (all fixed factors) on seedling number and richness. To account for the split-split-plot experimental design, i.e., that litter removal units were sub-subplots nested within subplots that in turn were nested within plots that were organized in blocks, our random effects included subplot nested within plot and plots nested

within block. We limited the amount of interactions to three-way interactions, since four-way interactions were not significant and did not change the results otherwise. Significance of the factors was tested with F-tests. We used model diagnostic plots to check the homogeneity of variances and the normality of errors (Crawley 2007) and both seedling number and richness were square-root transformed to meet the assumptions. We also tried running the same models as GLMMs with a Poisson error structure, but these models failed to converge. To additionally test for variation in effect sizes between light addition and litter removal we calculated their effect sizes on total seedling number and richness as log ratios of the treatment responses divided by the control. Data were pooled across exclosure and fertilization treatments for these analyses. We used linear mixed effect models to assess statistical differences of the effect sizes between the treatments. All models had the same random structure.

We used similar linear mixed effects models with the same random structure than above to test the effects of the treatments on individual seedling species that were common enough in the plots, i.e. had three or more observations in each treatment combinations. Of the 36 species observed we ran full models for six species. For the remaining 30 species, it was not possible to run models.

We assessed the relationship between (total and sown) seedling number and richness and the environmental variables (soil moisture, temperature and C:N and light intensity and quality) and litter depth using multiple linear mixed effects models with similar random structure as above. We standardized all explanatory variables to facilitate comparison of values with different units and orders of magnitude. Collinearity of the single factors in the models was tested using the variance inflation factor (VIF) and factor re-ordering. Since litter depth was measured only in units where litter was present (i.e. in half of the units compared to measurements taken for the other factors), the relationship between seedling number and richness (total and sown) and litter depth was tested in separate models. In these models, plot was nested within block, which accounts for the nested sampling design.

To investigate the interactive effects of herbivore exclusion, nutrient enrichment, light addition and litter removal on the community composition of seedlings we applied PERMANOVA (permutational multivariate analysis of variances) (Anderson 2001)with block as random structure, Bray-Curtis dissimilarity, and 999 permutations for both total seedling and sown seedling community separately. We used NMDS (non-metric multidimensional scaling) to illustrate significant community responses to the treatments.

We used the 'lme4' package (Bates *et al.* 2015) to run linear mixed effect models, the 'car' package for assessing the significance of the treatments effects (Fox & Weisberg 2019), the 'vegan' package for running PERMANOVA and NMDS (Oksanen *et al.* 2020), the 'tidyverse' package for data manipulation (Wickham *et al.* 2019) and the 'ggplot2' package for plotting (Wickham 2016) in R statistical software (R Core Team 2020 version 4.0.2).

Results

Effects of litter removal and light addition on seedling number and richness

13 out of 15 originally sown species were found in at least some of the experimental units. Only *Heracleum sphondyleum* and *Linaria vulgaris* did not germinate at all. The maximum number of seedlings (sown species only) in one unit was 65 and the maximum number of all seedlings (including unseeded species) in one unit was 85. The maximum seedling richness (sown species only) in one unit was 9 and the maximum seedling richness of all species (including unseeded species) in one unit was 16. In total we found 36 different seedling species in the entire experimental set-up.

Litter removal significantly increased both total and sown seedling number and richness (Figs. 2a and b, Table S2, Figs. S3a and b): total seedling number was on average 83% higher and total seedling richness 33% higher in litter removal units compared to intact units. Sown seedling number was on average 112 % higher and sown seedling richness 33 % higher in litter removal units compared to intact units.

Light addition had no significant main or interactive effects on either (total and sown) seedling number or seedling richness (Figs. 2a and b, Table S2, Figs. S3a and b), but fertilization significantly decreased total seedling number and richness (Fig. 2a and b, Table S2).

Comparing the effect sizes of litter removal and light addition, litter accumulation had a strong negative effect on both total and sown seedling number and richness regardless of light addition or unlighted conditions, whereas light addition had no effect independently or in combination with litter removal (Figs. S3a-d).
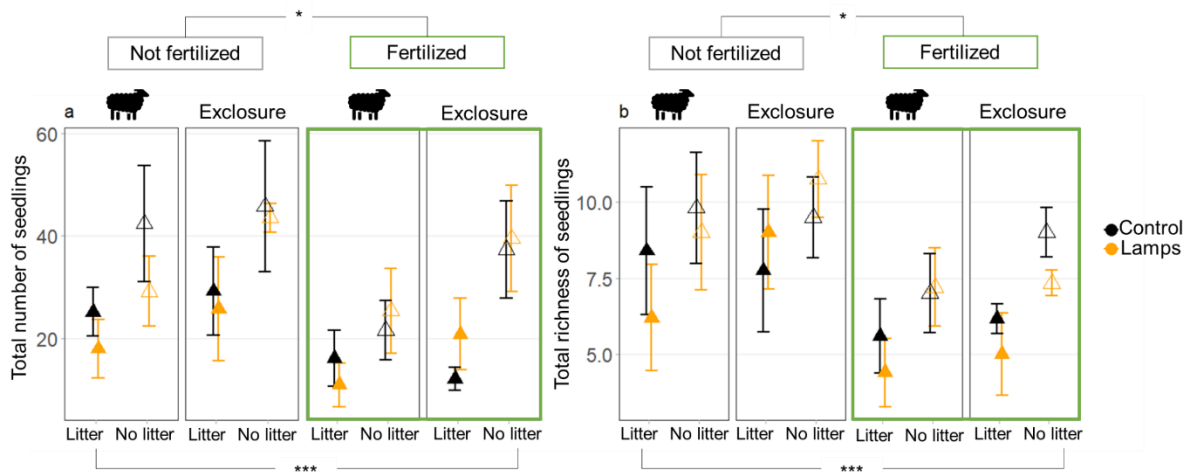

Figure 2. *(a) Total number of seedlings (mean ± SE) and (b) total seedling richness (mean ± SE) under light addition, litter removal, herbivore exclusion and fertilization sampled in May 2019. The asterisks indicate statistical significance (P < 0.05, main effect of litter removal, main effect of fertilization).*

Environmental changes in relation to seedling number and richness

Total and sown seedling number and richness were not significantly related to light intensity or light spectrum (Figs. 3d and e, Figs. 4d and e, Table S3), even though the range of measured light intensity values was high (11.54 to 1202.50 µmol/m²/s, Figs. 3d and 4d). In addition, neither total and sown seedling number nor richness were significantly correlated with soil moisture, soil temperature or soil C:N (Figs. 3b,c and f, 4b,c and f, Table S3). Sown seedling number decreased with increasing litter depth, but this effect was only marginally significant (Table S3). Total seedling number and total and sown seedling richness showed no significant relation to litter depth (Figs. 3a and 4a, Table S3).
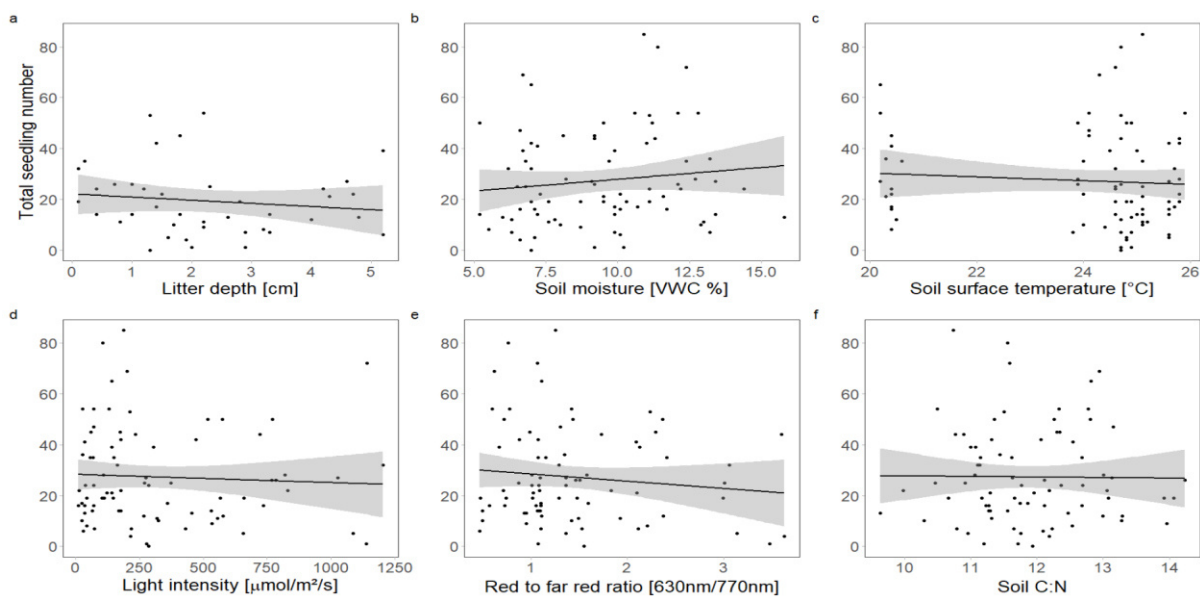
Figure 3. *Relationships between total seedling number and (a) litter depth, (b) soil moisture, (c) soil surface temperature, (d) light intensity at the ground (under litter and live vegetation when present), (e) red to far red ratio and (f) soil C:N. All measurements were taken at the seedling survey units. Note that litter depth was only recorded in half of the experimental units (those without litter removal treatment). Figures for sown seedlings (data not shown) are qualitatively the same.*
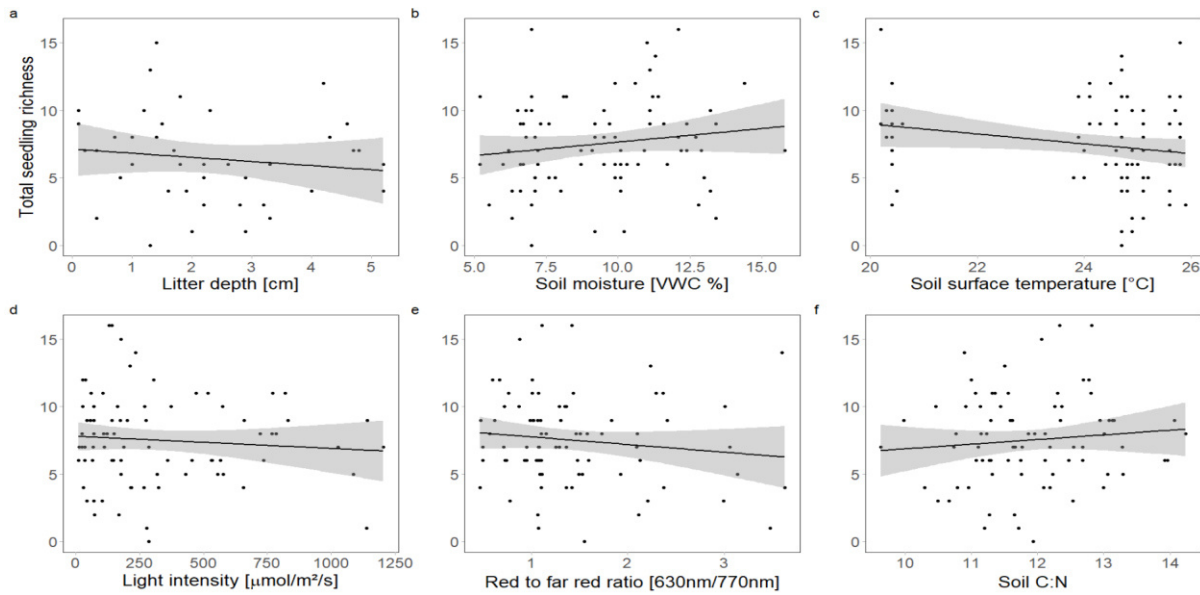
Figure 4. Relationships between total seedling richness and (a) litter depth, (b) soil moisture, (c) soil surface temperature, (d) light intensity at the ground (under litter and live vegetation when present), (e) red to far red ratio and (f) soil C:N. All measurements were taken at the seedling survey units. Note that litter depth was only recorded in half of the experimental units (those without litter removal treatment). Figures for sown seedlings (data not shown) are qualitatively the same.

Effects of litter removal and light addition on individual seedling species

Consistent with total seedling number, three of the tested species that responded to the treatments, were positively affected by litter removal: there was a significant positive main effect on *Achillea millefolium*, *Daucus carota* and *Plantago media* (Fig. S5a). In addition, herbivore exclusion had a positive impact on *Galium album* (Fig. S5b). *Pimpinella saxifraga* and *Silene latifolia* were tested but did not respond to any of the treatments.

Effects of the treatments on the seedling community

The total seedling species community composition was altered by litter removal and herbivore exclusion (PERMANOVA results; Table S4, Fig. S6a and b). The sown seedling species community was altered by an interaction and main effects of herbivore exclusion and litter removal (PERMANOVA results; Table S4, Fig. S6c). Light addition and fertilization had no effect on total and sown seedling community composition.

Discussion

We found that recruitment success (seedling number and richness) was strongly controlled by the presence of litter, while light addition exhibited no significant impact on early seedling recruitment neither independently nor in combination with litter removal. Furthermore, a large range of measured light intensity values did not correlate with recruitment success, reinforcing our experimental result of the importance of litter. These findings were independent of nutrient enrichment and herbivory. Our results therefore suggest that light limitation in the phase of

early recruitment is not the main driver of diversity loss in a wide variety of conditions, and not even under nutrient enrichment and exclusion of herbivores. Rather, a combination of factors associated with build-up of dense litter layer determines how many species and seedlings germinate. Conditions which promote accumulation of dead biomass can therefore be important filters preventing recruitment from the local species pool.

Our first prediction that litter removal would increase seedling recruitment was supported because the presence of litter greatly decreased seedling number and richness. It also increased the seedling number of most of the individual species that we tested. This is in line with earlier litter removal experiments which have shown an increase in seedling number or density in response to litter removal (Jensen & Meyer 2001; Wilsey & Polley 2003; Johnson *et al.* 2018). Litter addition studies also confirm these results (Foster & Gross 1998; Xiong *et al.* 2003; Zhang, Wang & Wan 2019). Together these findings highlight the important role of undecomposed litter, i.e. the legacy of previous years' vegetation, in suppressing recruitment from seed. Accumulated dead biomass can hamper seedling establishment by creating a mechanical barrier that prevents seeds from reaching soil surface (Facelli & Pickett 1991; Donath & Eckstein 2010; Ruprecht, Szabó & Collins 2012) and, on the other hand, can suppress seedlings that have already germinated. Litter can also inhibit germination through leachates (Ruprecht *et al.* 2008) or block incoming light and precipitation (Facelli & Pickett 1991). In addition, rodents may be more active under the protective cover of litter, since dead plant material can provide shelter and cover, increasing seed and seedling predation (Hulme 1996; Edwards & Crawley 1999; Fraser & Madson 2008; Smith *et al.* 2021). In our study, recruitment success was not associated with light intensity and quality, or soil moisture and soil surface temperature or soil C:N, suggesting that litter likely acted as a mechanical barrier, rather than affected seedling recruitment via any environmental variables. In addition, litter-driven recruitment patterns are likely to be controlled not only by one but by a combination of factors (Lamb 2008) which jointly affect recruitment, and subsequently influence community diversity.

Our second prediction that light addition would increase seedling recruitment was not supported as light addition did not significantly increase seedling number and richness. Moreover, light addition had no significant effect even when litter was removed, indicating that shading by surrounding vegetation is not an important factor affecting seed germination and early establishment. These experimental results were confirmed by our observational results that even though our light measurements spanned a great magnitude of light intensity values (11.54 to 1202.50 µmol/m^2/s), light intensity was not associated with seedling number and richness, supporting our conclusion that light does not have a significant impact on early recruitment success. In earlier studies manipulating light environment for seedlings indirectly (e.g. via cutting biomass, removing litter), positive treatment effects have been interpreted to at least partly reflect greater light limitation and competition for light with adults plants (Foster & Gross 1998; but see Jutila & Grace 2002; Xiong *et al.* 2003; Eskelinen & Virtanen 2005; Loydi *et al.* 2015). Our results of light addition, independently and in combination with litter removal, suggest that this is not the case and that litter rather than light availability determines early recruitment success.

Our study was not designed to examine the mechanisms by which litter affects early germination and we therefore cannot say for sure why litter hampered germination. It would be difficult to experimentally disentangle the variable effects of litter on seedling emergence. For example, adding light under litter without simultaneously increasing space, i.e., affecting the physical barrier that litter forms, would be challenging. However, even though light reduction could still be one mechanism through which litter inhibits germination, our result that light addition, even in the absence of litter, did not affect total recruitment suggests that light availability is not the main mechanism by which litter affects germination.

It is also possible that the mechanisms maintaining grassland plant coexistence may differ between early seedlings and later plant life stages. In mature plant communities light limitation has been associated with reduced diversity via species loss (Borer *et al.* 2014b; DeMalach, Zaady & Kadmon 2017b), though direct evidence of this mechanism in the field is still missing (Harpole *et al.* 2017). In experimental greenhouse communities, light addition did offset a decline in adult plant diversity under fertilization (Hautier, Niklaus & Hector 2009). While adult plants compete for light to maintain a positive carbon balance (Mooney 1972), early seedlings can tolerate low light levels; they do not compete with adult plants for light because they are morphologically inferior and have a less light demanding physiology (Kitajima & Myers 2008). Rather, newly emerging seedlings have evolved to develop under light-limited conditions by, for example, adapting the photosynthetic capacity of their cotyledons and first true leaves accordingly (Lawrence *et al.* 2020). Young seedlings can also live on seed resources for a while and therefore are not fully dependent on light for resource acquisition until photosynthesis is fully initiated (Fenner 1987; Kennedy *et al.* 2004; Kitajima & Myers 2008). Consequently, light availability might not be as critical in early seedling establishment as previously thought but likely increases in importance with plant maturation. This is supported by results from the same study system showing a positive response of diversity in adult plant communities to light addition (Eskelinen et al., submitted). The impacts of light limitation might therefore act through extinctions in later life stages; however, more research is needed to disentangle the effects of light in different life stages.

We expected stronger litter- or light-driven microsite limitation for seedlings under fertilization and exclusion of herbivores. In contrast to this prediction, litter removal and light addition did not have a stronger positive effect on seedling recruitment under fertilized and fenced conditions, even though especially herbivore exclusion increased the amount of dead biomass (Fig. 1). As litter removal and herbivory both affect recruitment via removal of biomass our statistical approach may not have been able to tease apart these two factors. Still, the strong effect of herbivore exclusion on litter biomass accumulation (Fig. 1) indicates that herbivore exclusion is an important factor for the litter build-up and thus indirectly does influence seedling recruitment. The fertilization treatment alone did not significantly increase litter biomass (Fig. 1) which may explain why suppression of seedling recruitment by litter was also not magnified by nutrient enrichment.

We found that fertilization alone, independent of litter removal and light addition, decreased seedling number and richness, which indicates that fertilization did not reduce recruitment via litter accumulation or light limitation as suggested in previous studies (Stevens *et al.* 2004b;

Myers & Harms 2009; Bergholz *et al.* 2015). Our result is therefore rather linked to physiological responses of seedlings to higher ammonium levels in fertilized plots (Fig. S7b), which can create a toxic environment for seedlings, or slightly reduced pH in fertilized plots (Fig. S7a) (Bardgett *et al.* 1999; Britto & Kronzucker 2002). Overall, our finding shows that potential direct effects of fertilization can be an additional obstacle to diversity via recruitment, but the effect is marginal compared to the effect of litter accumulation.

Seedling community responses to the treatments mostly followed the patterns of seedling number and richness, with litter removal being the most influential factor. In addition, herbivore exclusion altered seedling community composition, possibly via its effects on adult plant community composition and litter (Fig. 2), or via trampling. Also, even though herbivore exclusion did not directly affect seedling number and richness, it increased litter by 53 %, suggesting that it was an important factor contributing to the litter effects. One species, *G. album*, also directly suffered from grazing, emphasizing that individual species responses also vary.

To conclude, our results provide novel insights into the mechanisms that drive coexistence and diversity in the recruitment phase. We show that litter controls species richness and abundance on the seedling level via reduced species recruitment, while light availability did not matter for total community recruitment, neither independently nor in combination with litter removal. This contrasts with findings for adult plant communities where light addition has been shown to offset diversity decline in the greenhouse (Hautier, Niklaus & Hector 2009). However, to our knowledge this is the first study to directly manipulate light in the field to test its role on recruitment and thus separating the roles of litter accumulation and light availability in the early recruitment phase. These results contribute to the knowledge needed for planning restoration efforts by emphasizing the detrimental effect of litter accumulation for recruitment from seed. This is in particular important for restoration measures using seed addition to maintain diversity in natural and semi-natural grasslands that undergo different management practices (Johnson *et al.* 2018; Hernández *et al.* 2021; Török *et al.* 2021).

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SUPPORTING INFORMATION CHAPTER III

Table S1. Seeded species used in this experiment, their functional group and germination percentage in the laboratory. The germination percentage in the laboratory was determined by placing 100 seeds of each species in a Petri dish with regular irrigation regime, and counting all germinating seeds. *Linaria vulgaris*, *Pimpinella saxifraga* and *Ranunculus acris* were cold stratified in a refrigerator at 4°C for two weeks before germinating their seeds. The seeds for *Heracleum sphondyleum* were not available at the time of the test period. We grew the seeds in the lab prior to seeding in the field to ensure that the seed material was viable and to be able to identify germinating species in the field.

Species	Functional group	Max. germination % in lab
Achillea millefolium L.	Forb	80
Agrimonia eupatoria L.	Forb	2
Cynosurus cristatus L.	Grass	42
Dactylis glomerata L.	Grass	61
Daucus carota L.	Forb	23
Heracleum sphondyleum L.	Forb	-
Hypochaeris radicata L.	Forb	47
Knautia arvensis (L.) Coult.	Forb	33
Linaria vulgaris Mill.	Forb	0
Pimpinella saxifraga L.	Forb	6
Plantago lanceolata L.	Forb	39
Plantago media L.	Forb	90
Ranunculus acris L.	Forb	2
Silene latifolia Poir.	Forb	86
Tragopogon pratensis L.	Forb	14

Table S2. Results of the linear mixed effects models and subplot nested within plot nested within block as random factor, testing the effects of biomass removal, light addition, herbivore exclosure, fertilization and their interactions on total species number and richness across all recorded species (sown and naturally occurring seedlings) and on sown seedlings only. Significant results (P < 0.05) are in bold and marginally significant results (P < 0.1) are in italics. * Data are square-root transformed.

Source of variation	Total seedling number*			Sown seedling number *			Total species richness*			Sown species richness *		
	d.f.	F	p	d.f	F	p	d.f.	F	p	d.f.	F	p
Litter removal (LR)	1,33	21.52	**<0.001**	1,33	23.63	**<0.001**	1,33	15.74	**<0.001**	1,33	12.44	**0.001**
Light (L)	1,16	0.4	0.537	1,16	<0.1	0.879	1,16	1.66	0.216	1,16	0.22	0.648
Exclosure (E)	1,12	3.64	*0.081*	1,12	<0.1	0.911	1,12	1.53	0.240	1,12	<0.1	0.781
Fertilization (F)	1,12	4.98	**0.044**	1,12	1.21	0.292	1,12	5.32	**0.039**	1,12	0.82	0.384
LR x L	1,33	<0.1	0.765	1,33	0.17	0.681	1,33	0.64	0.429	1,33	0.24	0.630
LR x E	1,33	0.64	0.430	1,33	1.47	0.234	1,33	<0.1	0.850	1,33	0.3	0.589
LR x F	1,33	<0.1	0.823	1,33	0.83	0.369	1,33	0.11	0.747	1,33	0.99	0.328
L x E	1,16	1.16	0.298	1,16	3.07	*0.099*	1,16	0.36	0.556	1,16	2.50	0.133
L x F	1,16	1.26	0.278	1,16	0.78	0.390	1,16	0.27	0.610	1,16	2.00	0.176
E x F	1,12	< 0.1	0.876	1,12	0.12	0.740	1,12	<0.1	0.804	1,12	0.77	0.397
LR x L x E	1,33	0.26	0.617	1,33	0.19	0.667	1,33	0.55	0.465	1,33	0.9	0.351
LR x L x F	1,33	<0.1	0.873	1,33	<0.1	0.970	1,33	<0.1	0.947	1,33	<0.1	0.830
LR x E x F	1,33	0.26	0.615	1,33	<0.1	0.931	1,33	0.23	0.638	1,33	0.4	0.532
L x E x F	1,16	<0.1	0.944	1,16	1.96	0.181	1,16	2.26	0.152	1,16	2.62	0.125

Table S3. Results of multiple linear mixed effects models with subplot nested within plot nested within block as random effect assessing the relationships between (total and sown) seedling number and richness and light intensity at the ground level (below litter layer where present), light quality (R:FR), soil moisture, soil surface temperature and soil C:N across species. All predictors were standardized to facilitate comparison of values with different units and orders of magnitude. The relationship between litter depth and seedling number and richness was tested in a separate model, because data on litter depth were only recorded in half of the plots (those with litter present). Significant results are printed in bold (p < 0.05), tendencies are printed in italics (p<0.1). * Data are log transformed.

| Explanatory variable	Predictor	Variance inflation factor (VIF)	d.f.	F	p
Seedling number total*	Litter depth (cm)	-	1,32	0.42	0.521
	Light intensity (µmol/m²/s)	1.204	1,68	0.37	0.545
	R:FR	1.276	1,37	0.77	0.385
	Soil moisture (%VMC)	1.159	1,72	0.76	0.385
	Soil surface temperature (°C)	1.178	1,3	0.82	0.426
	Soil C:N	1.126	1,20	0.38	0.547
Seedling number sown*	Litter depth (cm)	-	1,30	3.70	*0.064*
	Light intensity (µmol/m²/s)	1.186	1,68	1.25	0.286
	R:FR	1.277	1,37	0.39	0.536
	Soil moisture (%VMC)	1.158	1,71	0.48	0.491
	Soil surface temperature (°C)	1.132	1,3	1.68	0.277
	Soil C:N	1.102	1,28	0.1	0749
Seedling richness total*	Litter depth (cm)	-	1,33	0.24	0.627
	Light intensity (µmol/m²/s)	1.191	1,68	2.09	0.153
	R:FR	1.280	1,36	1.15	0.291
	Soil moisture (%VMC)	1.162	1,71	0.76	0.386
	Soil surface temperature (°C)	1.142	1,3	1.47	0.305
	Soil C:N	1.109	1,26	<.1	0.962

Seedling richness sown*	Litter depth (cm)	-	1,28	1.36	0.253
	Light intensity (μmol/m^2/s)	1.143	1,72	1.63	0.206
	R:FR	1.239	1,41	0.93	0.340
	Soil moisture (%VMC)	1.134	1,69	0.26	0.609
	Soil surface temperature (°C)	1.097	1,3	1.48	0.302
	Soil C:N	1.085	1,39	<.1	0.948

Table S4. Results of permutational multivariate analysis of variance (PERMANOVA) for the total and sown seedling community in 2019. The analyses were based on Bray-Curtis dissimilarities. Only the significant effects (P < 0.05) are shown.

|	*F*	*P*
Total seedling community		
Litter	4.51	0.001
Exclosure	5.16	0.001
Sown seedling community		
Litter	6.32	0.001
Exclosure	1.91	0.049
Litter x Exclosure	2.30	0.014
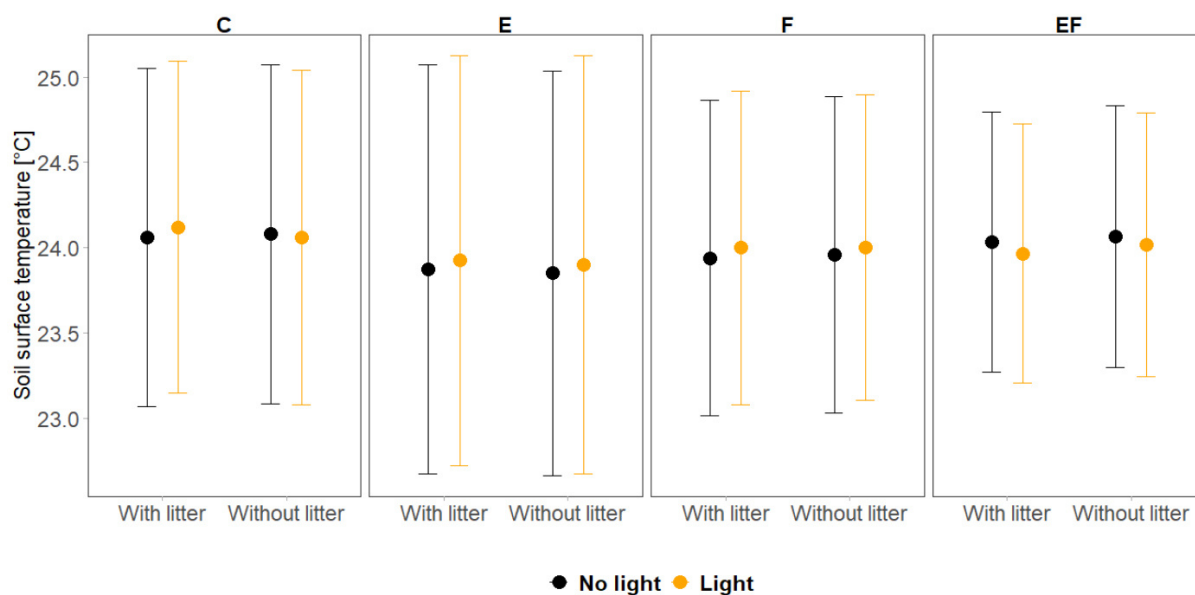
Figure S1. Soil surface temperature (means ± SE) in the different treatment combinations. Soil surface temperature was measured from all experimental units using a soil moisture probe (TDR 100, Spectrum Technologies, USA) in May 2019. Fertilization x litter interaction ($F_{1,32}$ = 4.21, P = 0.048). No main effect of any of the treatments. C = control, E = exclosure, F = fertilized, EF = exclosure + fertilized.
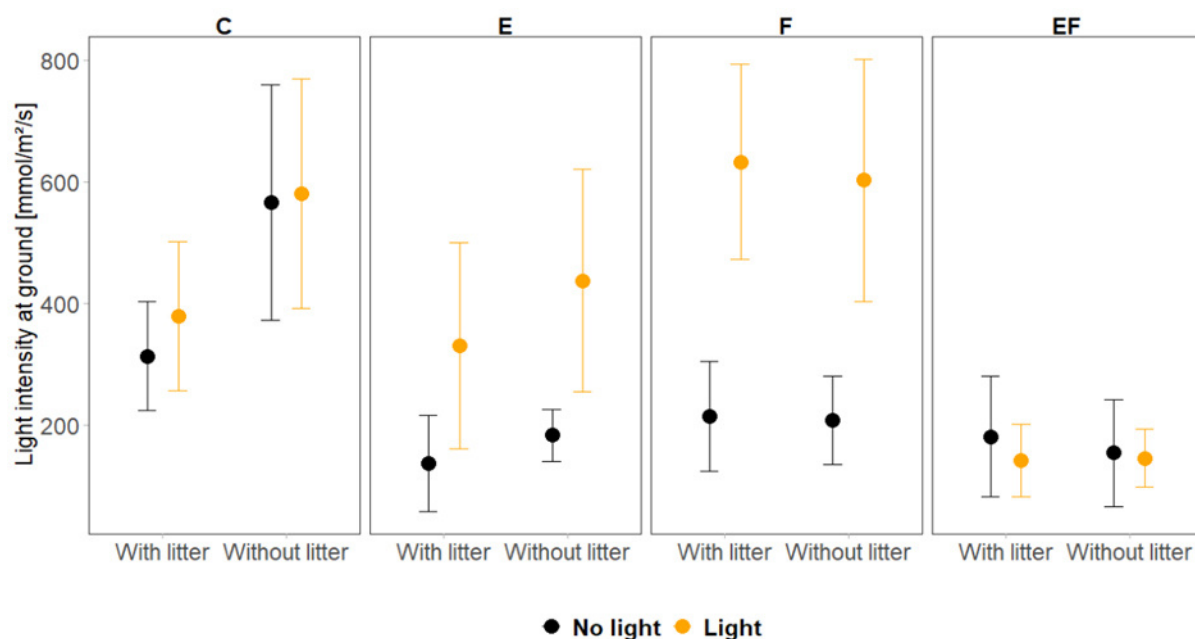
Figure S2. Light intensity (means ± SE) in the different treatment combinations. Light intensity was measured from all experimental units at ground level using a light meter (LI-250A, LI-190R, LI-COR, USA) in May 2019. Herbivory exclusion ($F_{1,12}$ = 16.13, P = 0.002), fertilization ($F_{1,12}$ = 4.87, P = 0.047) and light addition ($F_{1,16}$ = 6.43, P = 0.022) have a main effect on light intensity. C = control, E = exclosure, F = fertilized, EF = exclosure + fertilized.
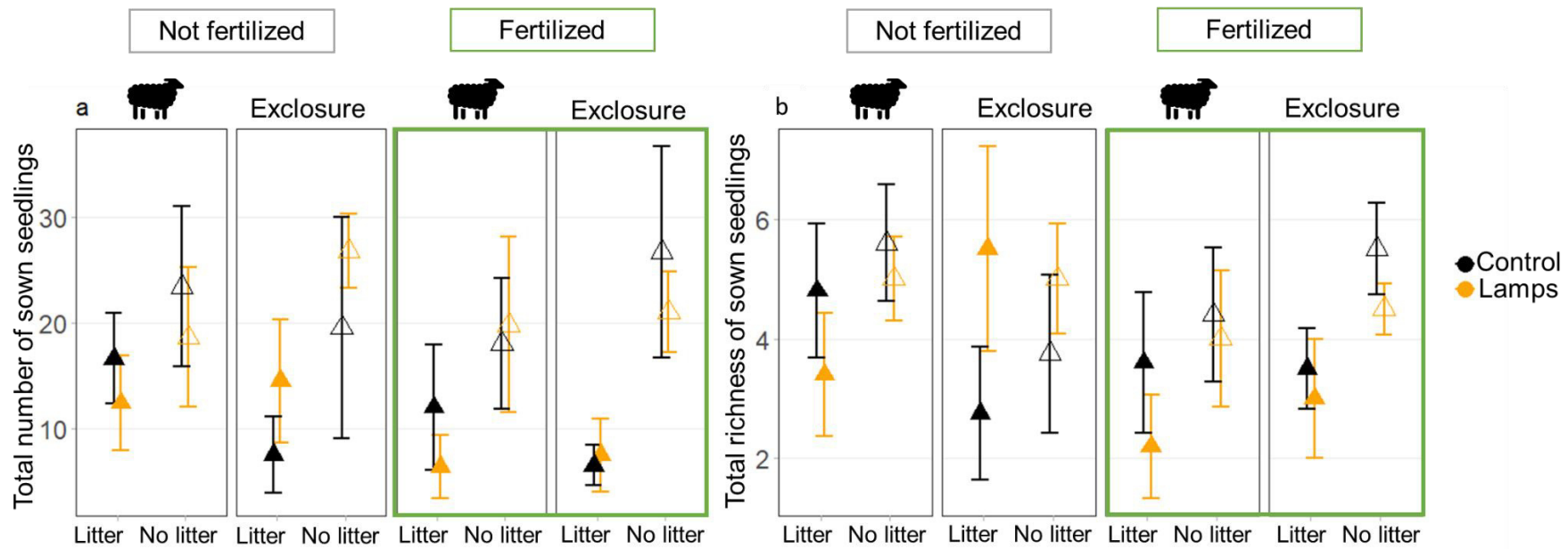
Figure S3. Number of (a) sown seedlings (mean ± SE) and (b) richness of sown seedlings (mean ± SE) under light addition, litter removal, herbivore exclusion and fertilization sampled in May 2019. The open triangles refer to litter removal, the filled triangles to litter present conditions.
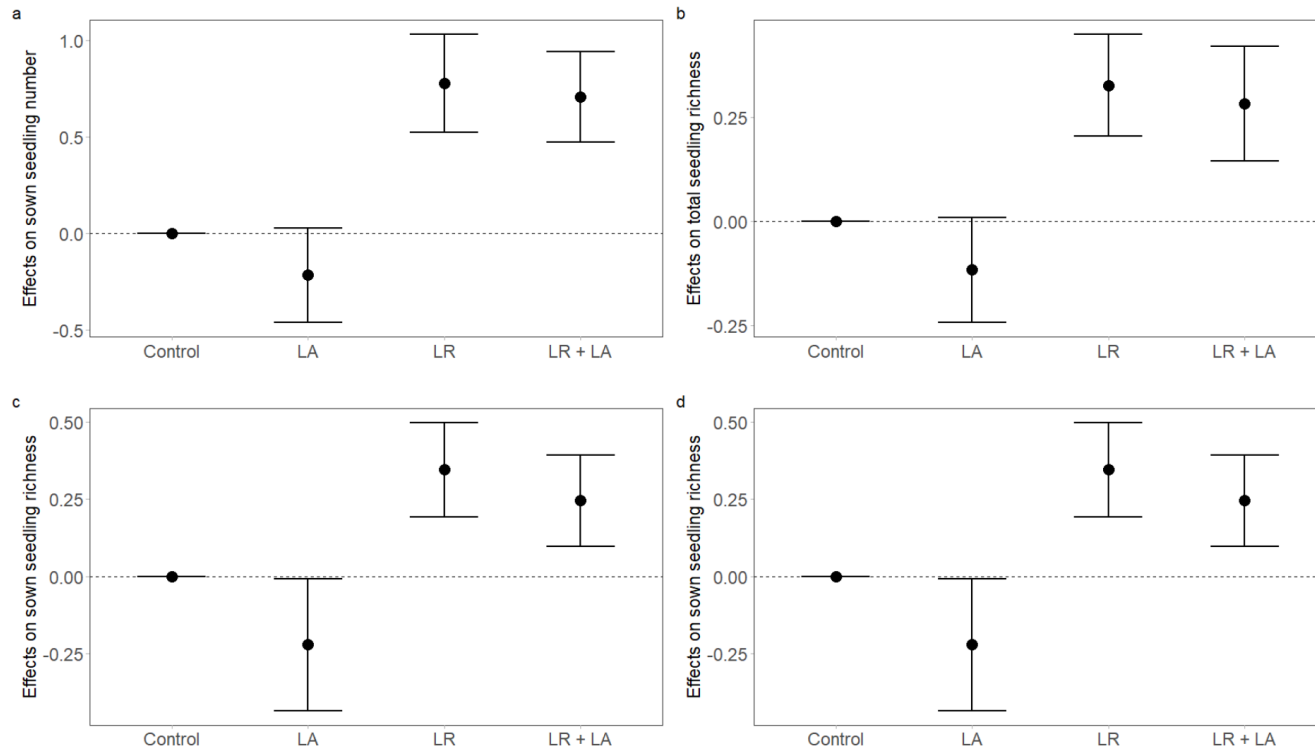
Figure S4. Effect sizes (mean ± SE) of light addition (LA = lamps + litter), litter removal (LR = no lamps + no litter) and light addition plus litter removal (LA + LR = lamps + no litter) on (a) total seedling number, (b) total seedling richness, (c) sown seedling number and (d) sown seedling richness Effect sizes were calculated as log ratios of the treatment responses divided by the control. Litter removal has a positive effect on total seedling number ($F_{1,38} = 25.47$, P <.001) and total seedling richness ($F_{1,38} = 17.06$, P <.001) and on sown seedling number ($F_{1,34} = 20.73$, P <.001) and sown seedling richness ($F_{1,34} = 12.26$, P =.001), whereas light addition has no effect independently and in interaction with litter removal.
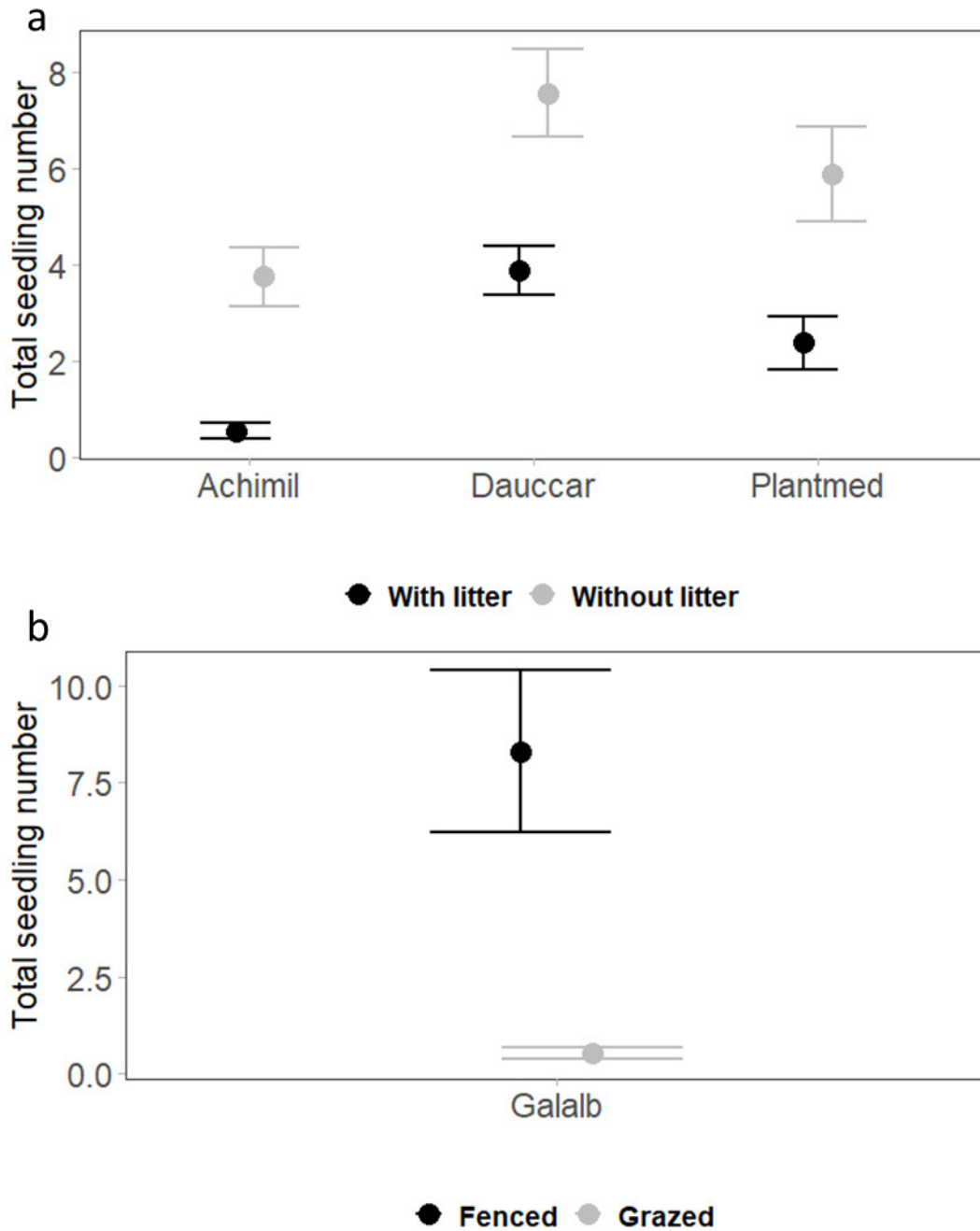
Figure S5. Main effect of (a) litter removal and (b) herbivore exclosure on the species shown. Data are means ± SE. Achillea millefolium (main effect of litter removal, $F_{1,33} = 24.03$, P < 0.001), *Daucus carota* (main effect of litter removal, $F_{1,33} = 15.49$, P < 0.001), *Plantago media* (litter removal main effect, $F_{1,33} = 10.45$, P = 0.003). Galium album (main effect of herbivore exclusion, $F_{1,12} = 9.25$, P = 0.010).
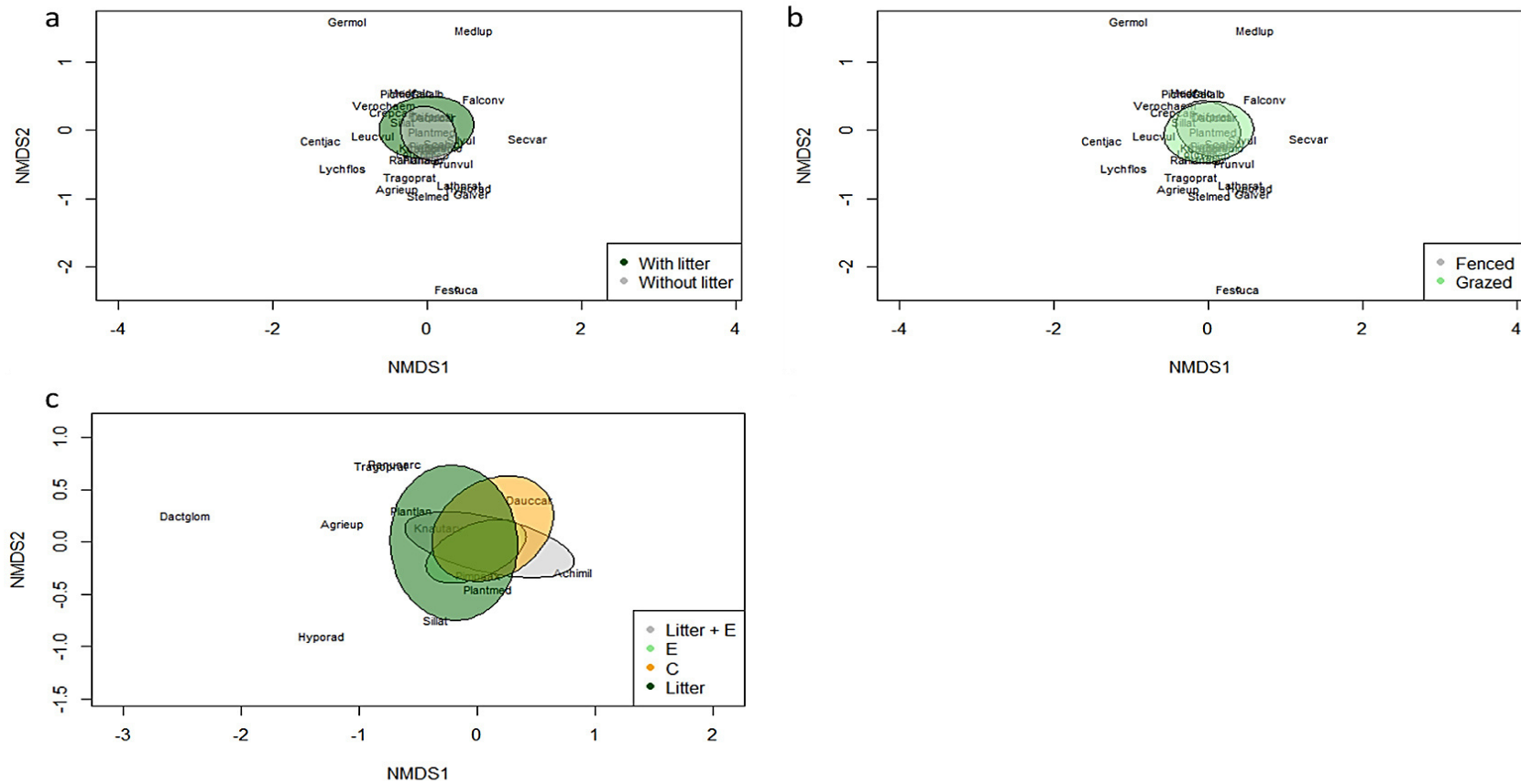
Figure S6. Non-metric multidimensional scaling (NMDS) of the total seedling community and its relationship with (a) litter removal and (b) herbivore exclusion. Non-metric multidimensional scaling (NMDS) of the sown seedling community and its relationship with (c) litter removal and herbivore exclusion (E) (C = control; no litter removal grazed). The ordinations were based on Bray-Curtis dissimilarity. We only show the treatments which were significant according to the permutational analysis of variance (PERMANOVA). The statistical results are shown in Table S4.
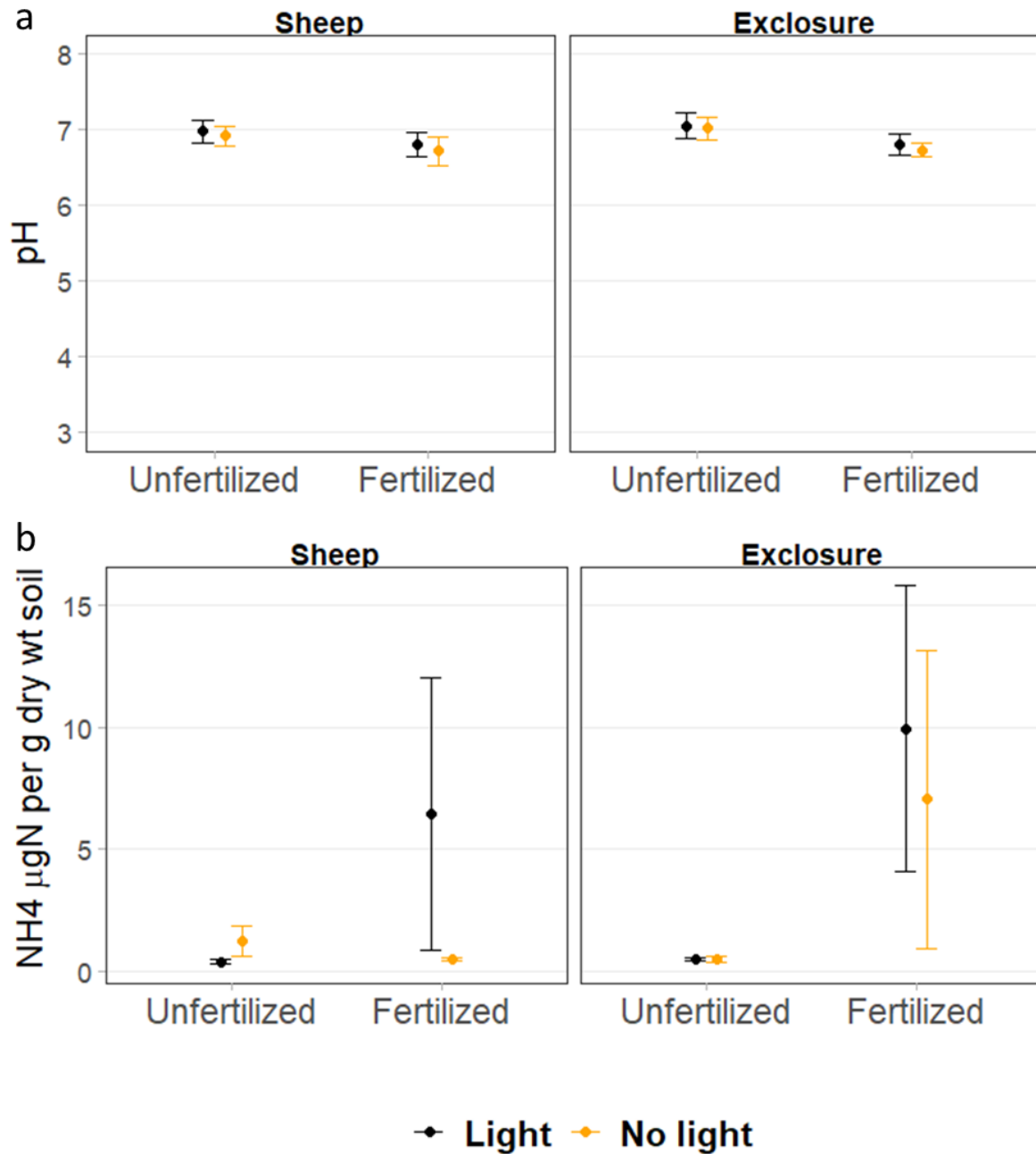
Figure S7. (a) PH and (b) NH4 in response to all combinations of grazing, fertilization and light. Data are means ± SE. Fertilization decreases pH ($F_{1,12}$ = 11.71, P = 0.005) and increases NH4 ($F_{1,12}$ = 5.59, P = 0.035). Note that the soil cores for these data were taken in 2020 on the plot level (i.e. one year later than the seedling survey and on bigger plot scale than the seedling survey units). Soil pH and NH4 concentration were analyzed at the University of Manchester.

CHAPTER IV

Silene latifolia responses to light and nutrients depend on grazing and future climate

Maria-Theresa Jessen[*,1,2,3,4], Harald Auge[1,2], Yann Hautier[5], Stan Harpole[1,3,4], Anu Eskelinen[1,3,6]

[1]*German Centre for Integrative Biodiversity Research – iDiv Halle-Jena-Leipzig, Puschstraße 4, D-04103 Leipzig, Germany*

[2]*Department of Community Ecology, Helmholtz Centre for Environmental Research - UFZ, Theodor-Lieser-Straße 4, D-06120 Halle, Germany*

[3]*Department of Physiological Diversity, Helmholtz Centre for Environmental Research – UFZ, Permoserstr. 15, D-04318 Leipzig, Germany*

[4]*Martin Luther University Halle-Wittenberg, Am Kirchtor 1, 06108 Halle (Saale), Germany*

[5]*Ecology and Biodiversity Group, Department of Biology, Utrecht University, Padualaan 8, 3584 CH Utrecht, The Netherlands*

[6]*Department of Ecology and Genetics, University of Oulu, FI-90014, Oulu, Finland*

Abstract:

Background and Aims: Altered climate, nutrient enrichment and changes in grazing patterns are important environmental and biotic changes in temperate grassland systems. Singly and in concert these factors can considerably influence individual plant performance and traits, with consequences on species competitive ability, species coexistence, community composition and diversity. However, experiments studying their combined effects on individual plant performance are rare. In addition, experiments directly testing the mechanisms that drive plant responses, such as light limitation, are missing.

Methods: We used *Silene latifolia*, an abundant and widespread grassland forb in Europe, palatable to grazers, as our phytometer species to study individual species responses to interactions among climate, nutrients, grazing and light. We recorded phytometer biomass, height, specific leaf area (SLA) and foliar C:N in full-factorial combinations of future climate treatment, fertilization, grazer exclusion and light addition via LED-lamps.

Key Results: Future climate and fertilization together increased plant height but only in unlighted plots. Further, plants had higher biomass in future climatic conditions when protected from grazers. In general, grazing had a strong negative effect on all measured variables regardless of resource availability (i.e. nutrients and light).

Conclusion: Our results show that light limitation may lead to greater height under densely vegetated conditions. Furthermore, our study suggests that plants may grow better (i.e. accumulate more biomass and grow taller) under future climate, but grazing may counteract the benefits of future climate. Therefore, grazers may modulate individual plant biomass and traits under future climatic conditions.

Keywords: climate change, exclosure, fertilization, experimental light addition, LED lamps, performance, phytometer, resources, sheep grazing, traits

Introduction

Grasslands are increasingly exposed to concurrent impacts of climate change, nutrient enrichment and changes in grazing practices (Gibson & Newman 2019). Singly and in concert these global change drivers can affect plant community composition and diversity (Gossner *et al.* 2016; Boutin *et al.* 2017; Borer *et al.* 2020). In a changing environment, plant communities should harbor species which are able to tolerate direct and interactive pressures of these drivers (Komatsu *et al.* 2019; Manning 2019). To predict and understand overall community responses, it is therefore essential to identify how abiotic and biotic changes influence the persistence and competitive ability of individual plants. One approach to assess plant vulnerability to current global change drivers is measuring intraspecific trait responses which can relate to plant performance (Liancourt *et al.* 2015; Jessen *et al.* 2020). However, while some studies have examined individual plant traits and performance in response to different land-use types (Herz *et al.* 2017; Breitschwerdt, Jandt & Bruelheide 2018), studies examining the combined impacts of nutrient enrichment, grazing and climate change are scarce (but see Kaarlejärvi, Eskelinen & Olofsson 2013; Jessen *et al.* 2020). In addition, not much is known about the mechanisms driving these trait-based plant responses.

Nutrient enrichment directly increases plant available nutrients and thus fuels plant growth and biomass accumulation (Stevens *et al.* 2015; Goldberg *et al.* 2017). Increased belowground resources can lead to larger SLA and higher leaf N content (Siebenkäs, Schumacher & Roscher 2015; Tatarko & Knops 2018). Fertilization-induced enhanced plant growth and leaf enlargement can lead to a reduction in light availability in the understory (Tilman 1987; Borer *et al.* 2014b). This should especially disfavor and limit the performance of small-statured species with resource-conservative traits (i.e. small SLA, high foliar C:N) (Suding *et al.* 2005). Consequently, tall-statured species with resource-acquisitive traits (i.e. large SLA, low foliar C:N) should dominate and perform better in nutrient-rich conditions (Keddy *et al.* 2002; Siebenkäs, Schumacher & Roscher 2015; Poorter *et al.* 2019; Wilfahrt *et al.* 2020). In a study conducted in forest understory (Blondeel *et al.* 2020), plant traits responded to light addition, but were unaffected by fertilization, suggesting that light was more limiting than nutrients for trait manifestation (Valladares *et al.* 2016). However, results from other systems, such as grasslands, might differ, because they lack shade created by trees and plants might be less well adapted to shaded conditions.

Grazing can reduce fertilization-induced light limitation which has, on the community level, a beneficial effect for biodiversity (Borer *et al.* 2014b). On the individual plant level, the direct effect of grazing on plant growth depends on grazing intensity (Hickman & Hartnett 2002), traits (i.e. stature, leaf size, leaf nutritional composition) and thus their vulnerability to herbivory (Diaz *et al.* 2007; Eskelinen 2008; Evju *et al.* 2009; Kaarlejärvi, Eskelinen & Olofsson 2013), and the time scale of grazing (Diaz *et al.* 2007; Volf *et al.* 2016; Thomann, Ehrlen & Agren 2018). In general, grazing affects plant growth by decreasing height and biomass and thus reduces plant performance (Ehrlen 1997; Van Der Wal *et al.* 2000; Eskelinen 2008), but it can also stimulate plant growth in a density-dependent manner (Penner & Frank 2021) and eventually lead to overcompensation (Lennartsson, Nilsson & Tuomi 1998; Hawkes & Sullivan 2001). However, abiotic conditions such as soil fertility can alter grazing effect on plants (Osem, Perevolotsky & Kigel 2004; Gough, Ramsay & Johnson 2007). Theory predicts that plants growing in resource-rich conditions should better compensate for grazing damage (McNaughton 1983; Strauss & Agrawal 1999). This emphasizes that the net effect of grazing on plant biomass and trait manifestation is likely dependent on resource availability (i.e. light and nutrients).

Climate change can change plant-herbivore interactions through direct effects on herbivores but also direct effects on plants (Hamann *et al.* 2021). Likewise, climate change may modify plant-resource interactions, for example, due to accelerated nutrient cycling in response to warmer temperatures (Luo 2007). For temperate grasslands in Central Germany, scenarios predict warmer temperatures throughout the growing season, increased spring and autumn precipitation, and reduced precipitation and increasing risk of drought spells during summer (Beniston *et al.* 2007; Christensen & Christensen 2007; Christensen *et al.* 2013; Helmholtz-Zentrum hereon 2021). Warmer temperatures and water surplus at the beginning of the growing season can stimulate vegetation growth, leading to increases in plant height and biomass (Frei, Ghazoul & Pluess 2014; Bjorkman *et al.* 2018) and in general promoting traits of fast resource use (Fridley *et al.* 2016). Herbivores, by targeting taller plants (Diaz, Noy-Meyr & Cabido 2001; Evju *et al.* 2009), can dampen the effect of warming on plant traits and thus alter plant performance in response to warmer temperatures (Kaarlejärvi, Eskelinen & Olofsson 2013; Jessen *et al.* 2020). On the other hand, reduced precipitation during summer can cause physiological stress with impacts on plant performance (Poirier, Durand & Volaire 2012; De Boeck *et al.* 2016; Funk, Larson & Ricks-Oddie 2021). To cope with drought induced stress, plants may profit from traits that minimize water loss such as smaller SLA (Weißhuhn, Auge & Prati 2011; Jung *et al.* 2014; Liancourt *et al.* 2015; Wellstein *et al.* 2017). Some studies have examined the interactive effects of climate change and nutrient enrichment in grassland systems (Shaw *et al.* 2002; Zavaleta *et al.* 2003; Eskelinen & Harrison 2015), but only a few have investigated how climate change induced changes in precipitation and nutrient enrichment interact with herbivory (Lang *et al.* 2020).

We used the widely distributed grassland species *Silene latifolia* (hereafter *Silene*) as a phytometer to study mechanisms by which individual forbs respond to interactions among nutrients, climate, light and grazing (future climate projected for Central Europe). *Silene* is palatable to herbivores (Marten, Sheaffer & Wyse 1987; Wolfe 2002) and highly important for

pollinators (Dotterl *et al.* 2006). It has also been shown to respond to environmental changes (Favre & Karrenberg 2011) and substantially contributes to the local recruitment from seed in our study system (Jessen & Eskelinen, personal observation). We therefore expect this species to be highly responsive to resource manipulations and herbivory, and changes in its performance should reflect to community dominance relationships. We measured two common traits (SLA and foliar C:N) linked to resource-use strategies (Westoby *et al.* 2002; Wright *et al.* 2004; Reich 2014), competitive ability (Keddy *et al.* 2002), and palatability to herbivores (Diaz, Noy-Meyr & Cabido 2001; Diaz *et al.* 2004). As a measure of performance, we collected data on plant aboveground biomass and plant height. We asked the following questions: 1) Do the effects of increased resources (nutrients and light) on the performance and traits of *Silene* depend on grazing? 2) Do the effects of increased resources on the performance and traits of *Silene* depend on climate? 3) Do the effects of climate on the performance and traits of *Silene* also depend on grazing?

We made the following predictions: 1a) Fertilization increases biomass, height and trait values of *Silene* more in fenced than unfenced plots because grazing offsets fertilization effects. 1b) Height and SLA of *Silene* are greater in unlighted than lighted plots because plants should respond to shade by growing taller and having larger SLA. These responses should be greater inside herbivore exclosures because shading by surrounding vegetation is much greater inside exclosures. 2a) Future climate interacts with fertilization on the biomass, height and traits of *Silene*; it either magnifies or offsets fertilization effects depending on which time of the year plants are limited by precipitation. 2b) Future climate either amplifies or reduces the effects of light addition, depending on whether it increases or decreases the biomass of surrounding vegetation. 3) Grazing amplifies or reduces the effects of climate, depending on whether climate increases or decreases the biomass, height and traits of *Silene*.

Material and Methods

Study site

The experiment is embedded in the Global Change Experimental Facility (GCEF) at Bad Lauchstädt Research Station (51°22060 N, 11°50060), Germany. In this area the long-term mean annual precipitation is 489 mm and the mean annual temperature is 8.9 °C (Schädler *et al.* 2019). The soils are fertile Haplic Chernozems (Altermann *et al.* 2005; Schädler *et al.* 2019). The GCEF combines research on different land-use types with ambient and future climate regimes in a split-plot design (Schädler *et al.* 2019). For this study we used ten extensively grazed pastures within the GCEF which represent species-rich grassland vegetation of dryer regions of Central Germany (Schädler *et al.* 2019). These pastures are grazed two to three times a year by a herd of about 20 German black-headed sheep, depending on the amount of vegetation biomass (Schädler *et al.* 2019). In 2018, 2019 and 2020 grazing was limited to two grazing events per year because of extreme drought conditions (Buras, Rammig & Zang 2020; Hari *et al.* 2020). Each pasture has a size of 16 x 24 m and is grazed by the sheep with high intensity for 24 hours (Schädler *et al.* 2019). To prevent other larger, naturally occurring grazing animals (e.g., deer) from entering the experimental site, the entire area was fenced. Rodents such as the European hare (*Lepus europaeus*) can enter the experimental area.

Five of the pastures are randomly assigned to the ambient climate, the other five to the future climate. For the climate manipulation, pastures under future climatic conditions are equipped with metal roof structures with foldable roof and side covers, as well as with a controllable irrigation system (Schädler *et al.* 2019). To control for any effect of the roof structure, pastures in ambient conditions have similar structures but with non-foldable roof and side covers. The intent of the climate treatment is to increase temperatures and to simulate decreasing precipitation in the summer and increasing precipitation in the spring and fall, consistent with predictions for this region (Schädler *et al.* 2019). The future climate treatment increases air and soil temperature using passive night warming for which the roof and side covers are automatically closed during the night. The amount of temperature increase varies over season and years (Schädler *et al.* 2019). To simulate increasing spring and autumn precipitation the weekly precipitation at ambient blocks is used as a reference to which ten percent is added to simulated the increase in precipitation in future blocks (Schädler *et al.* 2019). To simulate decreasing summer precipitation, future blocks receive 80 percent of the weekly precipitation that falls on ambient blocks (Schädler *et al.* 2019).

Experimental design

We established our experiment in 2017 using a full factorial design of herbivore (sheep) exclusion and nutrient enrichment in each of the ten pastures (ambient and future climate). In each of the ten pastures, we established four 1.4 × 1.4 m plots that were randomly assigned to the following treatment combinations: 1) unfertilized and grazed (e.g. control), 2) fertilized and grazed, 3) unfertilized and fenced, 4) fertilized and fenced. This resulted in 40 experimental plots, arranged in four-plot groups (called "blocks" in the statistical analyses), half of which received ambient climate and the other half future climate treatment. To fertilize, we manually added a slow-release NPK fertilizer mixture (Haifa Multicote 2 M 40-0-0 (40% N, Super Triple Phosphate TPS (45% P203), potassium sulfate fertilizer (50% K2O, 45% SO3) to each plot assigned to fertilization treatment two times per growing season (later March-May and June). We added 10 g N, 10 g P and 10 g K per m² (see the protocol of Borer *et al.* 2014a for grasslands around the globe) to experimentally relax nutrient limitation. The fertilization treatment started in May 2017, while the herbivore exclusion treatment started three months later, at the end of August. We used rectangular, mobile metal fences of 1.8 x 1.8 m size, 82 cm height and 10 cm mesh size to exclude the sheep from plots assigned to the herbivore exclusion treatments. The fences allowed small rodents like mice and voles (mainly *Apodemus sylvaticus* and *Microtus arvalis*), abundant in the experimental area, to pass (Jessen & Eskelinen, personal observation, Koch & Jakob, unpubl. data). In 2019, one plot originally intended for herbivore exclusion only was accidentally fertilized and one plot originally intended for herbivore exclusion and fertilization treatment was not fertilized. Both plots were treated as fertilized in the data analysis.

In addition to the fertilization and herbivore exclusion treatment we implemented a light addition treatment using modern LED lamps (C65, Valoya, Finland). For this purpose, the 1.4 × 1.4 m plots were divided into two 0.7 × 1.4 m subplots, one of which was randomly assigned to light addition treatment. resulting in total 80 experimental subplots. Each lighted subplot was equipped with two 120 cm long and 3.5 cm wide high intensity LED lamps that were

installed horizontally to the ground and parallel to each other. The light addition treatment started at the same time than fertilization treatment, i.e., at the end of May 2017. In the beginning of the growing season (February – April) the lamps were installed about 10 cm above the smallest plants and uplifted as vegetation grew. We set the lamps to switch on two hours after sunrise and switch off two hours before sunset, and they automatically switched off when the temperature exceeded 28°C to prevent overheating. In 2020, we switched on the lamps March 16. The light addition treatment added light throughout the active growing season and lamps were only removed during the grazing to prevent the sheep from damaging the lamps. Lamps in the fenced plots were switched off during the grazing. At the end of each growing season (October-November), the lamps were demounted to prevent frost damage. Using LED lamps that have a wavelength spectrum corresponding to natural sunlight we mimicked increased sunlight availability in a vegetation gap in a natural grassland, and were therefore able to test the role of light limitation.

Phytometer planting

In August 2019 we seeded local seeds of *Silene* (Saale-Saaten Stolle, Germany) in cultivation trays in a glasshouse. When the plants had grown for four months they were translocated into a cold house to allow them to adapt to outside conditions. In November 2019, when the plants had grown for five months, we planted one similar-sized individual into each experimental subplot. In lighted subplots we made sure the transplant was planted directly under the LED lamp. We planted five-month-old individuals as smaller/younger plants were often eaten by voles and mice (Moles & Westoby 2004; Barton & Hanley 2013). To protect the phytometers against vole and mice herbivory in the winter, they were each surrounded by a cylinder of green mesh (Netzhülle Bestklima, best4forst, Germany) with a height of 18 cm, a diameter of 12 cm and a mesh size of 3 x 3 mm. The mesh was attached to the ground with u-shaped nails. After transplanting we watered the plants. The protective mesh was removed in April 2020 when growing season and plant growth started.

Performance and trait sampling

To determine growth of *Silene* phytometers, we measured vegetative height (cm) from the ground to the highest point of each plant. Height was measured after the plants have been grazed, but had the chance to regrow since harvesting took place two months after the last grazing event. For data on SLA (mm² per mg dry mass) we collected a maximum of three healthy looking and well-developed leaves on each *Silene* individual. SLA was measured following the general protocol directly after harvesting (Cornelissen *et al.* 2003; Perez-Harguindeguy *et al.* 2013) and used as a surrogate for slow/fast resource uptake, response to light availability and attractiveness to herbivores (Diaz, Noy-Meyr & Cabido 2001; Diaz *et al.* 2004; Wright *et al.* 2004). We only sampled leaves that did not show any grazing damage. For most *Silene* phytometers it was not possible to collect the full number of leaves for SLA measurements because of severe leaf herbivory which led to strongly damaged leaves, or a few resprouting leaves at the stalk. Resprouting leaves were collected but labelled separately to distinguish them from "old" leaves collected from individuals inside the fences. Across "old" and resprouting leaves we obtain 48 samples from which we measured SLA (Table S1). In a

few cases, leaves were also severely wilted and could not be analyzed. Furthermore, we compiled all leaf material of each individual to determine foliar C:N (VarioEL CNHS analyzer, Elemental Analyse Systeme GmbH, Hanau, Germany). This was used as an indicator of resource uptake strategy and palatability to herbivores(Diaz, Noy-Meyr & Cabido 2001; Diaz *et al.* 2004; Evju *et al.* 2009). In total, we were able to use results from 65 leaf samples for the statistical analysis, as some samples had too little leaf material to provide reliable results (Table S1). In general, we got only a few leaf samples per treatment combination in the grazed plots, and had to omit testing for the effect of grazing on the foliar traits. After all measurements, we harvested the aboveground biomass of phytometer individuals. Overall, 78 out of 80 phytometers were still present at the point of harvest (i.e. after one year). The harvested plants were oven dried at 60°C for 48 hours and then weighed to obtain data on aboveground biomass allocation as a surrogate for plant performance (Liancourt *et al.* (2015), Kaarlejärvi, Eskelinen and Olofsson (2013). Both the trait sampling and the harvesting took place from the beginning to the middle of August 2020.

Statistical analysis

To assess performance responses of *Silene* to experimental treatments, we applied linear mixed effect models where height and aboveground biomass, each in their own model, were explained by herbivore removal, nutrient enrichment, light addition, climate treatment, and their interactions. Plot was nested in block as a random effect, to account for the split-plot experimental design. In addition, we ran these models for leaf traits in fenced plots only as herbivores had eaten most leaves and measuring SLA and C:N was not possible in most grazed plots (Table S1). The significance of the single factors and their interactions was tested with F-test. We used model diagnostic plots to check the homogeneity of variances and the normality of errors (Crawley 2007) and transformed the response variables to meet the assumptions when necessary (see Table 1 and 2 for transformed variables).

We used the 'lme4' package (Bates *et al.* 2015) to run linear mixed effect models, the 'car' package for assessing the significance of the treatments effects (Fox & Weisberg 2019), the 'tidyverse' package for data manipulation (Wickham *et al.* 2019), the 'ggplot2' package (Wickham 2016) and the 'patchwork' package (Pedersen 2020) for plotting in R statistical software (R Core Team 2020 version 4.0.3).

Results

Silene responses to resource additions modified by grazing

Fertilization increased height by 52 % (~ 12 ± 4.4 cm) and aboveground biomass by 89 % compared to unfertilized plots (Table 1). The fertilization effect tended to be greater in fenced plots, but this interaction was not statistically significant (Fig. 1a and b, Table 1). Addition of light had no main effect on *Silene* height or biomass and did not interact with grazing (Table 1). Grazing showed a strong main effect and reduced plant height by 83 % (~ 39 ± 3.6 cm) and total aboveground biomass by 95 % compared to fenced plots (Table 1, Fig. 1a and b).

Even though we could not test for grazing effects on leaf traits, leaves inside fences responded to resource additions: light addition increased relative foliar N content (i.e. decreased C:N) in unfertilized plots, but had no effect in fertilized plots (significant F x L, Table 2, Fig. 2a). Light addition alone increased SLA by 12.8 % (Table 2, Fig. S1) and fertilization alone decreased foliar C:N (i.e. increased relative foliar N content) by 21.9% (Table 2, Fig. 2).
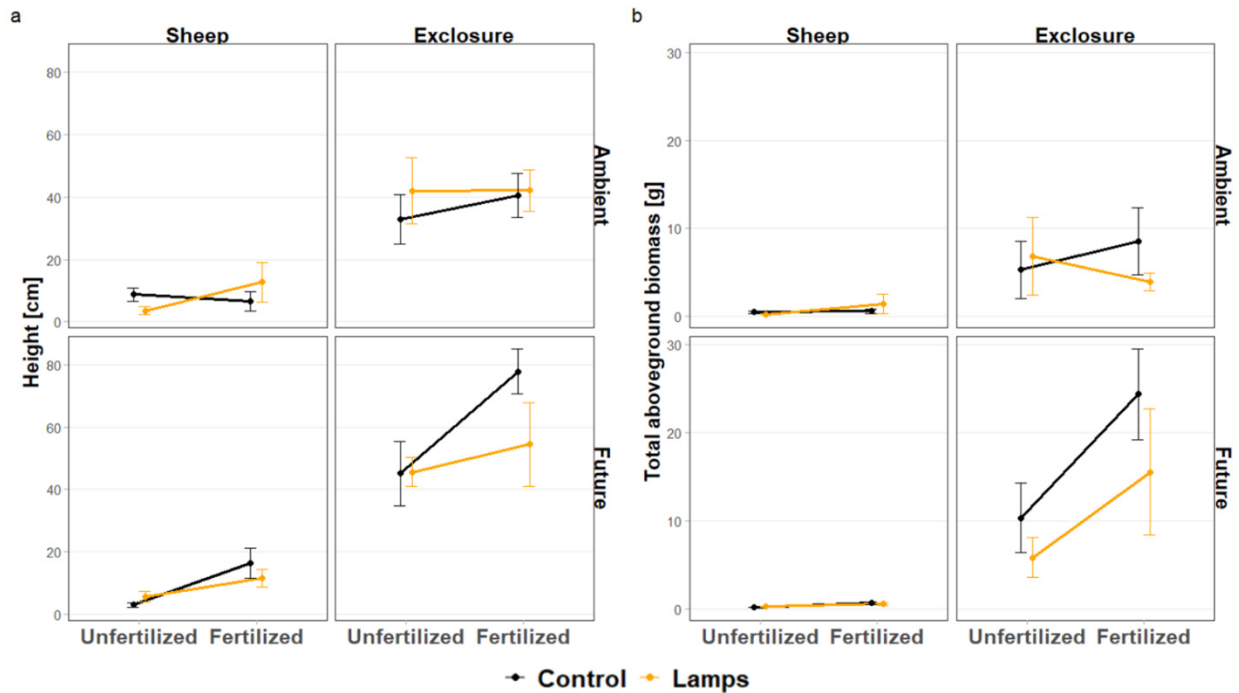
Figure 1. Height (a, n = 80) and biomass (b, n = 78) responses of Silene latifolia to combinations of grazing, fertilization, ambient and future climate and light addition. The data are means ± SE.

Silene responses to resource additions modified by climate

In support for predictions 2a and b we found that effect of light addition on height depended on the interaction between future climate and fertilization in such a way that *Silene* grew tallest under future climate and when fertilized but not lighted (significant F x C x L, Table 1, Fig. 1a). Furthermore, and according to prediction 2b, SLA increased with light addition, but only under ambient climate (significant C x L, Table 2). This effect was also greater in fertilized plots although the interaction with fertilization was not significant (Figs. 2b and Table 2). Climate had no main effect on *Silene* height, biomass, SLA and foliar C:N (Table 1 and 2).
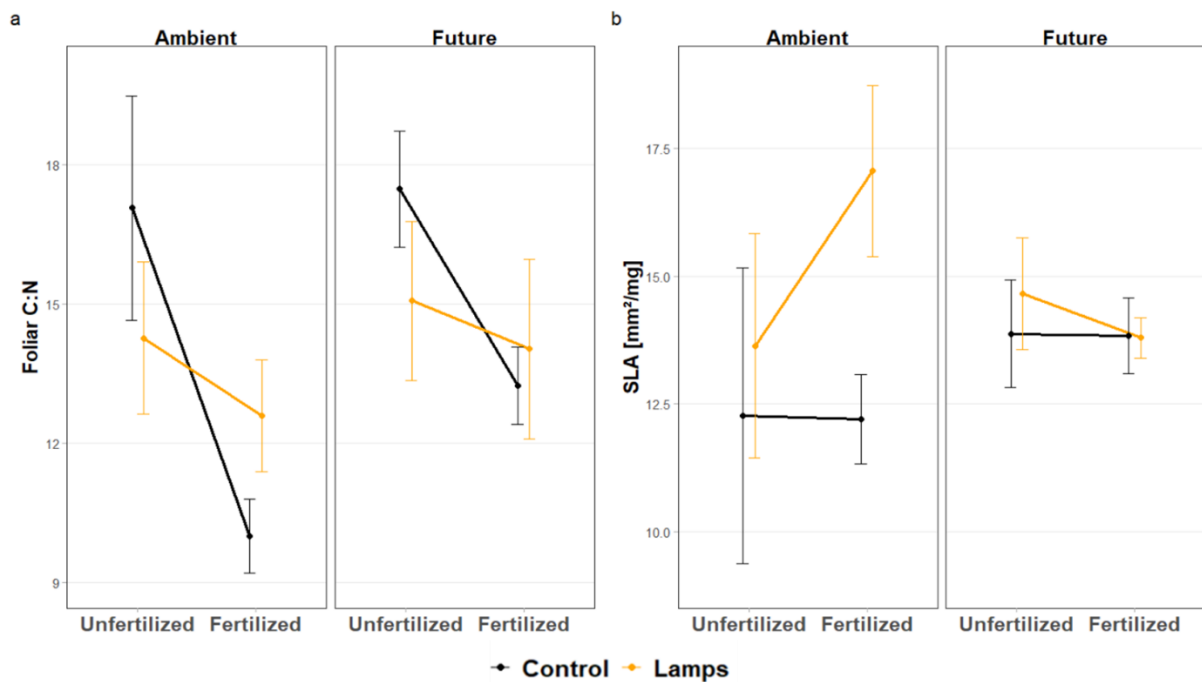
Figure 2. *Foliar C:N (a, n = 65) and SLA (b, n = 48) responses of Silene latifolia to combinations of fertilization, ambient and future climate and light addition. The data are from inside the fences and are means ± SE*

Phytometer responses to climate modified by grazing

Supporting prediction 3, *Silene* attained greater biomass in future climatic conditions compared to ambient conditions only in the absence of grazing (significant E x C, Table 1, Fig. 1b), i.e., grazing counteracted the effects of climate. There was no significant interaction between climate and grazing on the height of *Silene*, although the positive impact of future climate and fertilization in unlighted plots was especially pronounced inside fences (Fig. 1a).

Table 1. *Results of linear mixed effect models testing the effects of grazing (exclosure), fertilization, climate and light addition on the phytometer performance (height and total aboveground biomass). Significant results (p < .05) are printed in bold, marginally significant results (p < .1) are printed in italic. [a] data are log transformed.*

Source of variation	Height[a]			Biomass[a]		
	df	F	P	df	F	p
Exclosure	1,24	103.76	**<.001**	1,24	132.51	**<.001**
Fertilization	1,25	5.61	**0.026**	1,25	5.52	**0.027**
Climate	1,8	1.83	0.214	1,8	2.27	0.171
Light	1,32	0.35	0.558	1,31	3.76	*0.062*
E x F	1,25	1.14	0.296	1,25	<.1	0.951
E x C	1,24	<.1	0.813	1,24	4.30	**0.049**
E x L	1,32	<.1	0.965	1,31	1.00	0.232
F x C	1,25	2.43	0.132	1,25	1.50	0.231
F x L	1,32	<.1	0.851	1,31	0.45	0.508
C x L	1,32	<.1	0.818	1,31	<.1	0.797
E x F x C	1,25	1.36	0.254	1,25	<.1	0.797
E x F x L	1,32	2.52	0.122	1,31	0.76	0.390
E x C x L	1,32	2.06	0.161	1,31	2.50	0.124
F x C x L	1,32	7.19	**0.011**	1,31	0.55	0.464
C x E x F x L	1,32	3.59	*0.067*	1,31	0.86	0.362

Table 2. Results of linear mixed effect models testing the effects of fertilization, climate and light addition on the phytometer leaf traits (SLA and foliar C:N). Significant results (p < .05) are printed in bold, marginally significant results (p < .1) are printed in italic. ᵃ data are log transformed.

	SLA_fenced			Foliar CN_fenced[a]		
	df	F	p	df	F	p
Fertilization	1,8	0.2	0.644	1,11	5.84	**0.034**
Climate	1,7	<.1	0.805	1,7	1.75	0.225
Light	1,11	7.0	**0.023**	1,16	<.1	0.918
F x C	1,9	2.2	0.169	1,11	0.35	0.567
F x L	1,10	<.1	0.861	1,16	5.96	**0.027**
C x L	1,11	5.5	**0.038**	1,16	1.35	0.262
F x C x L	1,11	1.7	0.218	1,16	0.90	0.357

Discussion

We found that the presence of grazers had a strong influence on biomass, height and leaf traits of *Silene*; however, when grazers were excluded *Silene* also responded to nutrient, light and climate manipulations. Future climate increased plant biomass in fenced plots, suggesting that grazers can counteract the effects of climate on individual species in temperate grasslands. Furthermore, plants in fenced plots grew taller under fertilized and future climatic conditions without additional light. This empirically demonstrates that competition for light is an important mechanism affecting plant investment in height under densely vegetated conditions. In addition, strong responses to grazing highlight the important role of grazing animals for performance and traits of highly palatable forbs in grassland systems, both under current and future climatic conditions and under nutrient enrichment.

We found that plants grew tallest under future climate when fertilized but not lighted and this pattern was especially pronounced inside fences. Nutrient addition and exclusion of herbivores have previously been reported to increase the amount of live and dead plant material (e.g. Bakker *et al.* 2004; Stevens *et al.* 2015). In our experiment, total vegetation and in particular litter cover show a clear peak in fertilized and ungrazed plots (Fig. S2a and b), possibly explaining shoot elongation (Fig. S3a and b) as tall-stature can increase plant's ability to compete for light (Valladares & Niinemets 2008; Goldberg *et al.* 2017). Light limited conditions, which we experimentally created by fertilizing, excluding herbivores and providing no light, led to taller plants. We also found that this interactive effect of light addition, in terms of plant height and SLA, was only evident in the future climate. Increased spring precipitation and warmer temperatures in the future climate treatment may have promoted plant growth during the early growing season and life stage (Kahl *et al.* 2019). Our result suggests that

changes in seasonal precipitation and temperature patterns can be a decisive factor for species' trait manifestation under altered nutrient and grazing conditions (Le Bagousse-Pinguet *et al.* 2017; Lang *et al.* 2020).

We also found that the addition of light had a positive main effect on SLA in fenced plots, and this effect was prevalent in ambient climate only. Future climate with lower summer precipitation and higher temperature may have caused plants to invest less on expanding leaves during the summer months, resulting in lower SLA due to water scarcity (Wellstein et al., 2017). Nevertheless, the observed increase in SLA in response to light addition seems counterintuitive, as plants are expected to increase SLA in response to light limitation (Valladares & Niinemets 2008). However, also other factors than direct light intensity could have driven SLA responses which is supported by the fact that we did not find a significant relationship between light intensity and SLA (Fig. S4a). Instead, SLA was positively related to percentage total vegetation cover (Fig. S4b), suggesting that dense vegetation with high competition for space and drive leaf trait manifestation. Furthermore, also foliar C:N responded to light addition and this effect was contingent on fertilization such that the positive effect of light addition on foliar relative carbon content was prevalent only in fertilized but not in unfertilized plots. This shows that increased resources can promote investment on foliar carbon investment. In a meta-analysis, Poorter *et al.* (2019) find that total leaf carbon content increased in response to increasing light intensity and suggest that this is due to an increase of structural components such as lignin which have a high carbon content.

In addition, we found that future climate had a positive effect on the biomass of *Silene*; however, this positive effect was only evident in ungrazed plots as plants were completely eaten when not protected by fencing. Finding that herbivores can modulate plant responses to climate change is in line with previous studies from tundra which identified grazing as a key factor mitigating climate warming effects on plant growth (Olofsson *et al.* 2009; Kaarlejärvi, Eskelinen & Olofsson 2013). In particular, grazers have been found to limit the establishment of warm-adapted species (Kaarlejärvi, Eskelinen & Olofsson 2013; Eskelinen, Kaarlejärvi & Olofsson 2017), prevent upward shifts of treeline (Speed *et al.* 2010) and buffer diversity loss under warmer climate (Klein et al. 2004, Post & Pedersen 2008, Kaarlejärvi et al. 2017). Overall, these findings provide evidence that the effect of grazing can have stronger implications on individual plant and plant community performance than climate warming. To date, these previous studies are from high latitude or high elevation systems. Our results extend the important role of herbivores as climate response modulators to temperate grasslands. Our findings are especially important as natural grazing systems in temperate grasslands (e.g. in Central Germany) are in decline while climate change effects are increasing (Harrison *et al.* 2018).

Grazing had the strongest effect on *Silene* in our study. This finding is in line with previous research showing that grazers have strong short- and long-term effects on individual plant traits and performance (Eskelinen 2008; Kaarlejärvi, Eskelinen & Olofsson 2013; Kafle, Wurst & Dam 2018; Jessen *et al.* 2020; Lang *et al.* 2020). Reduced height and biomass are a direct consequence of plants being eaten. Smaller SLA, which under long-term grazing can be an adaptation to reduce the grazing risk (Firn *et al.* 2017), in this context results from short-

term, high intensity grazing. Grazed individuals sprouted leaves with smaller SLA and higher relative N content than leaves of intact plants within the fences. The addition of light and nutrients did not help plants to recover from grazing, suggesting that highly palatable plants to grazers, such as *Silene* (Marten, Sheaffer & Wyse 1987; Wolfe 2002), suffer from grazing regardless of resource supply and may not be able to compensate for the lost biomass at least during the same growing season. In our study, plants were harvested two months after the last grazing, which should have given some time to compensate. As a result, heavily grazed systems may lose species that are attractive to herbivores, especially if they do not enter the reproductive phase (Eskelinen & Oksanen 2006), as found in our study with only one flowering *Silene* individual in grazed plots.

In addition, we found that *Silene* individuals increased in height and biomass and their foliar C:N decreased in response to fertilization. These findings align with other studies investigating the effects of fertilization on individual plant performance and traits (Siebenkäs, Schumacher & Roscher 2015; Tatarko & Knops 2018). In contrast to C:N, SLA was unresponsive to fertilization. Our result is in line with Siefert and Ritchie (2016), who found that the responsiveness of SLA to nutrient addition decreases with plant height, and argue that tall-statured species are less adapted to shady conditions and therefore can be less plastic in their leaf traits (Rozendaal, Hurtado & Poorter 2006). This can explain why the SLA of *Silene*, which is a rather tall species, did not increase in fertilized plots.

In conclusion, our study highlights the role of light limitation on growth allocation of individual plants in highly competitive (i.e., densely vegetated) environments. Although we only studied one species, *Silene* is representative of a common and palatable grassland forb, and may therefore provide insights in the dynamics of similar species in grassland communities. Our study also provides evidence that future climate is likely to boost plant growth, but only if plants are not exposed to grazing. and therefore emphasizes the important role of grazers as modulators of plant performance under future climate This knowledge is particularly important in an era of rapidly advancing climate change and concurrent decline in natural grazing systems, not only at high latitudes but also at temperate latitudes (Harrison et al., 2018), and ideally can support grassland management that incorporates grazing measures.

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SUPPLEMENTARY INFORMATION CHAPTER IV

Table S1. Information on replicates per measured parameter and treatment combination. The maximum number of replicates per treatment combination is five, however, in EF/EFL the maximum number is six because two plots were accidentally fertilized for two subsequent growing seasons and since then additional considered as fertilized plots.

Climate	Treatment	Height	Biomass	SLA	Foliar C:N
Ambient	Control (C)	5	5	4	5
	Fenced (E)	4	4	3	4
	Fertilized (F)	5	5	3	3
	Lighted (L)	5	5	2	3
	EF	6	6	3	6
	EL	4	4	3	4
	FL	5	5	1	2
	EFL	6	6	5	6
Future	Control (C)	5	5	0	1
	Fenced (E)	4	4	4	4
	Fertilized (F)	5	5	3	4
	Lighted (L)	5	5	1	3
	EF	6	6	6	6
	EL	4	4	3	4
	FL	5	5	3	4
	EFL	4	6	5	6
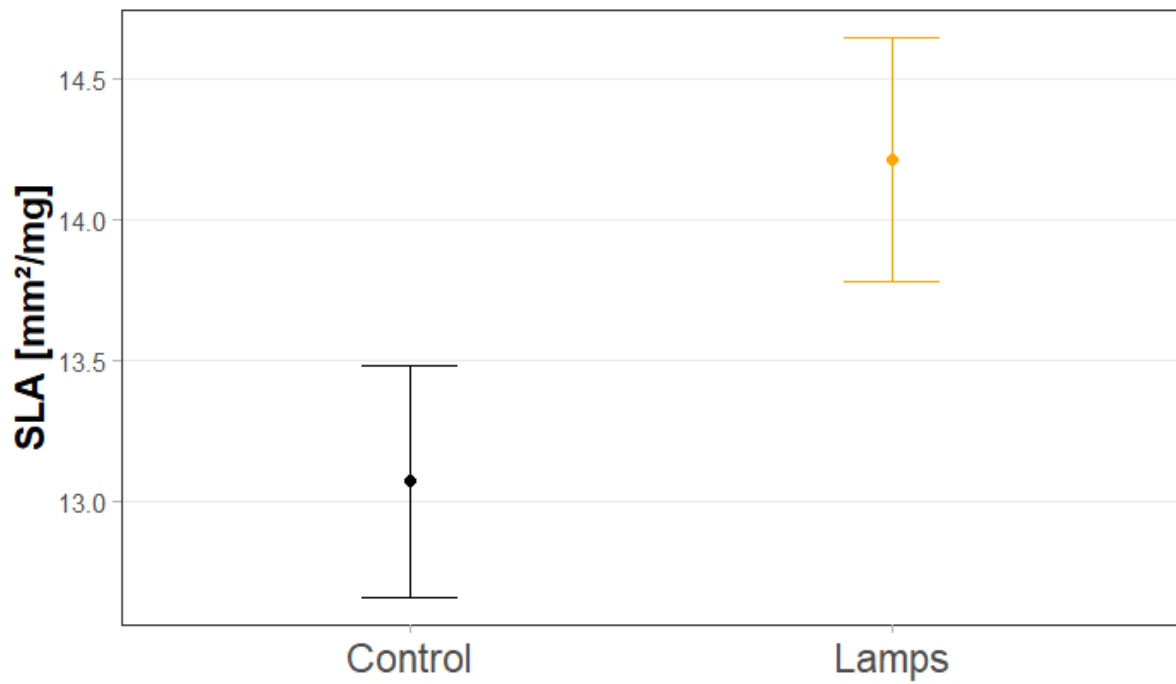
Figure S1. SLA under control and lighted conditions. The data are means ± SE from the leaves collected inside the fences.
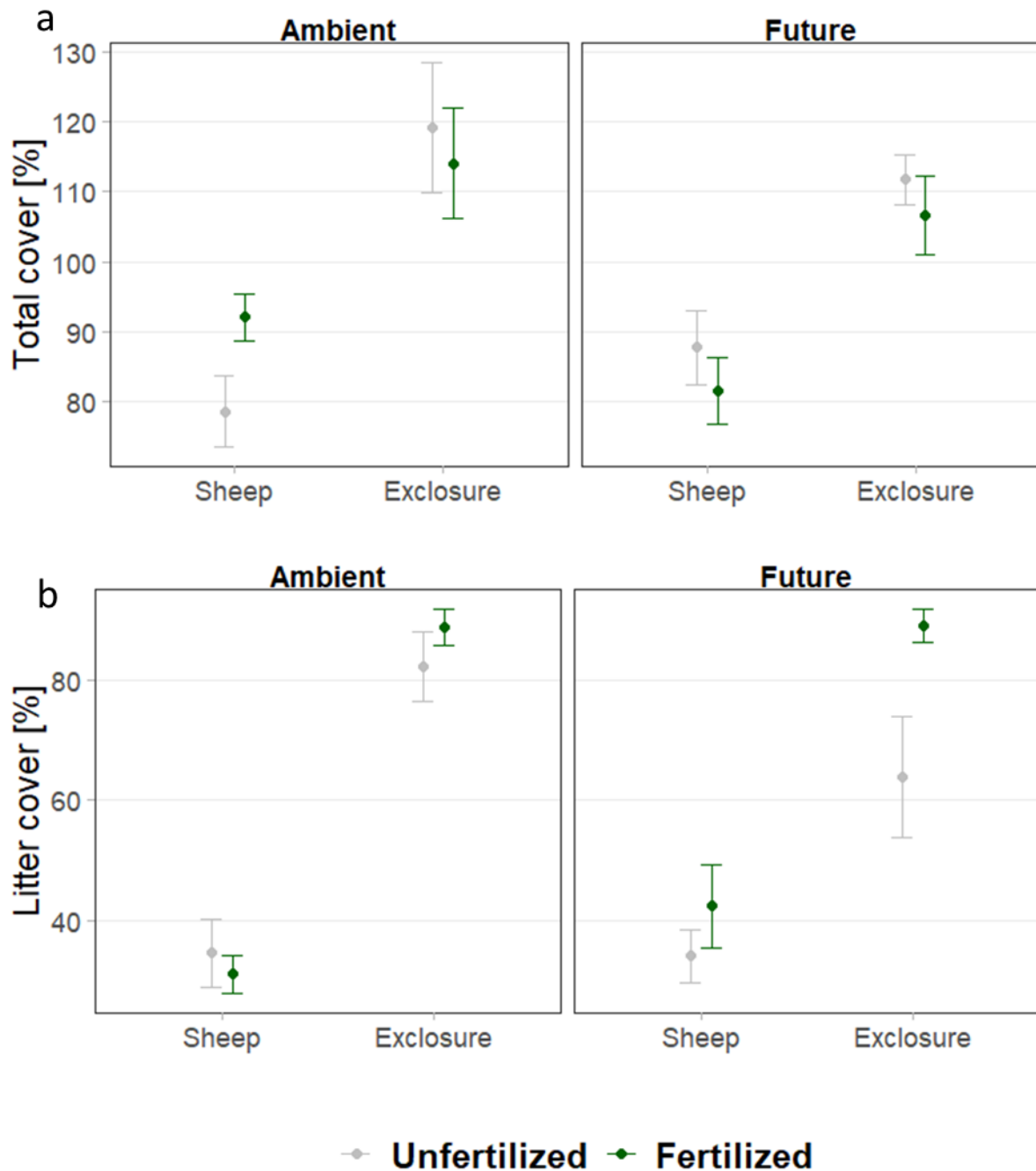
Figure S2. (a) Percent total vegetation cover and (b) percent litter cover in grazed (sheep) and ungrazed (exclosure), unfertilized and fertilized plots under ambient and future climate conditions. Data are mean ± SE. Total vegetation cover and litter cover were assessed by visual estimation on the experimental plots in June 2020.
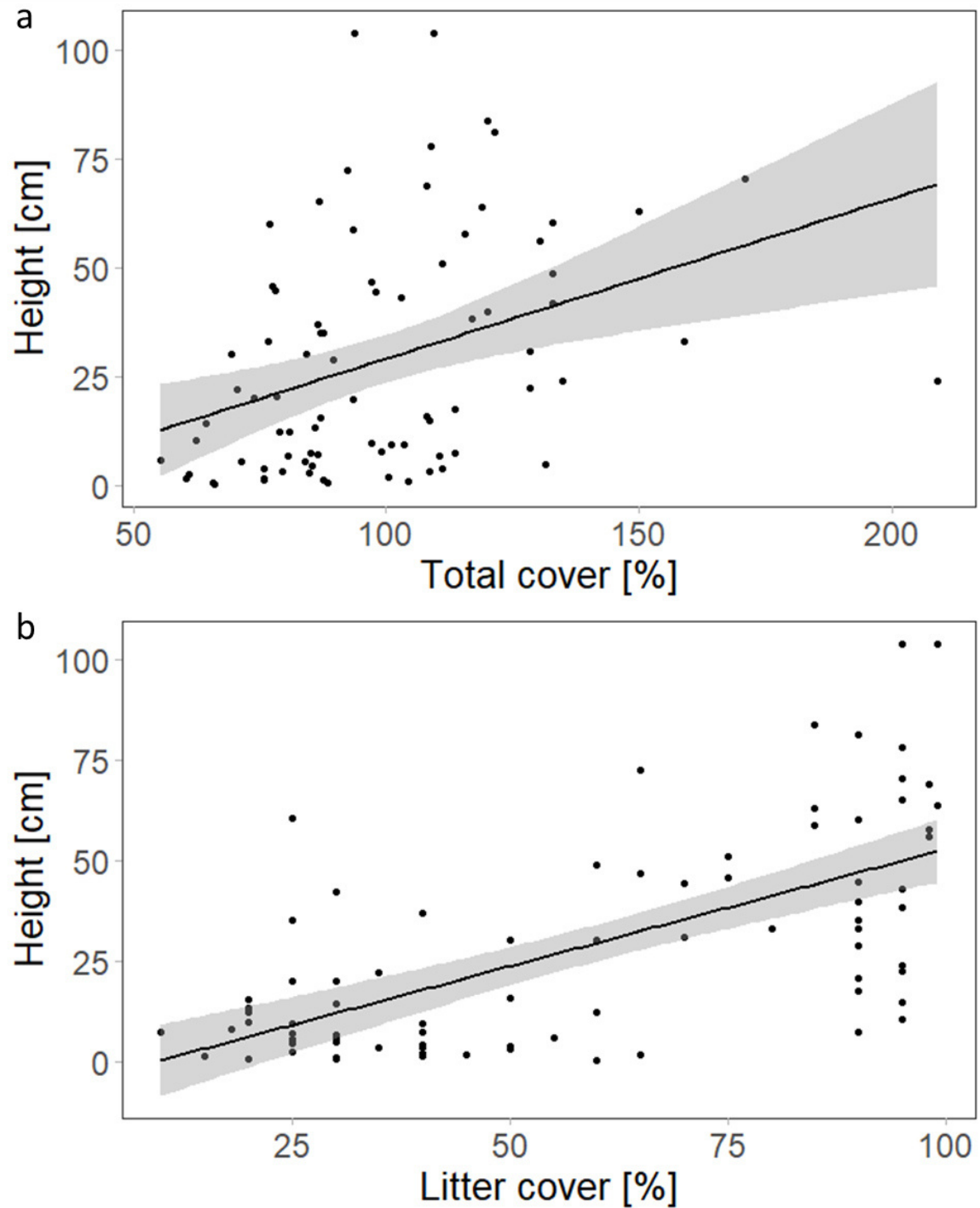
Figure S3. Regression of the visually estimated (a) total vegetation cover and *Silene* height and (b) litter cover and *Silene* height. The line represents a regression line with a 95% CI. The regressions are significant (a) $F_{1,74} = 7.58$, $P = 0.007$ (b) $F_{1,56} = 21.74$, $P < 0.001$.
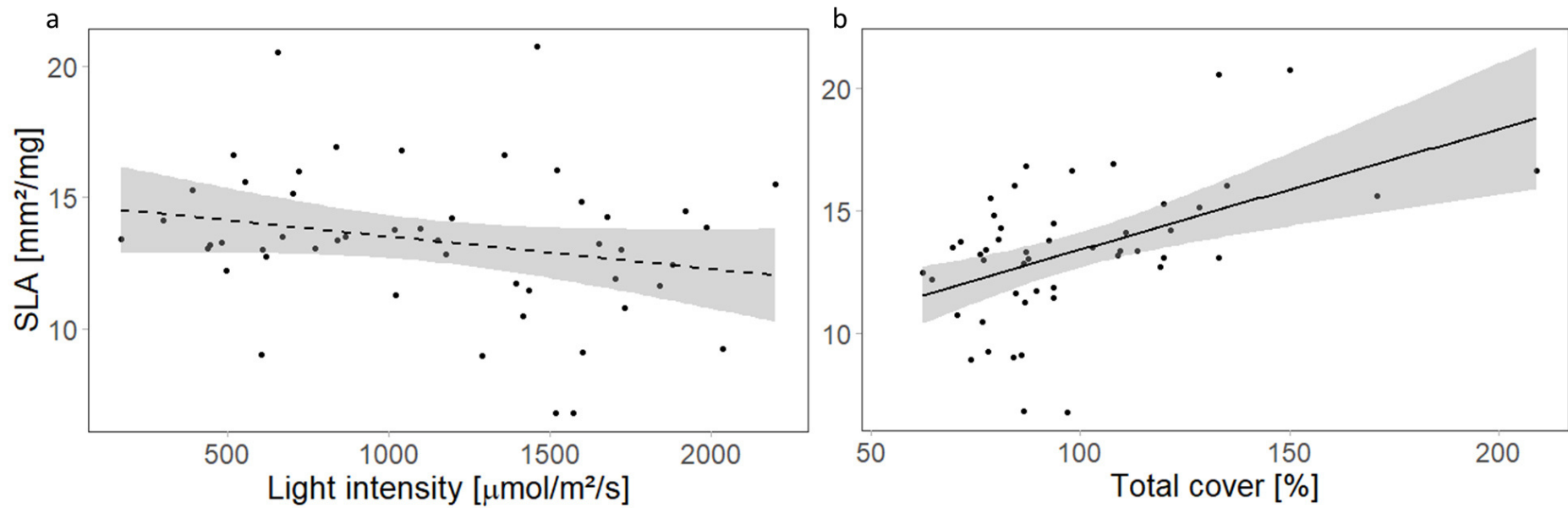
Figure S4. Regression of (a) the measured light intensity close to the ground and *Silene* SLA and (b) the visually estimated percentage litter cover and *Silene* SLA. The lines represent regression lines with a 95% CI. The dashed regression line is not significant ($F_{1,29} = 0.38$, $P = 0.544$), the solid regression line is significant ($F_{1,44} = 13.67$, $P < 0.001$).

CHAPTER V - SYNTHESIS

In this thesis, I studied the interactive effects of nutrient enrichment, grazing by mammalian herbivores and climate change on trait-based plant performance, recruitment success and phytometer responses, to gain an understanding of how these can translate into altered community composition and diversity. In particular, I investigated the role of light limitation as a mechanism explaining plant performance and community diversity responses to environmental change.

SUMMARY OF THE RESULTS

In the study described in **chapter II** I examined intraspecific trait manifestation as a long-term response to the combined influence of nutrient enrichment, herbivory exclusion and climate warming and related these trait changes to changes in relative plant abundance at the community level. First, I found that herbivores strongly controlled intraspecific trait responses *per se*, but also shaped trait responses to nutrient enrichment and warming. The latter pattern was especially strong at the species-specific level. Second, I found that changes in intraspecific trait values translated into changes in performance (i.e. relative abundance) and this was again contingent on the presence of herbivores.

In **chapter III** I teased apart the effect of litter accumulation and light limitation for early seedling recruitment combined with nutrient enrichment and exclusion of herbivory. I found that litter accumulation in general had a negative effect on both seedling number and richness unrelated to herbivory removal and fertilization. Light addition had no effect on recruitment, not even when litter was removed. But, I found a negative effect of fertilization decreasing recruitment, although this effect was marginal compared to the strong effect of litter removal.

In the research for **chapter IV** I looked at performance and trait responses of phytometer plants (*Silene latifolia*) to short-term impacts of experimental resource additions (light and nutrients) combined with herbivory exclusion and climate change (i.e. warming and seasonal precipitation changes). The phytometer grew taller under fertilized and future climate conditions in unlighted plots. Furthermore, climate change increased phytometer biomass, but only in fenced plots. In general, herbivory had a

strong negative effect on plant biomass and traits that could not be reversed by additional resources.

DISCUSSION

Nutrient enrichment, changes in grazing patterns and progressing climate change impact increasingly on grassland plant communities, but have been little explored from an interactive and also mechanistic perspective. In particular, the related mechanism of light limitation has never been investigated in the field by directly reducing light limitation by non-destructive and active light addition.

In the research for two of three chapters I found evidence that the abiotic and biotic factors considered in this thesis interactively affected the respective response variables. The most prevalent interactions were between herbivores and nutrient enrichment and herbivores and climate change. Besides these interactions, herbivory itself was the strongest factor driving plant trait and performance responses. Furthermore, I found strong evidence for litter accumulation as a mechanism driving early recruitment and diversity, opposed to light deficiency. However, competition for light explained height responses under densely vegetated conditions in adult *Silene latifolia* individuals.

Herbivores as modulators of plant traits, early recruitment and phytometer responses to nutrient enrichment and climate change

Herbivores shifted intraspecific trait responses towards smaller plants with small SLA and high foliar C:N (**chapter II**). This indicates that grazing is an important factor driving long-term (here nine years) trait responses and selects for plant characteristics that reduce the risk of being grazed (Evju *et al.* 2009). Similar results of intraspecific trait responses to grazing have been found on the local (Whitworth-Hulse *et al.* 2016) and global scale (Firn *et al.* 2019b). However, more importantly, herbivores also counteracted positive effects of fertilization and climate warming on species-specific intraspecific trait manifestation (**chapter II**). While intraspecific trait plasticity can be, *per se*, an important mechanism allowing plants to persist under novel conditions (Nicotra *et al.* 2010; Liancourt *et al.* 2015), these results show that herbivores have to be taken into account when assessing intraspecific trait responses to global change

drivers such as nutrient enrichment and climate warming. Herbivores have already been recognized as a key factor counteracting trait-based species loss in response to warming and fertilization (Kaarlejärvi, Eskelinen & Olofsson 2017), preventing warm-adapted species from invading tundra (Kaarlejärvi, Eskelinen & Olofsson 2013; Eskelinen, Kaarlejärvi & Olofsson 2017) and antagonizing warming-induced decline in species richness, shrub encroachment and biomass accumulation (Klein, Harte & Zhao 2004; Post & Pedersen 2008; Olofsson *et al.* 2009). The finding that herbivore-modulated trait responses of individual plants to global change drivers translated to plant performance on the community level (measured as relative abundance, **chapter II**) highlights that herbivores are important for the trait-based community assembly and in consequence community composition and diversity.

I also found that mammalian herbivores controlled plant biomass responses to future climate in a temperate system (**chapter IV**). Plants attained greater biomass in future climate conditions but only when they were protected from grazing. This is in line with the findings of the above-mentioned studies from tundra ecosystems and therefore extends the importance of mammalian grazers modulating the impact of climate change on plant communities to lower latitude systems.

Plant biomass and traits in **chapter IV** showed strong negative responses to the immediate net effect of grazing regardless of resource addition. The short-term herbivory led to there being almost no flowering individuals based on the phytometers sampled. In context with the results discussed in the previous paragraphs, this shows the context-dependent ambiguity of grazing: It can control influences of global change drivers on plant performance and traits, but at the same time it may also prevent mostly tall statured and highly palatable plants from reaching the reproductive stage as also found by Eskelinen and Oksanen (2006). This can potentially reduce local recruitment and change community composition. In particular, for grazer management decisions, it can therefore be important to be aware of the different effects of grazing on single plants and plant communities to be able to define a clear purpose for grazers in a managed system.

Concerning recruitment, **chapter III** revealed that herbivores had no main effect on early recruitment and diversity, neither did they interact with nutrient enrichment. Instead I found that litter accumulation controls recruitment, as discussed later in this

discussion. However, since grazing was the strongest driver of both vegetation and litter cover in the experimental plots (see Figure 1 in Chapter III) it essentially has the same effect as litter removal and was thus probably masked in the statistical analysis. This means that even though I did not find statistical support for an effect of grazing, it probably still facilitated recruitment via its effect on litter as shown by previous studies (Wilsey & Polley 2003; Eskelinen & Virtanen 2005; Wilsey & Martin 2015).

The role of light limitation for early recruitment and adult plants

According to the long-standing theory of the negative productivity-diversity relationship under high productivity (Grime 1973) and the 'resource-ratio hypothesis' (Tilman 1985), fertilized communities should be strongly light limited in the vegetation understory, which can explain diversity loss (Borer *et al.* 2014b; DeMalach, Zaady & Kadmon 2017b). My direct test of vegetation induced light limitation on early recruitment and diversity showed that light limitation was not the main mechanism explaining reduced recruitment emergence in the field. Instead, seedling recruitment was suppressed by litter accumulation (**chapter III**). Light addition also did not benefit recruitment when litter was removed, additionally indicating that light availability does not control diversity during the early recruitment phase. This result was also backed up by the finding that there was no relationship between seedling number or richness and light intensity measured at seedling level. To the best of my knowledge there are no other studies which directly test the role of light limitation during the seedling phase by adding light via additional illumination in the field. Still, this may suggests that mechanisms driving community diversity may differ between plant life stages, because light limitation has previously been found to explain diversity of adult plants (Hautier, Niklaus & Hector 2009). Hence, competition for light is certainly an ecologically relevant mechanism explaining diversity responses but its importance probably depends on the community life stage in question.

Studying the *Silene latifolia* responses to light addition in combination with nutrient enrichment, herbivory exclusion and climate change **(chapter IV)**, I found that plants grew tallest in fertilized plots under future climate conditions without additional illumination. This indicates that the combination of nutrient enrichment and altered climate created light limited conditions which the phytometer responded to by increasing in height. When light was added to these plots, and was therefore no longer

limiting, plants did not invest in taller growth. This response is indicative of the strategy of shade avoidance, which is typical for rather tall statured species (Gruntman *et al.* 2017).

Chapter IV had the caveat that I completely lost the second (small statured) phytometer, because of severe mice and vole disturbance. The second species was originally planted to explicitly compare the importance of light limitation in the full-factorial experimental setting between species of different stature. *Silene latifolia*, even though tall statured, can however also be light limited in densely vegetated conditions as shown here or also, in particular, prior to full maturity during the phase of establishment (i.e. as an older seedling or juvenile plant). To reinforce my findings, a follow-up study should ideally also look at small-statured species. Furthermore, studies on the role of light limitation could also cover the entire range of plant life stages and could, for example, link the importance of light limitation to the probability of recruitment into the next age class.

Litter accumulation controlling early recruitment

In **chapter III** I have shown litter accumulation strongly reduced seedling number and diversity. The findings discussed in the previous paragraph suggest that the mechanism by which litter hampers recruitment may not be light reduction. However, the experiment was not designed explicitly to examine the mechanisms by which litter drives seedling recruitment. Measurements of abiotic variables including light intensity at the ground, soil moisture and soil and air temperature were not associated with increased seedling number or richness. Therefore, I suggest that recruitment was reduced because of the physical barrier of litter, as proposed by Foster and Gross (1998) and Jensen and Meyer (2001). This means that the litter cover could have trapped the seeds added and prevented germination (Rotundo & Aguiar 2005; Ruprecht, Szabó & Collins 2012) or that germinated seedlings were not able to penetrate the dense litter layer and died. The latter could potentially be related to both seed and seedling traits since it is, for example, known that larger seeds support larger seedlings which could more easily break through the litter layer (Jensen & Gutekunst 2003). However, I did not find a seed size-dependent relationship for recruitment under litter (data not shown). Other than physical effects, litter could also have chemically inhibited recruitment (Facelli & Pickett 1991; Hovstad & Ohlson 2007; Bonanomi *et al.*

2011), provided shelter for seed and seedling consuming herbivores (Hulme 1996; Edwards & Crawley 1999; Fraser & Madson 2008) or supported pathogens (Veen *et al.* 2019). Regardless of the mechanism explaining the detrimental effect of litter accumulation on recruitment, my findings clearly highlight that litter is an obstacle for community diversity based on recruitment from seeds. In addition to earlier studies which arrived at the same conclusion (Foster & Gross 1998; Jensen & Meyer 2001; Wilsey & Polley 2003; Xiong *et al.* 2003). I can however add from a mechanistic perspective, that light limitation is not an explanation here. This knowledge could be considered, for example, in restoration projects using seed addition (Johnson *et al.* 2018). I did not find that the effect of litter was increased by fertilization or exclusion of herbivores, but herbivory exclusion increased litter biomass and therefore still indirectly influenced seedling recruitment.

Synergistic effects of global changes on plant and community responses?

Concurrent abiotic and biotic changes can potentially affect plants and plant communities synergistically and thus have a stronger effect in combination than singly. Experimental proof for such synergistic effects on plant communities already exist (Komatsu *et al.* 2019). In this thesis, I have found evidence for a synergistic effect of nutrient enrichment and climate change in terms of plant height in a Central European grassland system (**chapter IV**). In the Northern European system few of the studied plant species synergistically responded to an interaction of nutrient enrichment and climate warming with changes in leaf traits (**chapter II**). However, in both studies herbivores strongly controlled the effects of nutrient enrichment and climate change, therefore possibly preventing any stronger synergistic effects. Thus, as discussed earlier, a central message of this study is the antagonistic effect of herbivory in mitigating the effects of abiotic changes on plant traits influencing plant coexistence and community patterns.

Conclusion and Future Perspectives

In conclusion, this thesis highlights that current and ongoing abiotic and biotic changes interact to affect individual plants and plant communities. Furthermore, my results show that herbivores can dampen effects of both nutrient enrichment and climate change on plant intraspecific traits and biomass accumulation and, therefore,

markedly influence plant competitive abilities, performance, and, as a result, coexistence and community composition. While such findings are already known to some extent from high-latitude ecosystems, my results extend the importance of mammalian herbivores as climate change modulators to temperate systems. This information shows that grazer management, beyond economic considerations, is also of great ecological importance (Bakker & Svenning 2018), not only in terms of landscape conservation preventing natural succession (Middleton 2013), but also to dampen or counteract anthropogenically driven changes in the environment.

On a mechanistic level, I have been able to show that litter accumulation rather than light limitation drove early seedling success and thus diversity in the early recruitment phase. To evaluate when light limitation starts acting as the main constraint on seedling recruitment, more research using light addition experiments is needed. This research could follow the different recruitment phases in a plant's life cycle and connect these to light-related performance measures. One key aspect could be information about seedling traits (Larson & Funk 2016; Larson *et al.* 2020) from the early to the juvenile phase to explain species-specific performance in relation to light limitation. Since it is logistically, technically and economically difficult to implement multiple and globally distributed field-based light addition experiments using LED lamps, it would be interesting and of great value for the scientific community to explore alternative methods of non-destructive and minimally confounding light addition possibilities in the field. This could lead to an experiment replicated at several sites with different abiotic conditions and different species pools, allowing the investigation of how community responses change along environmental gradients and disentangling general from context-dependent responses.

In general, the role of competition for light as a mechanism structuring communities and their diversity under nutrient enrichment and future climate could also be studied in the context of rising CO_2 levels, extreme weather events such as droughts during different seasons or changes in invertebrate or small rodent populations. Mice and vole herbivory has been a strong disturbance factor in the experimental plots located in Bad Lauchstädt, Germany, which clearly affected vegetation structure and thus light availability in the community due to movement and consumption patterns. Given that the population dynamics of small mammals depend

on food availability (i.e. community productivity) and climate conditions (Cardenas *et al.* 2021), there may be interesting interactions to explore.

Another finding from this research is that I was able to corroborate the recognition of the importance of intraspecific trait change (e.g. Moran, Hartig & Bell 2016; Des Roches *et al.* 2018; Donelson *et al.* 2018) as a possibility for plants to cope with and persist under multiple and interacting global changes. While experimental observations and thus data on intraspecific trait variation increase, it is still little incorporated into ecological modelling, but could clearly allow for more robust models of species distributions and community compositions under interacting global changes. Such improved models could have implications for restoration, conservation and overall ecosystem management planning (Zakharova, Meyer & Seifan 2019). Furthermore, the role of intraspecific trait variation is not yet well studied in terms of ecosystem functions and services which are an important link between ecological processes and the human perspective on ecosystems.

In summary, my research has shown that biotic and abiotic environmental changes can interactively affect plant functional traits and performance and that dead plants or plant parts can have an important detrimental legacy effect on early seedling recruitment. All these findings add important knowledge to the scientific community, but as always can be reinforced and extended with follow-up studies.

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APPENDICES

CURRICULUM VITAE

Personal Information

Name: Maria-Theresa Jessen

Email: maria-theresa.jessen(at)idiv.de

Education

2017 – present	**PhD student,** Department of Community Ecology/Physiological Diversity at Helmholtz Centre for Environmental Research (UFZ)/German Centre for Integrative Biodiversity Research (iDiv)- Halle, Jena, Leipzig
	Research topic: Can competition for light explain diversity loss under herbivory exclusion and fertilization?
	Main supervisor: Assoc. Prof. Dr. Anu Eskelinen
	Co-Supervisor: Dr. Harald Auge, Prof. Dr. Stan Harpole, Asst. Prof. Dr. Yann Hautier
2015 – 2017	**Master of Science Ecology**, Umeå University, Sweden
	Thesis title: Effects of climate warming on the performance of three boreal tree seedling species in interaction with moss cover and fire history
	Supervisor: Assoc. Prof. Dr. Ellen Dorrepaal
2011 – 2015	**Bachelor of Science International Forest Ecosystem Management**, University of Sustainable Development Eberswalde, Germany
	Thesis title: Dendrologische Untersuchungen an *Pinus sylvestris*, *Pinus nigra* und *Fagus sylvatica* in Bezug auf Trockenereignisse
	Supervisor: Prof. Dr. Harald Schill

PUBLICATIONS AND CONFERENCE CONTRIBUTIONS

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Jessen, M.T., Kaarlejärvi, E. & Eskelinen, A. (2019): Competition for light in the land of the midnight sun – Grazing strongly impacts on intraspecific trait variation. Oikos Finland Meeting, Oulu, 05/02 – 06/02/2019 (Poster)

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EIGENSTÄNDIGKEITSERKLÄRUNG

Hiermit erkläre ich, dass ich die vorliegende Doktorarbeit mit dem Titel „Interactions among herbivory, nutrient enrichment and climate change as drivers of plant traits, performance and community diversity" 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.

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