Herbivory, predation and pest control in the context of climate and land use

Herbivorie, Prädation und Schädlingskontrolle im Kontext von Klima und Landnutzung

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Ute Fricke

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“Just don't give up trying to do what you really want to do. Where there is love and inspiration, I don't think you can go wrong.”

Ella Fitzgerald

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Summary

Chapter 1 – General introduction

Anthropogenic land-use and climate change are the major drivers of the global biodiversity loss. Yet, biodiversity is essential for human well-being, as we depend on the availability of potable water, sufficient food and further benefits obtained from nature. Each species makes a somewhat unique contribution to these ecosystem services. Furthermore, species tolerate environmental stressors, such as climate change, differently. Thus, biodiversity is both the "engine" and the "insurance" for human well-being in a changing climate. Here, I investigate the effects of temperature and land use on herbivory (Chapter 2), predation (Chapter 3) and pest control (Chapter 4), and at the same time identify features of habitats (e.g. plant richness, proximity to different habitat types) and landscapes (e.g. landscape diversity, proportion of oilseed rape area) as potential management targets in an adaptation strategy to climate change. Finally, I discuss the similarities and differences between factors influencing herbivory, predation and pest control, while placing the observations in the context of climate change as a multifaceted phenomenon, and highlighting starting points for sustainable insect pest management (Chapter 5).

Chapter 2 – Plant richness, land use and temperature differently shape invertebrate leaf-chewing herbivory on major plant functional groups

Invertebrate herbivores are temperature-sensitive. Rising temperatures increase their metabolic rates and thus their demand for carbon-rich relative to protein-rich resources, which can lead to changes in the diets of generalist herbivores. Here, we quantified leaf-area loss to chewing invertebrates among three plant functional groups (legumes, non-leguminous forbs and grasses), which largely differ in C:N (carbon:nitrogen) ratio. This reseach was conducted along spatial temperature and land-use gradients in open herbaceous vegetation adjacent to different habitat types (forest, grassland, arable field, settlement). Herbivory largely differed among plant functional groups and was higher on legumes than forbs and grasses, except in open areas in forests. There, herbivory was similar among plant functional groups and on legumes lower than in grasslands. Also the presence of many plant families lowered herbivory on legumes. This suggests that open areas in forests and diverse vegetation provide certain protection against leaf damage to some plant families (e.g. legumes). This could be used as part of a conservation strategy for protected species. Overall, the effects of the dominant habitat type in the vicinity and diverse vegetation outweighed those of temperature and large-scale land use (e.g. grassland proportion, landscape diversity) on herbivory of legumes, forbs and grasses at the present time.

Chapter 3 – Landscape diversity and local temperature, but not climate, affect arthropod predation among habitat types

Herbivorous insects underlie top-down regulation by arthropod predators. Thereby, predation rates depend on predator community composition and behaviour, which is shaped by temperature, plant richness and land use. How the interaction of these factors affects the regulatory performance of predators was unknown. Therefore, we assessed arthropod predation rates on artificial caterpillars along temperature, and land-use gradients. On plots with low local mean temperature (≤ 7°C) often not a single caterpillar was attacked, which may be due to the temperature-dependent inactivity of arthropods. However, multi-annual mean temperature, plant richness and the dominant habitat type in the vicinity did not substantially affect arthropod predation rates. Highest arthropod predation rates were observed in diverse landscapes (2-km scale) independently of the locally dominanting habitat type. As landscape diversity, but not multi-annual mean temperature, affected arthropod predation rates, the diversification of landscapes may also support top-down regulation of herbivores independent of moderate increases of multi-annual mean temperature in the near future.

Chapter 4 – Pest control and yield of winter oilseed rape depend on spatiotemporal crop-cover dynamics and flowering onset: implications for global warming

Winter oilseed rape is an important oilseed crop in Europe, yet its seed yield is diminished through pests such as the pollen beetle and stem weevils. Damage from pollen beetles depends on pest abundances, but also on the timing of infestation relative to crop development as the bud stage is particularly vulnerable. The development of both oilseed rape and pollen beetles is temperature-dependent, while temperature effects on pest abundances are yet unknown, which brings opportunities and dangers to oilseed rape cropping under increased temperatures. We obtained measures of winter oilseed rape (flowering time, seed yield) and two of its major pests (pollen beetle, stem weevils) for the first time along both land-use and temperature gradients. Infestation with stem weevils was not influenced by any temperature or land-use aspect considered, and natural pest regulation of pollen beetles in terms of parasitism rates of pollen beetle larvae was low (< 30%), except on three out of 29 plots. Nonetheless, we could identify conditions favouring low pollen beetle abundances per plant and high seed yields. Low pollen beetle densities were favoured by a constant oilseed rape area relative to the preceding year (5-km scale), whereas a strong reduction in area (> 40%) caused high pest densities (concentration effect). This occurred more frequently in warmer regions, due to drought around sowing, which contributed to increased pollen beetle numbers in those regions. Yet, in warmer regions, oilseed rape flowered early, which possibly led to partial escape from pollen beetle infestation in the most vulnerable bud stage. This is also suggested by higher seed yields of early flowering oilseed rape fields, but not per se at higher

temperatures. Thus, early flowering (e.g. cultivar selection) and the interannual coordination of oilseed rape area offer opportunities for environmental-friendly pollen beetle management.

Chapter 5 – General discussion

Anthropogenic land-use and climate change are major threats to biodiversity, and consequently to ecosystem functions, although I could show that ecosystem functions such as herbivory and predation barely responded to temperature along a spatial gradient at present time. Yet, it is important to keep several points in mind: (i) The high rate of climate warming likely reduces the time that species will have to adapt to temperature in the future; (ii) Beyond mean temperatures, many aspects of climate will change; (iii) The compensation of biodiversity loss through functional redundancy in arthropod communities may be depleted at some point; (iv) Measures of ecosystem functions are limited by methodological filters, so that changes may be captured incompletely. Although much uncertainty of the effects of climate and land-use change on ecosystem functions remains, actions to halt biodiversity loss and to interfere with natural processes in an environmentally friendly way, e.g. reduction of herbivory on crops, are urgently needed. With this thesis, I contribute options to the environment-friendly regulation of herbivory, which are at least to some extent climate resilient, and at the same time make a contribution to halt biodiversity loss. Yet, more research and a transformation process is needed to make human action more sustainable. In terms of crop protection, this means that the most common method of treating pests with fast-acting pesticides is not necessarily the most sustainable. To realize sustainable strategies, collective efforts will be needed targeted at crop damage prevention through reducing pest populations and densities in the medium to long term. The sooner we transform human action from environmentally damaging to biodiversity promoting, the higher is our insurance asset that secures human well-being under a changing climate.

Zusammenfassung

Kapitel 1 – Allgemeine Einleitung

Intensive Landnutzung und Klimawandel sind die Hauptursachen des globalen Rückgangs der biologischen Vielfalt. Diese ist jedoch wichtig für das menschliche Wohlergehen, da wir von der Verfügbarkeit von trinkbarem Wasser, Nahrungsmitteln und weiteren Leistungen der Natur abhängig sind. Dazu leistet jede Art einen gewissermaßen einzigartigen Beitrag. Darüber hinaus kommen verschiedene Arten unterschiedlich gut mit umweltbedingten Stressfaktoren wie z.B. dem Klimawandel aus. Dadurch ist die biologische Vielfalt sowohl der "Motor" als auch die "Versicherung" für das menschliche Wohlergehen in einem sich verändernden Klima. Hier untersuche ich die Auswirkungen von Temperatur und Landnutzung auf Pflanzenfraß („Herbivorie", Kapitel 2), Räuber-Beute-Beziehungen („Prädation", Kapitel 3) und die Regulation von Schädlingen im Raps (Kapitel 4), und betrachte gleichzeitig Merkmale von Lebensräumen (z.B. Reichtum an Pflanzenarten und -familien, Nähe zu unterschiedlichen Lebensraumtypen) und Landschaften (z.B. Vielfältigkeit der Landschaft, Anteil der Rapsanbaufläche) als mögliche Ansatzpunkte für Anpassungsstrategien an den Klimawandel. Abschließend erörtere ich die Gemeinsamkeiten und Unterschiede der Faktoren, die Herbivorie, Prädation und Schädlingskontrolle beeinflussen, ordne diese in den Kontext des Klimawandels als vielseitiges Phänomen ein, und betone mögliche Ansatzpunkte für den nachhaltigen Pflanzenschutz (Kapitel 5).

Kapitel 2 – Pflanzenreichtum, Landnutzung und Temperatur beeinflussen die Schädigung verschiedener funktioneller Pflanzengruppen durch blattfressende Wirbellose unterschiedlich

Wirbellose Pflanzenfresser (z.B. Grashüpfer) sind temperaturempfindlich. Steigende Temperaturen erhöhen ihre Stoffwechselrate und damit ihren Bedarf an kohlenstoffreichen im Vergleich zu proteinreichen Ressourcen, was zu einer Ernährungsumstellung von pflanzenfressenden Generalisten führen kann. Hier erfassten wir die Blattschädigung durch kauende Wirbellose an drei funktionellen Pflanzengruppen (Leguminosen, andere krautige Pflanzen, Gräser), welche sich in ihrem C:N (Kohlenstoff:Stickstoff) Verhältnis unterscheiden. Die Erfassung führten wir entlang von räumlichen Temperatur- und Landnutzungsgradienten in offener krautiger Vegetation angrenzend an verschiedene Lebensraumtypen (Forst, Grünland, Ackerfläche, Siedlung) durch. Die Blattschädigung verschiedener funktioneller Pflanzengruppen variierte stark und war an Leguminosen höher als an krautigen Pflanzen oder Gräsern, außer auf Offenflächen im Forst. Dort waren die Blattschädigungen der funktionellen Pflanzengruppen ähnlich und die Schädigung an

Leguminosen niedriger als im Grünland. Auch das Vorhandensein vieler Pflanzenfamilien verringerte die Blattschädigung an Leguminosen. Dies legt nahe, dass Offenflächen im Forst und vielfältige Vegetation einen gewissen Schutz gegen Blattschädigung an manchen Pflanzenfamilien (z.B. Leguminoses) bieten. Dies könnte im Rahmen des Artenschutzes einen Beitrag zum Erhalt geschützter Arten leisten. Insgesamt überwogen die Auswirkungen des vorherrschenden Lebensraumtyps in der näheren Umgebung und vielfältiger Vegetation zum jetzigen Zeitpunkt den Einfluss von Temperatur und großräumiger Landnutzung (z.B. Grünlandanteil, Vielfältigkeit der Landschaft) auf die Blattschädigung an Leguminosen, krautigen Pflanzen und Gräsern.

Kapitel 3 – Vielfältige Landschaften und die lokale Temperatur, jedoch nicht das Klima, beeinflussen die Prädationsleistung von Gliederfüßern in verschiedenen Lebensräumen

Pflanzenfressende Insekten unterliegen der Top-Down-Regulation durch räuberisch-lebende Gliederfüßer. Der Beitrag, den diese zur Top-Down-Regulation leisten hängt jedoch unter anderem von der Zusammensetzung ihrer Artengemeinschaft und von ihrem Verhalten ab. Beides wird durch Temperatur, Pflanzenreichtum und Landnutzung beeinflusst. Wie sich das Zusammenspiel dieser Faktoren auf die Regulationsleistung von Räubern auswirkt war bis dato unbekannt. Deshalb untersuchten wir die Attackierung von räuberischen Gliederfüßern auf Beuteattrappen (Knetraupen) entlang von Temperatur- und Landnutzungsgradienten. Auf Studienflächen mit niedriger lokaler Mitteltemperatur (≤ 7°C) wurde oft keine einzige Knetraupe attackiert, was sich möglicherweise auf die temperatureabhängige Inaktivität von Gliederfüßern zurückführen lässt. Die Durchschnittstemperatur im mehrjährigen Mittel, das Pflanzenreichtum und der vorherrschende Lebensraumtyp hingegen zeigten keinen substanziellen Einfluss auf die Attackierung der Knetraupen durch räuberische Gliederfüßer. Am höchsten waren die Attackierungsraten in vielfältigen Landschaften (2-km Skala) unabhängig vom lokal vorherrschenden Lebensraumtyp. Da vielfältige Landschaften, nicht jedoch die Durchschnittstemperatur im mehrjährigen Mittel, die Attackierungsraten beeinflussten, können Maßnahmen zur Diversifizierung von Landschaften möglicherweise unabhängig von moderat steigenden mehrjährigen Mitteltemperaturen in naher Zukunft die Top-Down-Regulation von Pflanzenfressern begünstigen.

Kapitel 4 – Schädlingskontrolle und Ertrag im Winterraps sind von der räumlich-zeitlichen Dynamik der Rapsanbaufläche sowie vom Blühzeitpunkt abhängig: Implikationen für die globale Erwärmung

Winterraps ist eine wichtige Ölpflanze in Europa, doch die Erträge werden insbesondere durch Schädlinge wie Rapsglanzkäfer und Stängelrüssler gemindert. Die Schädigung durch den Rapsglanzkäfer ist abhängig vom Schädlingsaufkommen, aber auch vom Befallszeitpunkt in Bezug zum Entwicklungsstadium des Winterraps, wobei das Knospenstadium besonders empfindlich ist. Die Entwicklung von Raps und Rapsglanzkäfer ist temperaturabhängig, wohingegen Temperatureffekte auf Schädlingsabundanzen unbekannt sind, sodass höhere Temperaturen sowohl Chancen als auch Gefahren mitsichbringen. Wir führten Messungen an Winterrapspflanzen (Blühzeitpunkt, Samenertrag) und zwei seiner Hauptschädlinge (Rapsglanzkäfer, Stängelrüssler) erstmalig entlang von Landnutzungs- und Temperaturgradienten durch. Der Befall mit Stängelrüsslern wurde nicht von den untersuchten Temperatur- und Landschaftsparametern beeinflusst und die natürliche Schädlingskontrolle von Rapsglanzkäferlarven in Bezug auf Parasitierungsraten war mit Ausnahme von drei von 29 Standorten gering (< 30%). Nichtsdestotrotz konnten wir Bedingungen identifizieren, die niedrige Befallszahlen mit Rapsglanzkäfern und hohe Samenerträge begünstigen. Geringe Rapsglanzkäferdichten wurden durch eine konstante Rapsanbaufläche relativ zum Vorjahr (5-km Skala) begünstigt, wohingegen eine starke Reduktion in der Anbaufläche (> 40%) zu hohem Befall führte (Konzentrationseffekt). Aufgrund von Trockenheit in warmen Regionen rund um den Saattermin trat dies häufiger in warmen Regionen auf, was zu einem stärkeren Befall mit Rapsglanzkäfern in diesen Regionen beitrug. In wärmeren Regionen kam der Raps jedoch auch früher zur Blüte, was es ihm vermutlich ermöglichte, dem Rapsglanzkäferbefall im empfindlichsten Knospenstadium einigermaßen zu entgehen. Dies zeigte sich auch daran, dass eine frühe Blüte, nicht jedoch höhere Temperaturen, zu höheren Erträgen führte. Eine frühe Blüte (z.B. durch Sortenwahl) und die jahresübergreifende Koordination der Rapsanbaufläche bieten Möglichkeiten für die umweltfreundliche Schädlingskontrolle von Rapsglanzkäfern.

Kapitel 5 – Allgemeine Diskussion

Der durch den Menschen verursachte Landnutzungs- und Klimawandel stellt eine große Gefahr für die biologische Vielfalt und damit auch für die Funktionalität von Ökosystemen dar, obwohl ich zeigen konnte, dass natürliche Abläufe wie Pflanzenfraß und Räuber-Beute-Beziehungen kaum auf Temperaturunterschiede entlang eines räumlichen Gradients reagierten. Dennoch ist es wichtig mehrere Punkte zu beachten: (i) Die Rate, mit der sich die Erde erwärmt, wird Arten in Zukunft weniger Zeit lassen sich an die herschende Temperatur anzupassen; (ii) Neben der Erderwärmung werden sich viele weitere Aspekte des Klimas verändern; (iii) Die Aufrechterhaltung von

natürlichen Abläufen unter Artenverlust durch funktionale Redundanz könnte irgendwann erschöpft sein; (iv) Die Messung natürlicher Abläufe ist durch methodische Filter limitiert, sodass Änderungen unter Umständen unvollständig abgebildet werden. Obwohl Ungewissheiten bezüglich der Auswirkungen des Landnutzungs- und Klimawandels auf natürliche Abläufe bestehen bleiben, werden dringlich Maßnahmen benötigt, die zum Erhalt der biologischen Vielfalt beitragen und die es ermöglichen umweltfreundlich in natürliche Abläufe einzugreifen wie z.B. die Abmilderung von Pflanzenfraß an Kulturpflanzen. Mit dieser Doktorarbeit, zeige ich Ansatzpunkte für Maßnahmen zur umweltfreundlichen Regulation von Pflanzenfraß auf, die zumindest zu einem gewissen Grad Klima-resilient sind und zugleich einen Beitrag zur Eindämmung des Artensterbens leisten. Um das menschliche Handeln nachhaltiger zu machen, bedarf es neben weiterer Forschung eines Transformationsprozesses. Für den Pflanzenschutz bedeutet dies, dass die gängigste Methode der Schädlingsbekämpfung mit schnell wirkenden Pestiziden nicht unbedingt die nachhaltigste ist. Um nachhaltige Strategien zu realisieren werden gemeinschaftliche Bemühungen nötig sein, die sich der Vorbeugung von Schäden an Kulturpflanzen durch die mittel- bis langfristigen Reduktion von Schädlingspopulationen und -dichten widmen. Je früher wir das menschliche Handeln von umweltschädigend zu biodiversitätsfördernd umwandeln, desto größer ist unser “Versicherungswert”, der das menschliche Wohlergehen in einem sich änderndem Klima gewährleistet.

Chapter 1

General introduction

Life on Earth in transition

Billions of years ago the Earth was a barren planet. Yet over time and due to evolution, biodiversity and diverse ecosystems emerged (Cazzolla Gatti 2016). This created conditions under which the human species could establish. Rapid human population growth and inventions to overcome resource limitations made *Homo sapiens* the dominating species on Earth. Important milestones to overcome resource limitations were the agricultural, the industrial and the green revolution. The agricultural revolution denotes the transition from nomadic to sedentary life 10,000 BC, and the birth of agriculture (Barker 2006). The invention of machines, at the onset of industrial revolution, brought a radical change in the way food and goods were produced (Hudson 2009). As a consequence, the working population in the agricultural sector in Germany decreased from 62% in 1800 to 34% in 1914 (Bpb 2012), with further declines to 1.3% by 2019 (Statistisches Bundesamt 2022). Despite the decreasing labour force in the agricultural sector, food production increased rapidly, known as green revolution (Pingali 2012). This was driven by breakthroughs in crop breeding but also by increasing agricultural inputs, e.g. applying fertilizers and pesticides. The success story of the human species was complemented by advances in medicine, which strongly increased human life expectancy (Crimmins 2015). However, the rapid increase of the human population, accompanied by developments such as the conversion of land for human food production on a large scale, imposed severe threats to biodiversity, and thus to most living beings on this planet (Díaz et al. 2019; IPBES 2019; Wagner 2020).

Living beings modify their environment. These modifications can lead to conditions under which new species can establish (Cazzolla Gatti 2011). For example, herbivory can alter microclimatic conditions through modifying plant canopy (Classen et al. 2005), which potentially creates suitable conditions for some species. Yet, some modifications threaten a multitude of species (Díaz et al. 2019). This is the case when humans convert a natural forest into a crop field which gets frequently ploughed and sprayed with pesticides thereafter. This does not only reduce many niches in the three dimensional space, but also leads to frequent resets of the ecosystem, which both can contribute to species impoverishment (Cazzolla Gatti 2016). Besides, species depletion at one trophic level, e.g. when diverse vegetation is replaced by a single crop species, may trickle through the trophic cascade, as the richness of herbivorous and to a lesser extent also of predatory arthropods depends on plant richness (Schuldt et al. 2019). On top, human-associated greenhouse gas emissions cause global warming (Cook et al. 2016; IPCC 2018, 2022), which will increasingly impact biodiversity (Thomas et al. 2004; Díaz et al. 2019). Thus, both anthropogenic land-use and climate change threaten biodiversity (Díaz et al. 2019; IPBES 2019). Under current conditions, the Earth will likely lose more than 75% of its biodiversity, which means facing the 6th mass extinction in just a few centuries (Barnosky et al. 2011; Ceballos et al. 2015; Cowie et al. 2022). Biodiversity loss through human activities, from large to very small organisms such as insects (Barnosky et al. 2011; Ceballos et al. 2015; Wagner 2020), illustrates the impact humans exert upon life on Earth. However, human activities harnessed to promote biodiversity and to adapt to climate change may facilitate to halt or reverse the current declines.

When biodiversity continues to decline, this will have devastating consequences for human existence (IPBES 2019). Human well-being depends on the availability of potable water and sufficient food, as well as on clean air, and further benefits obtained from nature, known as ecosystem services (Millenium Ecosystem Assessment 2005). Many of these services from nature can be replaced by human efforts to a certain extent, e.g. through water treatment systems, fertilizers, hand pollination and pesticides. However, replacing all at a large scale, to supply 9.7 billion people by 2050 (United Nations 2019), is merely impossible. Therefore, biodiversity – and particularly of invertebrates (Wilson 1987) – is essential to the maintenance of the underlying processes such as water purification, resource provisioning and air filtration (IPBES 2019). This is because each species occupies a certain niche space and interacts with a certain set of other organisms in its environment, which makes species to some extent functionally unique (Gamfeldt and Roger 2017). The presence of multiple species results in enhanced provisioning of ecosystem functions when complementary niches are occupied, species interactions are positive and influential species are comprised (Gamfeldt and Roger 2017). The entirety of provided functions in an ecosystem, powers ecosystem processes and make up its structure (Sandhu and Wratten 2013). Thus, biodiversity and the provided ecosystem functions are the foundation of human well-being, but more importantly also of human existence, which makes the threat of a 6th mass extinction a question of both human well-being and survival.

Climate and land use – Drivers of transition

The legacy of intensive land use

At present, land-use conversion for agricultural production is the major driver of biodiversity decline in terrestrial ecosystems (Díaz et al. 2019). This is because the conversion of pristine to anthropogenic habitat reduces the local amount of semi-natural habitat, which is accompanied by an increased local extinction risk, and increases the distance between habitats of the same type, which reduces the immigration rate depending on the dispersal ability of species (MacArthur and Wilson 1963; Cazzolla Gatti 2016). Therefore, land conversion and landscape simplification in the course of agricultural intensification is accompanied by biodiversity loss (Landis 2017). Besides, pesticides are commonly applied onto crop fields, which reduces population sizes of both pests and non-target organisms (Aktar et al. 2009; Krauss et al. 2011), and contributes to biodiversity loss (Wagner 2020).

To halt biodiversity loss and to secure the supply of an increasing human population (United Nations 2019), a key challenge will be to increase agricultural production without causing environmental harm. This will require to rethink pest management as more target-specific mortality agents (e.g. dsRNA and entomopathogens), as well as biological pest control (e.g. parasitism), act more slowly than conventional chemical pesticides (Ulber et al. 2010b; Slater et al. 2011; compare: Hokkanen and Menzler-Hokkanen 2017; Willow et al. 2021a). However, the currently dominating pest management strategy focuses on the treatment of pest-infested crop plants, and thus depends on quick mortality of the pests. When pest reduction occurs outside the vulnerability window of the crop, economic benefits are likely limited within the season, yet the investment contributes to crop damage prevention in the following year. Therefore, the benefit of implementing such a pest management strategy may be small for the individual farmer, but high when farmers act collectively. A shift in thinking from pest treatment to crop damage prevention, accompanied by collective farming approaches, facilitates to move towards sustainable agriculture, which ensures both high crop yields and biodiversity.

Yet, not only agricultural land use but also urbanization leads to species declines as urbanization is also accompanied by the conversion of semi-natural habitats and the emission of pollutants (Piano et al. 2020; Wagner et al. 2021). As biodiversity is important to the provisioning and resilience of ecosystem functions under changing environments (Oliver et al. 2015; IPBES 2019), biodiversity loss due to anthropogenic land-use change, puts humanity in a challenging starting position for climate change.

Climate change – A risk or chance for biodiversity and ecosystems

Climate change alters geographic distributions, abundances and extinction rates of species with consequences for local and regional species pools and biotic interactions (Bale et al. 2002; Thomas et al. 2004; Oliver et al. 2015). Thereby, changes in temperature play a key role (Bale et al. 2002). Elevated temperatures alter nutrient requirements of insects, development times across the trophic cascade, and thus also interactions between plants, herbivores and predators (Bale et al. 2002; Rasmann and Pellissier 2015; Rosenblatt and Schmitz 2016). Plant-herbivore interactions change with rising temperatures, for example, when generalist herbivores shift their diet towards plants with higher C:N ratio to meet higher carbon demands at increased metabolic rates, but also when the plants' defences change depending on temperature (Rosenblatt and Schmitz 2016; Schmitz et al. 2016). Also consumption rates of herbivores can increase with temperature (Rosenblatt and Schmitz 2016), as well as the attack and consumption rates of their predators (Nève 1994; Honěk 1997; Rosenblatt and Schmitz 2016). Besides, temperature-dependent changes in life cycle timing can release herbivores from their natural enemies (Rosenblatt and Schmitz 2016), but may also allow a host plant to pass the stage that is most susceptible to damage before the herbivore occurs

(Williams 2010). Thus, climate change likely affects trophic interactions and thereby also ecosystem functions, such as herbivory and predation, and crop damage by pests. Yet, biodiversity-friendly land use may buffer climate change effects on ecosystem functions (Oliver et al. 2015), and perhaps, climate change may be a chance for biodiversity and ecosystems, when climate change flips the switch, which turns the dominating human behaviour from destruction into restoration of life on Earth.

Combined effects of climate and land use on biodiversity and ecosystem functions

Evidence accumulates that effects of climate and land use interactively act on biodiversity, e.g. land use can have positive, negative or neutralizing effects on climate effects and vice versa (Mantyka-Pringle et al. 2012; Santos et al. 2021). For instance, higher temperatures may amplify biodiversity loss in case of habitat destruction (Mantyka-Pringle et al. 2012). Yet, whether climate change also affects ecosystem functions depends on various mechanisms at species, community and landscape level, which can confer resilience to ecosystem functions under environmental change (reviewed in Oliver et al. 2015). Thereby, biodiversity is the ‘insurance’ for ecosystem functions (Folke et al. 1996; Yachi and Loreau 1999; Oliver et al. 2015). For instance, when there are many species with an overlap in function, which respond differently to a stressor (Biggs et al. 2020). Besides, when stressors or altered abiotic conditions lead to local extinction of a species, a diverse species pool at the landscape scale, which is well connected to the local community, ensures that the free niche space and associated functions are quickly taken on by an immigrating species (Oliver et al. 2015). These are two mechanisms through which biodiversity can modulate effects of changing environmental conditions on ecosystem functions. Conditions favouring biodiversity based on ecological and evolutionary theory are more habitat amount and more niche spaces in the habitat, e.g. three-dimensional space such as forests (MacArthur and Wilson 1963; Fahrig 2013; Cazzolla Gatti 2016). Besides, plant species richness promotes species richness of higher trophic levels, e.g. arthropod herbivores and to some extent also predators (Schuldt et al. 2019), with effects on ecosystem functions such as herbivory (Meyer et al. 2017) and predation (Griffin et al. 2013; Barnes et al. 2020). Yet, beyond species richness also community composition does play a role for ecosystem functions (Rossetti et al. 2017; Alhadidi et al. 2018). Therefore, irrespective of species richness, different community composition may also modulate temperature effects on ecosystem functions. Community compositionof arthropod predators, for instance, differs between grasslands and adjacent forests, albeit some species occur in both and disperse across the habitat border (Magura 2002; Magura et al. 2017). The population size of organisms that move between habitat patches may benefit from complementary or supplementary resources provided by diverse landscapes that comprise more different habitat types, more similar proportions of habitat types or both (Dunning et al. 1992). Thus, conditions affecting community composition may modulate temperature effects on ecosystem functions. This makes tailored habitat and landscape management a powerful tool to promote biodiversity and ecosystem functions under climate change (Mantyka-Pringle et al. 2012). Thus, it is urgent to understand the combined effects of climate and land use on biodiversity and ecosystem functions to develop adaptation strategies to climate change. This is the direction taken by the LandKlif project.

The LandKlif project

Aims

The main aims of the LandKlif project (2018-2023) are to disentangle the combined effects of climate and land use on biodiversity, ecosystem functions and related ecosystem services, and to develop viable management strategies for adaptation to climate change (https://www.landklif.biozentrum.uni-wuerzburg.de). LandKlif comprises natural and social scientists with experimental, theoretical and empirical research approaches in Bavaria, Germany (**Fig. 1A, B**). The experimental approach contained an extensive joint field campaign of collaborating universities (**Fig. 1A**), and was complemented by computer simulations on landscape elements promoting the adaptation of communities to climate change (theoretical approach) and surveys on the perception of landscapes, ecosystem services and climate change of multiple societal actors such as farmers, nature managers and citizens (empirical approach). The LandKlif project is funded by the Bavarian Ministry of Science and the Arts via the Bavarian Climate Research Network (bayklif, https://www.bayklif.de).

Study design

Within LandKlif, an innovative experimental study design was developed, which allowed to investigate the influence of climate and land use on biodiversity and ecosystem functions independently of each other on multiple spatial scales (Redlich et al. 2021). The LandKlif study design combined climate zones, landscape-scale land-use types, and a wide range of local habitat types (**Fig. 2**). Combinations of five climate zones (< 7.5 °C, 7.5–9.0 °C in 0.5 °C steps, > 9.0 °C, multi-annual mean temperature 1981–2010, 'MAT') and three regional land-use types (near-natural, agriculture and urban) were chosen from 5.8 km x 5.8 km grid cells covering Bavaria, each with four replicates (= 60 'regions'). Regional land-use types were defined as follows: > 85% land cover by near-natural vegetation and minimum 50% forest (near-natural), > 40% land cover by arable land and managed grassland (agriculture), and > 14% land cover by housing, industry and traffic infrastructure (urban; Redlich et al. 2021). In each region, plots were established in the three dominating habitat types out of four typical habitat types in the temperate region (forest, grassland, arable field, settlement). On each plot, an experimental strip of 30 m x 3 m was established on open herbaceous vegetation, such as forest glades and clearings, grazed, mown and mulched grasslands,

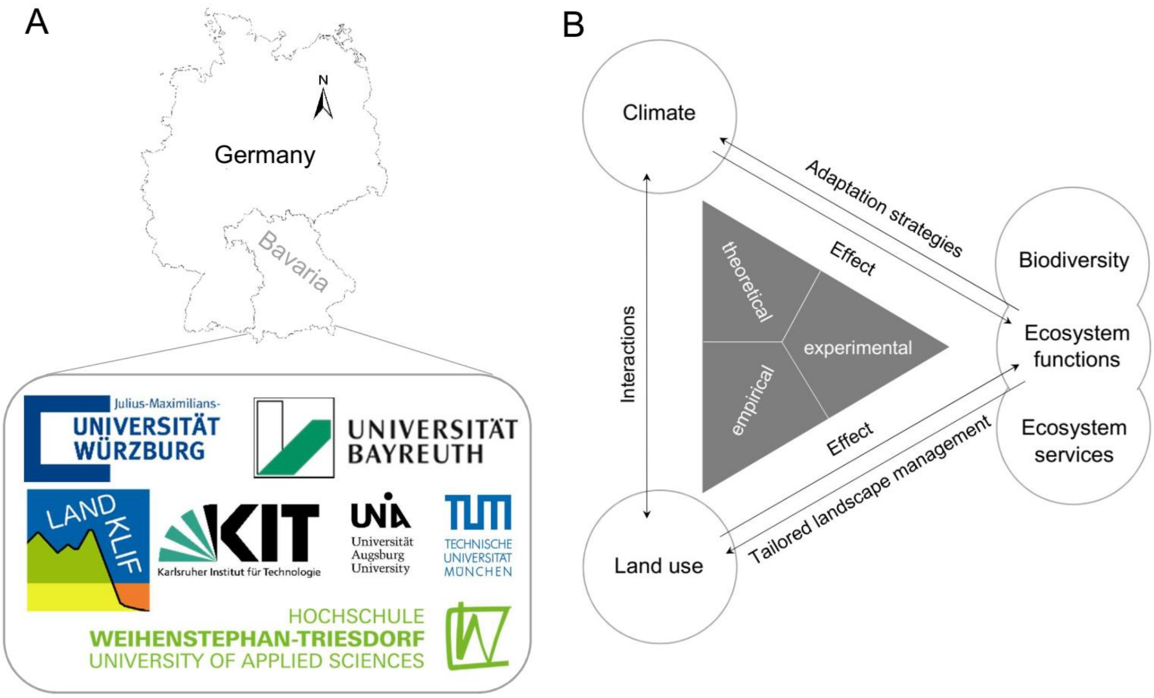

Figure 1 Overview of the LandKlif project. (A) The partner universities in Bavaria, Germany (B) conducting experimental, theoretical and empirical research to disentangle combined effects of climate and land use on biodiversity, ecosystem functions and ecosystem services, and on the perception of nature and climate change by society. From this, recommendations were derived on climate-adapted or climate-resilient management strategies to promote biodiversity and ecosystem functions.

field margins and grasslands in proximity to crop fields, and parks and meadows within settlement areas. Experimental strips were placed with at least 50 m distance to larger roads and other habitat types (e.g. between experimental strip on a field margin and forest). For the placement of agricultural plots, proximity to winter oilseed rape fields was preferred, which were used to assess ecosystem service provisioning in crop fields (pollination, pest control, crop yield production).

The LandKlif study design is based on a space-for-time approach, which was previously demonstrated to provide valuable and appropriate results of climate-change effects on biodiversity comparable to studies along the time trajectory (Blois et al. 2013). Thus, the LandKlif study design delivers results on combined climate and land-use effects in a timely manner (Redlich et al. 2021).

Field campaign

On the selected plots, an extensive joint field campaign was conducted in 2019 including biweekly visits to the plots as well as farmer surveys at the agricultural offices in whose catchment areas the plots were located (**Table 1**). Field work teams were formed collecting data on subsets of plots (**Fig. 2A**), which encompassed various measures of biodiversity (e.g. using Malaise traps, pitfall traps

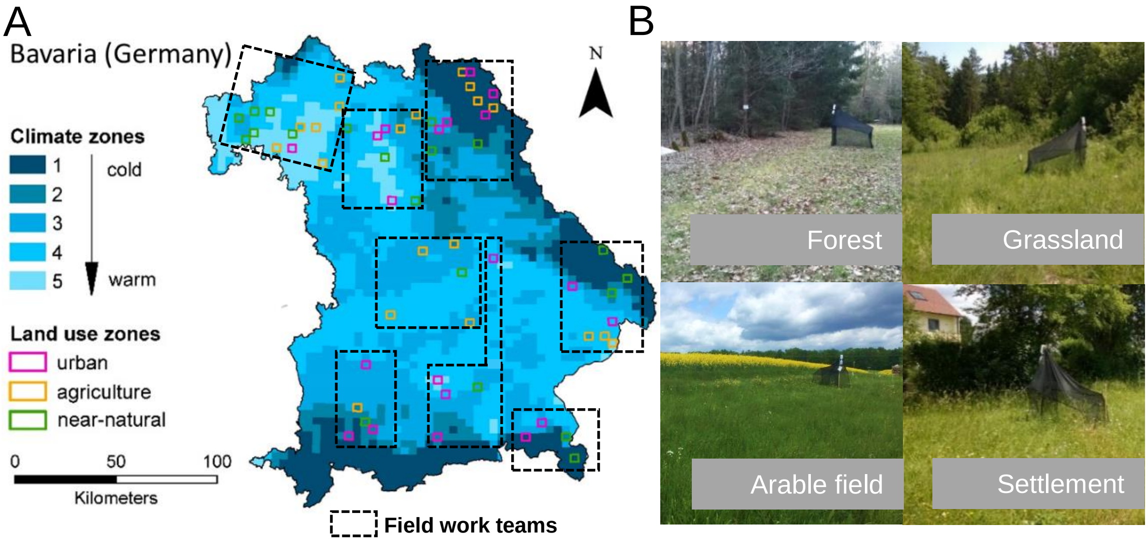

Figure 2 The LandKlif study design (A) covered 60 study regions along a climate and land-use gradient in Bavaria, Germany, indicated by coloured squares. Dashed rectangles illustrate the logistic units of field work teams. (B) In each study region, plots were established in the three dominant out of four possible habitat types (forest, grassland, arable field, settlement) as experimental strips on open herbaceous vegetation resulting in a total number of 180 plots. Map was extracted from Redlich et al. (2021) and modified: Legend position was moved from bottom to left, map was overlayed with dashed rectangles. Photo credit: LandKlif Team

and transect surveys of dung pellets), ecosystem function assessment (e.g. pollinator exclosure, decay experiments and sentinel prey), and ecosystem service assessment (e.g. proportion of parasitized pests), collated in **Table 1**. Experimental data obtained encompassed, for example, data on the biomass of flying insects, species richness of several arthropod groups, decay rates of rat carcasses and several dung types, leaf area loss to invertebrate herbivores, predation rates on sentinel prey (here: artificial caterpillars) and parasitism of pests (**Table 1**). Besides, we performed phenological observations on European Beech (*Fagus sylvatica*) and winter oilseed rape (*Brassica napus*), took soil samples and recorded local weather conditions. Plant richness and cover data were obtained by one field work team for all plots. Surveys on societal actor groups other than farmers (forester, nature manager and citizens) were conducted by the team leading this part of LandKlif research. I led the research on herbivory (Chapter 2), predation (Chapter 3) and pest control (Chapter 4) within LandKlif, which included designing experiments, providing protocols and materials, being responsible for sample processing, data analysis and manuscript writing of the respective parts within LandKlif. Regarding data collection, I shared the responsibility in the North-Western region of the study area with my colleague Cristina Ganuza (**Fig. 2A**), but supported field work teams in other regions, when needed.

Public outreach

To engage with land managers (e.g. farmers, forester), and to promote exchange on biodiversity and biodiversity-friendly management practices – which likely increase resilience of ecosystems to climate change (see Oliver et al. 2015) –, I initiated an online event for land managers involved in the LandKlif project (research on their land) and for everyone interested on the topic. Based on a short survey among some land managers (I made calls) on their interests in participating in an online event, we – a team of PhD candidates within LandKlif (Cynthia Tobisch, Jana Englmeier, Maria Hänsel, Johannes Uhler, and me) – presented results on differences in species composition across Bavaria and in different habitat types (forest, grassland, arable field and settlement). Besides, we informed about the role of different functional groups in ecosystems (e.g. pollination, pest control, decomposition) and three external speakers reported on their experiences with biodiversity-friendly management in urban green spaces, agriculture and forestry. The talks were the foundation for a lively and fruitful discussion among practitioners and between practitioners and scientists. About 25 participants joint the online event. A summary of the event is available in German (https://www.landklif.biozentrum.uni-wuerzburg.de/News/ViewNews.aspx?NewsId=24).

Table 1 Overview of data obtained on biodiversity, ecosystem functions, ecosystem services and more within the LandKlif project under indication of relevant methods and my contribution to data collection (FA = first author – led research from planning to writing of the manuscript, CA = co-author – contributed to data collection and writing of the manuscript, DC = data collection – contributed to data collection but not yet to manuscript writing).

Category	Data obtained	Field sampling/ assessment	Processing	Publication	My role
Biodiversity					
Plants[1]	• Plant richness (species and family level) • Plant cover • Vegetation biomass	• Vegetation survey • Cover estimates by Braun-Blanquet • Biomass sampling	• Expert identification • Drying and weighing vegetation samples	(Tobisch et al. under review)[2]	CA
Vertebrates	Relative abundance of roe deer	Pellet group counts along transects	Modelling	(Benjamin et al. 2022)	CA
Flying insects	• BINs (species equivalents) • Insect pollinator richness • Flying-insect biomass	Malaise traps	• DNA metabarcoding • Obtaining drained net weight	(Uhler et al. 2021; Ganuza et al. 2022) (Uphus et al., prepared)[3]	CA
Ground-active arthropods	Species richness and abundance of selected orders	Pitfall traps	Expert identification	-	DC
Microorganisms	• Estimate of microbial species richness contributing to decay processes • Microbial diversity in soils	• Microbial swabs of dung and carcasses • Soil samples	DNA sequencing	-	DC
Ecosystem functions					
Herbivory	Proportion of leaf area loss to invertebrate herbivores	Sampling and preserving leaves in books	App-based assessment of leaf area loss	(Chapter 2)	FA
Predation	Arthropod predation rates	Assessing attack marks on plasticine caterpillars	Assessing attack marks in the lab (double check)	(Chapter 3)	FA
Pollination	Proportion of seed set augmentation of wild plants through pollinator access	Pollinator exclusion using gauze bags	Seed yield assessment	-	DC
Decomposition	Decay rate of dung (bison, lynx, deer) and rat carcasses	• Decomposition of standardized dung and carcasses • Photos documenting decay stages of carcasses	• Weighing dung • Modelling decay	(Englmeier et al. 2022) (Englmeier et al., under review)[4]	CA

Table 1 (continued)

Category	Data obtained	Field sampling/ assessment	Processing	Publication	My role
Ecosystem services					
Pest control	• Pest abundances of pollen beetles and stem weevils • Parasitism of pollen beetle larvae • Bud and stem damage on winter oilseed rape plants	Sampling of winter oilseed rape plants at flowering	Assessment of pest abundances, parasitism and crop damage in the lab	(Chapter 4)	FA
Pollination	Proportion of seed set augmentation of winter oilseed rape through pollinator access	Pollinator exclusion using microperforated polypropylene bags	Seed yield assessment	-	DC
Crop yield	Winter oilseed rape yield	Sampling of winter oilseed rape plants at crop maturity	Seed yield assessment	(Chapter 4)	FA
Cultural services	Perceived value of landscapes by farmers, nature managers, citizens	Surveys		(Küchen et al., under review)[5]	CA
Phenology					
European beech	Start of the season of under- and overstory	• Estimating percentage of “budburst” and “leafout” per individual tree (weekly in situ ground observations) • Time lapse cameras	Modelling	(Uphus et al. 2021)	CA
Winter oilseed rape	Onset of flowering (field-level)	Biweekly determination of the growth stage applying to ≥ 50% of plants	Modelling	(Chapter 4)	FA
Societal perception					
	Perception by farmers, nature managers and citizens: • value of ecosystem services • climate change	Surveys		(Landwehr et al., submitted)[6] (Thiemann et al., under review)[7]	CA

[1] Data on plant richness and cover were obtained in the field by a team of botanists; [2] Tobisch et al. (under review) Plant species composition as primary determinant of terrestrial arthropod assemblages, Oecologia; [3] Uphus et al. (prepared) Spring greening variability affects insect richness and biomass on a land use and temperature gradient, Nature Ecology & Evolution; [4] Englmeier et al. (under review) Dung beetle diversity is mainly affected by land use, while community specialization is driven by climate, Ecology & Evolution; [5] Küchen et al. (under review) Where and why is landscape considered valuable? Societal actors’ perceptions of ecosystem services across Bavaria, Germany, Ecosystems and People; [6] Landwehr et al. (submitted) Climate change perceptions in Bavaria – Revealing the influence of socio-demographic and environmental factors, GAIA Master Students Award; [7] Thiemann et al. (under review) Perceptions of ecosystem services: comparing socio-cultural and environmental influences, PLOS ONE; status: 2022/05/09

Thesis in brief

This thesis presents the research I led within the LandKlif project. I aimed to increase the understanding of abiotic and biotic drivers of the ecosystem functions herbivory (Chapter 2) and predation (Chapter 3), and the related ecosystem service pest control (Chapter 4), in the context of climate and land use, and to derive adaptation strategies to global warming. I discuss management strategies to regulate herbivory, or pest abundances and crop damage, and predation under a range of temperatures (Chapters 2–4), and address potential differences between spatial temperature gradients and predicted multifaceted climate change (Chapter 5).

Chapter 2 concerns drivers of arthropod leaf-chewing herbivory on three plant functional groups (legumes, non-leguminous forbs, grasses) on open herbaceous vegetation. I investigated the effects of local temperature, multi-annual mean temperature, the dominant habitat type in the vicinity (forest, grassland, arable field, settlement), local plant richness (species and family level), and proportion of grassland area and landscape diversity (multiple scales) on herbivory among plant functional groups. Based on this, I elucidate differential effects among plant functional groups and refuges for plants from leaf-chewing herbivory, which may be used for species protection.

Chapter 3: I estimated arthropod predation rates in open herbaceous vegetation, using artificial caterpillars. I investigated the response of predation rates to short-term weather conditions (mean temperature, relative humidity), multi-annual mean temperature, local plant richness (species and family level), landscape diversity (multiple scales), dominant habitat type in the vicinity and interactive effects of habitat type with other drivers. The results enter considerations of landscape management to promote top-down control of arthropod herbivores, and possibly also of insect pests to crops.

Chapter 4 addresses pest control and seed yield of winter oilseed rape along a temperature gradient. Onset of flowering, abundances of pollen beetles and stem weevils, parasitism rates of pollen beetles, crop damage to buds and stems, and crop yield were assessed. From this, I discuss potential adaptation strategies of winter oilseed rape production to climate change, particularly with respect to the phenological (mis)alignment of crop vulnerability and pest invasion, and the reduction in oilseed rape area in years of adverse climatic conditions.

Chapter 5 conflates the findings of the previous chapters and puts them into the wider context. In particular, I elucidate similarities and differences between drivers of herbivory, predation, pest control and LandKlif results on biodiversity, discuss the findings relative to climate change as multifaceted phenomenon beyond warming, and highlight management options to regulate ecosystem functions and to promote biodiversity (e.g. sustainable pest management).

Chapter 2

Plant richness, land use and temperature differently shape invertebrate leaf-chewing herbivory on plant functional groups

Ute Fricke, Sarah Redlich, Jie Zhang, Cynthia Tobisch,
Sandra Rojas-Botero, Caryl S. Benjamin, Jana Englmeier,
Cristina Ganuza, Rebekka Riebl, Johannes Uhler, Lars Uphus,
Jörg Ewald, Johannes Kollmann, Ingolf Steffan-Dewenter

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Abstract

Higher temperatures can increase metabolic rates and carbon demands of invertebrate herbivores, which may shift leaf-chewing herbivory among plant functional groups differing in C:N (carbon:nitrogen) ratios. Biotic factors influencing herbivore species richness may modulate these temperature effects. Yet, systematic studies comparing leaf-chewing herbivory among plant functional groups in different habitats and landscapes along temperature gradients are lacking. This study was conducted on 80 plots covering large gradients of temperature, plant richness and land use in Bavaria, Germany. We investigated proportional leaf area loss by chewing invertebrates (‘herbivory’) in three plant functional groups on open herbaceous vegetation. As potential drivers, we considered local mean temperature (range: 8.4–18.8 °C), multi-annual mean temperature (range: 6.5–10.0 °C), local plant richness (species and family level, ranges: 10–51 species, 5–25 families), adjacent habitat type (forest, grassland, arable field, settlement), proportion of grassland and landscape diversity (0.2–3-km scale). We observed differential responses of leaf-chewing herbivory among plant functional groups in response to plant richness (family level only) and habitat type, but not to grassland proportion, landscape diversity and temperature – except for multi-annual mean temperature influencing herbivory on grassland plots. Three-way interactions of plant functional group, temperature and predictors of plant richness or land use did not substantially impact herbivory. We conclude that abiotic and biotic factors can assert different effects on leaf-chewing herbivory among plant functional groups. At present, effects of plant richness and habitat type outweigh effects of temperature and landscape-scale land use on herbivory among legumes, forbs and grasses.

Introduction

Anthropogenic land-use and climate change pose threats to biodiversity with consequences for ecosystem functioning (Oliver et al. 2015). An important ecosystem function, which facilitates energy flux from primary producers to higher trophic levels, is herbivory (Cebrian and Lartigue 2004; Turcotte et al. 2014). In many ecosystems, insect herbivores are among the major contributors to herbivory and play a key role in food webs and nutrient cycles (Schowalter 2016). Land-use and climate change may affect herbivory, as they shape species composition and physiology of invertebrate herbivores, but also of their interaction partners such as plants and predators (Rosenblatt and Schmitz 2016; Díaz et al. 2019; Martin et al. 2019). Yet, large-scale experimental studies on individual and interactive effects of temperature, plant richness and land-use factors on invertebrate herbivory are lacking, though important for identifying factors, which possibly buffer effects of higher temperatures on herbivory.

Invertebrate herbivory of a plant strongly depends on its nutritious quality and palatability (Loranger et al. 2012; Njovu et al. 2019), which varies substantially among plant functional groups, namely legumes, non-leguminous forbs and grasses (Scherber et al. 2006). Legumes contain more nitrogen, e.g. higher crude plant protein content and lower leaf C:N ratio, than forbs and grasses (Perez Corona et al. 1995; Leingärtner et al. 2014), whereas silica acts as feeding deterrent in grasses (Massey et al. 2006). Consequently, from legumes to non-leguminous forbs and grasses in general, a decreasing intensity of leaf-chewing herbivory intensities is observed (Scherber et al. 2006; Leingärtner et al. 2014).

At the same time, insect herbivory is also strongly affected by abiotic factors, in particular temperature (Bale et al. 2002). Elevated temperatures affect herbivores and their interaction partners, i.e. plants and predators, in multiple ways, including alterations in nutrient requirements, development time and interactions between them (Bale et al. 2002; Rasmann and Pellissier 2015; Rosenblatt and Schmitz 2016). Over time, this can lead to local extinction of species and shifts in their geographic distribution (Bale et al. 2002; Thomas et al. 2004; Rasmann and Pellissier 2015), resulting in altered plant, herbivore and predator communities in a habitat patch. As herbivores are regulated both by resource availability (bottom-up) and predators (top-down) (Barnes et al. 2020), different temperature effects at multiple levels of the trophic cascade can lead to increased, decreased or unchanged herbivory by invertebrates (Rosenblatt and Schmitz 2016), while the pattern may differ among plant functional groups with largely differing C:N ratios. For instance, when temperatures rise, the metabolic rates of invertebrate herbivores may increase and cause a shift in the diet of generalist herbivores towards plants with higher C:N ratio (Rosenblatt and Schmitz 2016; Schmitz et al. 2016), such as from legumes to grasses or non-leguminous forbs.

Thus, studying herbivory among plant functional groups may provide novel insights into the effects of temperature.

However, adverse temperature effects on ecosystem functions may be buffered in more diverse herbivore communities (Oliver et al. 2015). Herbivore richness and abundance (Ebeling et al. 2014; Schuldt et al. 2019), and possibly invertebrate herbivory (Ebeling et al. 2014; Meyer et al. 2017), are favoured by higher plant species richness. On the other hand, plant species richness can also decrease herbivory (Unsicker et al. 2006; Jactel and Brockerhoff 2007), as specialist invertebrate herbivores, which often feed within a plant genus or family (Haddad et al. 2001), are less likely to encounter their host plant and to form dense populations in more diverse patches (Root 1973). Therefore, diverse plant communities comprising more taxonomic distant species can result in a reduction of herbivory (Jactel and Brockerhoff 2007), thereby potentially counteracting processes where plant species richness increases herbivory (Dinnage 2013).

Beside plant richness characterizing the local habitat and shaping the local invertebrate community, habitat amount is relevant to sustain high species richness (MacArthur and Wilson 1963; Fahrig 2013), e.g. of invertebrate herbivores. For instance, for a herbivore community on a local patch of herbaceous vegetation, the amount of available habitat can be approximated as the proportion of managed grassland in the area. However, the accuracy of this approximation depends on the plant functional group, as grasses are more commonly present on managed grasslands than legumes. Thus, with increasing grassland proportion, herbivory may increase more strongly on grasses than legumes. This increase of invertebrate herbivore richness with larger habitat amount (MacArthur and Wilson 1963; Fahrig 2013) could modulate temperature effects on herbivory (Oliver et al. 2015).

Open herbaceous vegetation occurs as part of grasslands or adjacent to other habitats such as forests (e.g. clearing), arable fields (e.g. field margin) and settlements (e.g. parks). The habitat type adjacent to a patch of open herbaceous vegetation may affect the available amount of habitat (e.g. open herbaceous vegetation), habitat isolation as well as the herbivore community composition. For example, forests can constitute barriers to dispersal of invertebrate herbivores (Schmitt et al. 2000), which can lead to species impoverishment in small herbaceous patches embedded in forests (Rösch et al. 2013). Thus, herbivore communities may differ depending on the adjacent habitat type, which may result in differences in invertebrate herbivory, but also in the response of herbivory to temperature.

Diverse landscapes promote richness and abundance of generalist invertebrate herbivores (Jonsen and Fahrig 1997). Thereby, high landscape diversity (Shannon index) refers to the presence of more different habitat types, more similar proportions of habitat types or both. Generalist herbivores may benefit from more than one habitat type due to supplementary or complementary resource use, when moving between habitat types (Dunning et al. 1992). Thus landscape diversity may be a better approximation of habitat availability to generalist herbivores. Increases in generalist richness and abundance may increase herbivory. Therefore, diverse landscapes may indirectly modulate temperature effects on herbivory as well as increased proportions of generalists may favour temperature-induced shifts in herbivory from legumes (low C:N ratio) to grasses or forbs.

Here, we aim to disentangle the combined effects of temperature, plant richness and land use on invertebrate leaf-chewing herbivory among three plant functional groups. For this purpose, we studied herbivory on open herbaceous vegetation adjacent to typical habitat types in the temperate region (forest, grassland, arable field, and settlement) along large geographic gradients of local mean temperature, multi-annual mean temperature, plant richness at species and family level, and proportions of grassland and landscape diversity. In particular, we address the following questions:

1. How does temperature affect herbivory on three plant functional groups with largely differing C:N ratios?
2. How does plant richness and land use at multiple scales (habitat type, grassland proportion, landscape diversity) affect invertebrate herbivory among plant functional groups?
3. Do temperature and plant richness or land use interactively affect invertebrate herbivory on plant functional groups?

Materials and methods

Study area and plot selection

Research was conducted on 179 plots across Bavaria, Germany. To disentangle the combined effects of climate and land use on herbivory in three plant functional groups, we used a novel multi-scale study design which combined climate zones, regional land-use types, and a wide range of local habitat types (Redlich et al. 2021). Fifteen combinations of climate zones (multi-annual mean temperature between 1981–2010; < 7.5 °C, in 0.5 °C steps until 9 °C, > 9 °C) and regional land-use types (near-natural, agriculture and urban) were chosen from 5.8 km x 5.8 km grid cells covering Bavaria, each with four replicates (= 60 'regions'). Regional land-use types were defined by land cover: near-natural by > 85% near-natural vegetation with a minimum of 50% forest, agriculture by > 40% arable land and managed grassland, and urban by > 14% housing, industry and traffic infrastructure. In each region, plots were placed in the three dominant out of four possible habitat types (forest, grassland, arable field, settlement), and in the more contrasting habitat types if regional land cover was similarly distributed among habitat types. Additional plot selection criteria were avoiding overlap of 1-km 'buffer zones' among plots and keeping at least 50 m distance to larger roads and other habitat types (Redlich et al. 2021). Plots were established as 30 m x 3 m strips on open herbaceous vegetation, such as forest glades and clearings, grazed, mown and mulched grasslands, field margins and grasslands in proximity to crop fields, and parks and meadows within settlement areas.

Assessment of herbivory by leaf-feeding invertebrates

Aboveground invertebrate herbivory was measured in the plots once in the period from end-May until mid-June 2019 (spring season). We assessed the dominant leaf damage type, with respect to damaged leaf area proportion by invertebrates from different feeding guilds (chewer, sucker, miner, unknown) for three herbaceous plant functional groups: legumes, non-leguminous forbs (following 'forbs') and grasses (**Table S1**). Chewing leaf damage dominated across plant functional groups, supporting the importance of this study. To refer to herbivory by leaf-chewing invertebrates, we use in the following the terms 'herbivory' and 'leaf area loss' interchangeably. We quantified proportional leaf area loss to leaf-chewing invertebrates for the above mentioned three herbaceous plant functional groups. Legumes contained representatives of the plant family Fabaceae only. Forbs encompassed species of various herbaceous angiosperm families except for the plant family Fabaceae and for plant families within the order Poales. Grasses included graminoids of the plant family Poaceae and occasionally species of the Cyperaceae family. These three plant functional groups are commonly distinguished and differ largely in several traits, particularly in C:N ratio and protein content (Perez Corona et al. 1995; Leingärtner et al. 2014), and commonly differ in herbivory levels (Scherber et al. 2006; Leingärtner et al. 2014).

Per plant functional group, three plant individuals of three 'plant species' were haphazardly selected for the collection of three leaves (total of 27 plant individuals and 81 leaves per plot). This approach assured that multiple plant species were sampled within plant functional groups, but due to the large number of fieldworkers involved in this project, this was done based on morphological traits without determining individual species identity. Therefore, we use quote marks to refer to 'plant species' in the context of our herbivory assessment. The plant species list provided as supporting information (**Table S2**) was based on separate vegetation surveys, and were only available after the leaf sampling. Since no single plant species occurred across all plots, e.g. the third most frequent legume species occurred on only on 46 out of 179 plots (**Table S2**), 'plant species' assessed for leaf-chewing herbivory differed among plots. Due to the haphazard selection of 'plant species', abundant species within plant functional groups were more likely to be sampled.

From each individual plant, leaves from the apical, middle and basal nodes – in case of grasses, top, middle and bottom blade on the stem of tillers – were pinched off, mounted in a notebook with transparent tape, pressed and dried for later assessment of leaf damage. Both leaf position as selection criterion and digital assessment in the lab were chosen to minimize observer bias and also to include leaves of different ontogenetic stages that may be disproportionately affected by herbivory (Sand-Jensen et al. 1994). Leaf-chewing herbivory was higher on basal than apical, aka older than younger, leaves across plant functional groups (**Table S1**).

Proportional leaf area loss was determined using the BioLeaf app (Machado et al. 2016), which automatically transformed colour images to binary images (only black and white pixels) and calculated proportional leaf area loss based on white parts enclosed by black leaf area. Therefore, some prior image adjustments were needed: i) Nibbled leaf margins were straightened or adjusted to restore the pre-damage leaf contour with a thin black line in order to capture nibbled leaf margins as missing leaf area; and ii) overlapping leaf parts were separated with a thin white line connecting the white space to the surroundings of the leaf to not falsely be assigned as missing leaf area by the Bioleaf app. Images were adjusted using GIMP software (The GIMP Development Team 2017).

Measures of plant richness

Vegetation surveys were conducted between May and July 2019 (seven subplots on each plot, adding up to 10 m^2 total sampling area per site). Recorded plant species and families were summed up per plot to achieve plant richness at species and family level. Ferns, horsetails and woody plants as part of the herb layer were considered for total plant richness measures but not for herbivory assessment. A list of plant species and families present on plots is provided in **Table S2**.

Measures of land use at multiple spatial scales

Local similarities among plots of open herbaceous vegetation were captured by the predictor ‘habitat type’, which denotes the adjacent habitat to the plots, i.e. forest, grassland, arable field and settlement.

As landscape predictors, we considered landscape diversity and proportion of grassland at multiple scales around the centre of the plots (0.2 km, 0.5–3.0 km in 0.5-km steps; seven spatial scales). Landscape diversity was calculated as Shannon Index from detailed land-cover maps distinguishing six land-use categories: natural/semi-natural, forest, grassland, arable, urban and water (combination of ATKIS 2019, CORINE 2018 and IACS 2019; for details see **Fig. S1**). Proportion of grassland mirrors the proportion of the respective land-use category.

Measures of temperature

Local mean temperatures were derived from thermologgers (ibutton, type DS1923) attached to the north side of wooden poles, at 1.1 m above ground and roughly 0.15 m below a wooden roof, preventing direct solar radiation. We established one thermologger per plot and extracted the local mean temperature during the study-site specific 1-month period prior to leaf sampling from hourly temperature measurements.

We retrieved 30-year multi-annual mean temperatures per plot based on gridded monthly averaged mean daily air temperatures with a horizontal resolution of 1 km from 1981–2010 (Deutscher Wetterdienst 2020). This climate variable was chosen to study climate and land-use effects in a space-for-time framework (Blois et al. 2013; Redlich et al. 2021).

Data analysis

Data on proportional mean leaf area loss to chewing invertebrates were averaged per plant individual, ‘plant species’ and plant functional group for each plot to equally account for individuals and species despite missing leaves and plant individuals. Sampling of different plant species was assured due to morphological traits. As we did not intend to conduct a plant species-specific assessment of the leaf-chewing herbivory data, exact plant species identity was not determined. Averaging leaf area loss per plot was favoured over a multiple-nested random term accounting for nested sampling structure to avoid model fitting issues related to missing values and information, e.g. missing recordings of leaf position or missing leaves due to processing damage. We also excluded data from all plots of which we obtained proportional mean leaf area loss data of <10 leaves of each plant functional group prior to herbivory analysis, to cover identical predictor ranges among plant functional groups. The application of exclusion criteria resulted in data from 80 plots in 39 regions being included in the analysis.

Invertebrate leaf-chewing herbivory data were analysed with beta regression to cope with continuous proportional data (Yellareddygari et al. 2016; Douma and Weedon 2019). In preparation for beta regression, zeros were replaced with a small value (0.00001; slightly lower than the smallest value; Douma and Weedon 2019). Leaf damage by leaf-chewing invertebrates on legumes and forbs was absent on a single plot each, and was absent on grasses on two plots.

As candidate predictors, we included plant functional group, local mean temperature, multi-annual mean temperature, land use at local (habitat type) and landscape-scale (proportion of grassland area, landscape diversity; seven spatial scales in separate models), and local plant richness (species and family level). Predictor values were z-transformed prior to analysis, while the selected best models are presented with untransformed predictor variables. Ten separate models were created, each of them containing plant functional group, multi-annual mean temperature, one of the four land-use and plant-richness variables (at different spatial scales, if applicable) and all interactions up to the three-way interaction term. Separate models were preferred over one model containing all land-use and plant-richness variables to avoid over-parameterization.

The model including the three-way interaction of plant functional group, multi-annual mean temperature and habitat type indicated a trend in grassland, which was further explored using a data subset of grassland plots. This was also done for comparison with other studies, as herbivory studies are commonly conducted on grasslands. An additional model containing multi-annual mean temperature, habitat type and their interaction term, was fitted to the subset with the rest of the analysis approach being equal. For comparison, an additional model containing local mean temperature instead of multi-annual mean temperature was fitted to the grassland subset.

A nested random term for ‘plot’ in ‘region’ (three plots per region) was included to account for plant functional groups on the same plots and clustering of plots (Redlich et al. 2021). When grassland subsets were analysed only ‘plot’ was used as a random term. This nested random term was retained throughout the model selection process (Bolker et al. 2008).

The majority of maximum variance inflation factors were < 4, which falls below the commonly applied threshold for collinearity of variance inflation factor > 10 (Chatterjee and Price 1991). Variance inflation factor exceeded the threshold in some models containing interaction terms with habitat type. Additionally, a correlation matrix of continuous predictor variables was calculated (**Table S3**) and continuous predictors were plotted by habitat type (**Fig. S2**) to visually assess relationships between continuous and categorical predictor variables. Continuous predictors were not or only weakly correlated except for a strong positive correlation between plant richness at species and family level (Pearson’s $r = 0.76$, $P < 0.001$, **Table S3**). For a comparison of continuous predictor ranges among habitat types see **Fig. S2**.

Models with all possible predictor combinations were compared by the goodness of fit based on Akaike’s information criterion corrected for small sample size (AICc). The lower AICc, the better the relative goodness of model fit. Competing multivariate models with a difference of less than two ($\Delta\text{AICc} < 2$) were considered equal (Burnham and Anderson 2002), and then the more parsimonious model was chosen. Model selection of fixed effects (predictors) was done with models fitted by maximum likelihood, while the selected best model was fitted and is presented by restricted maximum likelihood (Zuur et al. 2009). Tukey posthoc analysis was used to compare herbivory between levels of categorical variables (i.e. plant functional groups, habitat types) and to correct for multiple comparisons.

To gain further insights on the relative importance (sum of Akaike weights) of the candidate predictors for herbivory of the single plant functional groups, multimodel averaging was conducted for each plant functional group separately, including plant richness either at species or family level (**Fig. S3 + text**).

Data analysis was done with R version 4.0.3 (R Core Team 2020) using the packages ‘glmmTMB’ (Brooks et al. 2017), ‘emmeans’ (Russell 2020), ‘Hmisc’ (Harrell 2020), ‘MuMin’ (Barton 2020), ‘ggeffects’ (Lüdecke 2018), ‘DHARMa’ (Hartig 2020) and ‘performance’ (Lüdecke et al. 2020).

Results

Effects of plant richness and land use on herbivory among plant functional groups

Damage by leaf-chewing invertebrates on legumes, forbs and grasses ranged between 0–83%, 0–59% and 0–19% area loss of individual leaves, respectively (**Fig. S4**). Among plant functional groups, plot-averaged leaf area loss on legumes (2.5%) was on average 2.3 times higher than on forbs (1.1%) and 5.9 times higher than on grasses (0.4%; **Fig. 1a**). This pattern was mirrored in most habitats except forests, where herbivory was similar across plant functional groups and herbivory on legumes was lower than in grassland (**Fig. 1b**). Herbivory on forbs and grasses was not substantially different among habitat types.

Invertebrate leaf-chewing herbivory did not depend on plant richness at species level (**Fig. 2a, Table S4+5**), but with increasing total numbers of plant families, herbivory on legumes decreased while herbivory on forbs and grasses increased (**Fig. 2b**). As plant richness at family level was higher in forests than in other habitat types (**Fig. S2**), the differential effects of habitat type and of family-level plant richness among plant functional groups cannot be clearly separated. However, when assessing the relative importance of all candidate predictors on leaf-chewing herbivory separately per plant functional group means multimodel averaging, and including plant richness at species and family level in separate models (**Table S3**). Habitat type was the relatively most or second most important predictor of herbivory on all three plant functional groups (**Fig. S3**). Relative importance of habitat type was especially high ($\Sigma wi \geq 0.8$) for herbivory on legumes, and on forbs and grasses only when family-level plant richness was not included. Family-level plant richness was the relatively most important predictor ($\Sigma wi = 0.7$) or second most important predictor ($\Sigma wi = 0.4$) for leaf-chewing herbivory on forbs and legumes, respectively, but not for grasses (**Fig. S3**). Thus, habitat type was relatively more important than family-level plant richness for legume herbivory, but not for herbivory on forbs. Nonetheless, the pattern of decreasing leaf-chewing herbivory on legumes towards higher plant richness at family-level seemed to persist across habitat types (**Fig. S5**), which supports a weak effect of plant richness at family level also on legumes.

At multiple spatial scales, invertebrate herbivory among plant functional groups was similar across the observed ranges of proportions of managed grassland and landscape diversity (**Table S4+5, Fig. S3**).

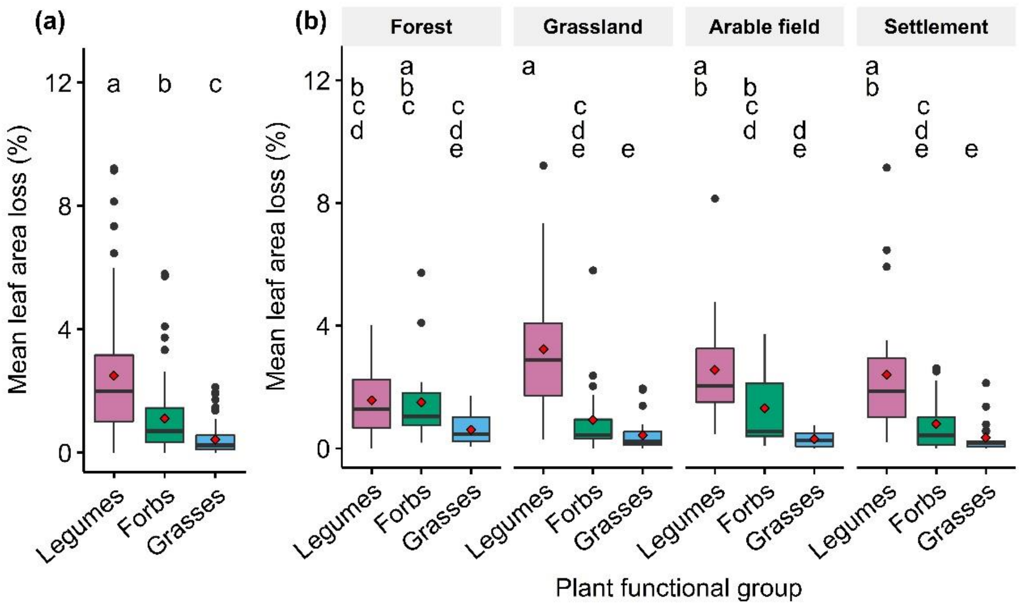

Figure 1 Effects of plant functional group (a) and interactive effects of plant functional group and habitat type (b) on mean leaf area loss to chewing invertebrates per plot. Red diamonds highlight mean values per plant functional group. Different lower case letters indicate differences between habitat types and plant functional groups evaluated by post hoc tests with Tukey correction after evaluation of the overall effects in beta regression models by ΔAICc and parsimony.

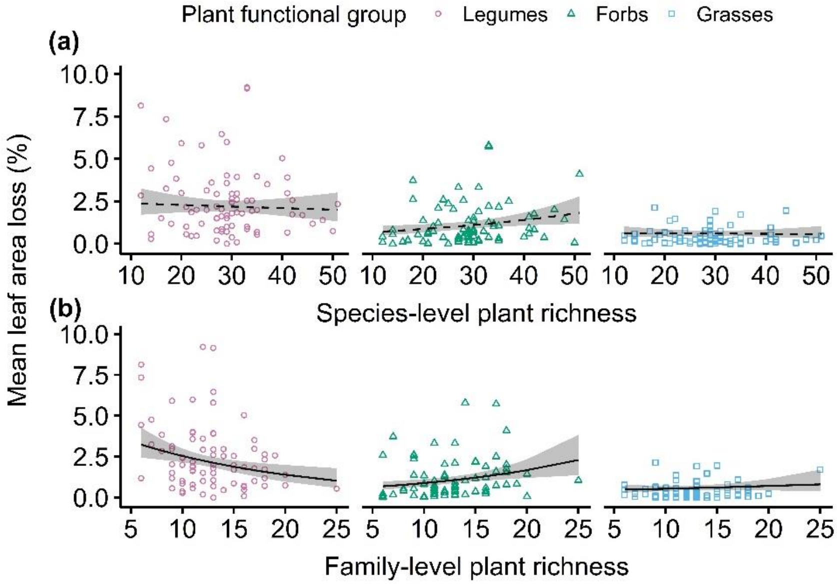

Figure 2 Interactive effects of plant richness with plant functional group (legumes: pink circles, non-leguminous forbs: green triangles: grasses: blue squares) on plot-averaged leaf area loss to chewing invertebrates. Panels show interactive effects with (a) plant richness at species level and (b) family level. Lines present predictions of full beta mixed models (solid when interaction term supported, else dashed). Grey shades indicate 95% confidence bands. Model selection was based on ΔAICc and parsimony.

Interactive effects of temperature and land use on herbivory of plant functional groups

Both local mean temperature of the 1-month period prior to leaf sampling (**Fig 3a**) and multi-annual mean temperature (**Fig 3b**) did not substantially affect mean herbivory among plant functional groups (**Table S4+5**).

Three-way interactions of plant functional group, any of the temperature variables and single land-use or plant richness predictors were not supported by ΔAICc and parsimony (**Table S4+5**). Yet in grassland plots, herbivory on legumes, forbs and grasses decreased, increased and slightly increased with higher multi-annual mean temperature, respectively (**Fig. 3c, Fig. S6, Table S6**). However, local mean temperature did not affect herbivory among plant functional groups in grassland plots (**Fig. S7, Table S6**).

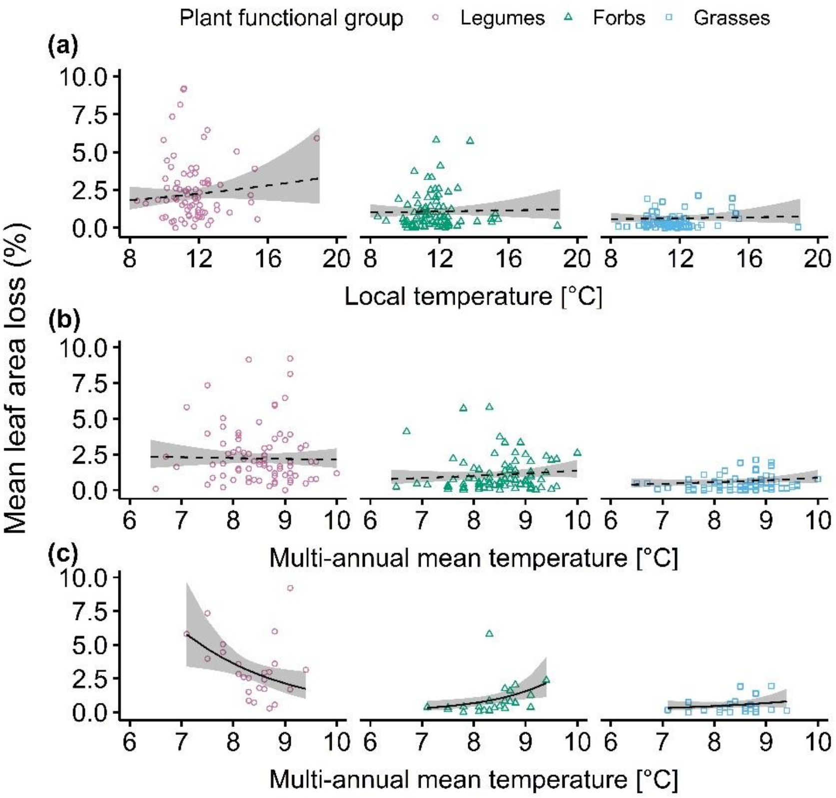

Figure 3 Interactive effects of temperature with plant functional group (legumes: pink circles, non-leguminous forbs: green triangles: grasses: blue squares). Panels show interactive effects with (a) local mean temperature (80 plots), (b) multi-annual mean temperature (80 plots) and (c) multi-annual mean temperature including grassland plots only (24 plots). Lines indicate predictions of the full beta mixed model (solid when interaction supported, else dashed) based on the complete data set (a, b) or the grassland subset (c). Model selection was done using ΔAICc and parsimony.

Discussion

We compared invertebrate leaf-chewing herbivory – the dominant type of leaf damage in our study – among three major plant functional groups across geographic gradients of plant richness, land use and temperature, and elucidated the potential of biotic conditions to modulate temperature effects on herbivory. Herbivory differed among plant functional groups, and among plant functional groups in response to local habitat types and plant richness at family level, but showed no general response to plant richness at species level, proportion of grassland, landscape diversity, local mean temperature and multi-annual mean temperature, at the studied gradients. We found a differential effect of multi-annual mean temperature among plant functional groups in grassland plots (grassland subset). In the following we discuss the presence or absence of differential temperature, plant richness and land use effects among plant functional groups, future research directions arising from our study and potential consequences of global warming on invertebrate leaf-chewing herbivory.

Plant richness at family level decreased invertebrate leaf-chewing herbivory on legumes and increased herbivory on non-leguminous forbs and (slightly on) grasses. In this study, higher family-level plant richness implies more plant families other than legumes (Fabaceae) and grasses (Poaceae), e.g. more plant families of forbs, horsetails, ferns and woody seedlings (part of the herb layer, particularly in forests). The observed pattern in herbivory suggests that invertebrate herbivores feeding on legumes are more negatively impacted by the presence of more plant families compared to more plant species, and that herbivores on legumes are more affected than those feeding on grasses. The first could result from herbivorous invertebrates often being specialized on feeding within plant families (Haddad et al. 2001), e.g. on legumes (Fabaceae), and from a reduced likelihood that a specialized herbivore will find and build-up high population densities on its host plants in diverse vegetation (Root 1973). Herbivory on grasses may respond less to plant richness compared to legumes for several reasons: i) despite the higher plant richness, the proportion of grasses in the community may have remained high, ii) grasses may be more prone to generalist rather than specialist chewing invertebrates, which depend less on plant richness (Shinohara and Yoshida 2021), and iii) proportional leaf area loss to chewing invertebrates was generally very low on grasses compared to legumes with a much larger range of leaf area losses (see also Leingärtner et al. 2014), which means that any change in herbivory on grasses results in a small effect. The increased herbivory on forbs (functional group rich in plant families) towards higher plant richness at the family level may result from an increased likelihood of palatable plant families being among the forb species on a plot and being sampled (sampling effect). Thus, albeit community-level herbivory may increase with plant species richness (Ebeling et al. 2014; Meyer et al. 2017), herbivory on individual plant families may decrease, and even more strongly with plant richness at family-level.

The proportion of grassland did not affect herbivory on any plant functional group. Larger proportions of grassland, and thus more habitat area of open herbaceous vegetation, was expected to increase herbivory, as species richness increases with increasing habitat amount (MacArthur and Wilson 1963; Fahrig 2013). The absence of an effect of grassland proportion may result from the measure of grassland proportions comprising managed grasslands, but not all landscape elements of open herbaceous vegetation (forest clearing, parks, etc.). Besides, managed grasslands harbour different herbivore communities depending on the specific management (Shinohara et al. 2019). Therefore, the habitat amount available to a herbivore community may have diverged from the measured grassland proportion. Alternative explanations are that grassland proportion may have equally benefitted herbivores and predators, which cancelled out grassland effects on herbivory, or that different herbivore communities can provide similar levels of herbivory (Rossetti et al. 2017). Although we did not observe an effect of grassland proportion on leaf-chewing herbivory, landscape elements may be relevant to herbivory, but their effect may only become visible using higher resolution maps, which better capture habitat amount (e.g. also forest clearings), and including measures on the herbivore and predator community.

Habitat type affected leaf-chewing herbivory among plant functional groups. Herbivory on legumes was lower in forests than in grasslands and intermediate in settlements and arable fields, and therefore herbivory was similarly low among plant functional groups in forests, compared to higher herbivory levels on legumes than on forbs and grasses in typical ‘open’ habitat types (grassland, arable field, settlement). The difference in herbivory on legumes between grasslands and forests cannot clearly be assigned to a single mechanism, but may result from lower habitat amount of open herbaceous vegetation in forests (Fahrig 2013), dispersal barriers constituted by forests (Schmitt et al. 2000) or both, reducing the probability of legume specialists to be present. Studies comparing herbivory on open habitat and inside forests also reported higher herbivory levels for open than forested habitats (Maron and Crone 2006; Dostálek et al. 2018). This may apply in particular to plant species or plant families that suffer from specialist herbivory and that are less prone to generalist herbivory, for example legumes (Fabaceae) compared to grasses (Poaceae). Common leaf-chewing generalist herbivores on open herbaceous vegetation are grasshoppers, which consume much more grasses than legumes (Unsicker et al. 2005). Thus, plant species of certain plant families may find refuge from invertebrate leaf-chewing herbivory in forests.

Landscape composition, here landscape diversity at various spatial scales (0.2–3.0 km), did not substantially affect invertebrate chewing herbivory among plant functional groups. Particularly generalist species benefit from diverse landscapes (Jonsen and Fahrig 1997). Thus species richness of generalist herbivores may increase with landscape diversity at the expense of specialists, as communities tend towards equilibrium (MacArthur and Wilson 1963; Cazzolla Gatti 2016). Besides, differences in landscape diversity may also go along with more or less disturbance and higher or lower species richness and size of the herbivore community. However, a small number of common generalist herbivorous invertebrate species have the potential to maintain herbivory levels provided by more diverse herbivore communities (Rossetti et al. 2017). Thus, invertebrate herbivore community composition may have changed along the landscape diversity gradient without visible changes in invertebrate leaf-chewing herbivory.

Although warmer climates are expected to increase herbivory pressure (Rasmann and Pellissier 2015), we observed neither a general increase of invertebrate leaf-chewing herbivory in response to higher local mean temperature (1-month period prior to leaf sampling) nor to higher multi-annual mean temperature covered by our study design. However, in grassland plots herbivory on legumes decreased towards warmer climates, while herbivory increased on forbs and (slightly on) grasses. Why this pattern occurs only in grasslands cannot be clearly explained, but it may originate from differences in invertebrate communities among plots in different habitat types, which is suggested by differences in richness and biomass of flying insects among habitat types (Uhler et al. 2021). Differential responses of herbivory among plant functional groups in grasslands to multi-annual temperature, but not to local mean temperature, suggest temperature effects related to the herbivore community rather than to short-termed changes in herbivore physiology. However, more research will be needed to provide further evidence on differential rates of invertebrate leaf-chewing herbivory among plant functional groups (or plant families) towards higher temperatures and to identify the underlying mechanisms. Still, this observation in grassland plots provides further – albeit weak – evidence for differential responses in invertebrate herbivory among plant functional groups and habitat types, which should be considered in future studies (e.g. studying herbivory adjacent to different habitat types), as traditionally herbivory research is much focused on grasslands.

As the majority of plot-averaged leaf area losses to leaf-chewing invertebrates fell below 4% across our large climatic temperature gradient, it is unlikely that any other temperature measure not addressed in this study, elicited strong effects on herbivory under the studied conditions. However, herbivory on individual plant species or families – other than legumes (Fabaceae) and grasses (Poacea) – was not captured in this study, but may have responded more clearly to temperature. This is likely to be particularly true for plant species or families whose defences are highly temperature-sensitive or which are damaged by highly temperature-sensitive herbivores (reviewed in Rosenblatt and Schmitz 2016). Thus, albeit herbivory at the level of plant functional groups was not (or only in grasslands) affected by temperature, we cannot exclude that single plant species – e.g. relevant from a conservationist perspective – were not affected, particularly as we did observe proportional leaf area loss of up to 83% on individual leaves. Besides, herbivore communities may have adapted to the current temperature conditions over a long period of time, potentially contributing to similar herbivory levels across the studied multi-annual mean temperature gradient, but temperature effects may become apparent when global warming maintains its current pace and further exacerbates biodiversity loss (Thomas et al. 2004; Wagner 2020). With this study, we captured the current pattern of invertebrate leaf-chewing herbivory at the level of plant functional groups in response to a large multi-annual mean temperature gradient (6–10 °C), and found no evidence – except for grasslands – that leaf-chewing herbivory would be affected by higher temperatures.

The herbivory pattern among plant functional groups observed in this study – i.e. in response to family-level plant richness and habitat type – can be best explained through differences in legume specialists between those sites. Relationships of forb herbivory with plant richness, land use and temperature were much less clear, which may result from this plant functional group comprising multiple plant families. This emphasises the relevance of studying herbivory on a taxonomic level, distinct from community-level herbivory. Our results suggest that the plant family level is suitable, e.g. as many herbivores are specialized within plant genus or family (Haddad et al. 2001). Besides, matching herbivory on a taxonomic level with measures of the herbivore community (e.g. richness and abundance of leaf-chewing herbivores feeding on a specific plant family) will likely provide valuable mechanistic insights into effects of plant richness, land use and temperature on herbivory.

Conclusion

Overall plot-averaged herbivory by leaf-chewing invertebrates was rather low (< 4% leaf area loss) and often similar across the studied geographic gradients of abiotic and biotic factors (i.e. local mean temperature, grassland proportions, landscape diversity), suggesting that largely different herbivore communities provide similar levels of herbivory at plot-level. However, invertebrate leaf-chewing herbivory among plant functional groups – particularly on single plant families (e.g. legumes) – responded differentially to plant richness at family-level, land use (i.e. habitat type) and temperature (i.e. multi-annual mean temperature in grassland plots) across large geographic gradients, which may have consequences for the competitive relationships among plant families. This suggests that herbivory assessment at taxonomic level (e.g. plant families) provides more differential insights into responses of herbivory to biotic and abiotic factors than community-level herbivory. We found no evidence that local plant richness, habitat type, grassland proportion or landscape diversity modulate sensitivity of herbivory on three plant functional groups to temperature (e.g. indirectly via herbivore community), but also little evidence of both local mean temperature and multi-annual mean temperature effects on herbivory. Thus currently, effects of local plant richness and habitat type seem to be more relevant than temperature and landscape-scale land use to variation in invertebrate leaf-chewing herbivory among three plant functional groups.

Acknowlegements

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Supplement

Figure S1 + Text: Creating the detailed land-cover map

We distinguished six land-use categories within the state of Bavaria, i.e. natural/semi-natural habitat, forest, grassland, arable, urban and water, and created a detailed land-cover map based on these categories. For this purpose, we used three different data sources (IACS 2019, CORINE 2018, ATKIS 2019) that complemented each other and provided different levels of detail, as required for additional characterization of the landscape in further analysis (i.e. ‘subcategories’, not used here). We used ATKIS to define the boundary of different land-use types, IACS and CORINE to provide additional details for further characterization. In case of overlaps of data sources and land-use layers we prioritized specific land-use categories (semi-natural > forest > grassland > arable > urban > water) and data sources (see legend **Fig. S1**) to enhance spatial resolution and details related to subcategories used for additional spatial analysis. Land-use categories were then used to calculate landscape diversity and proportion of grassland around the center of each study site.

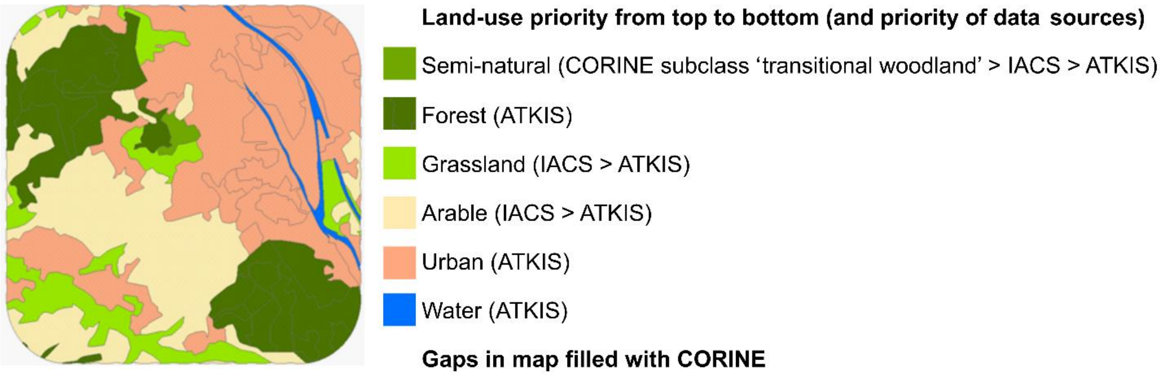

Figure S1 Creation of detailed land-cover maps based on six main land-use categories within Bavaria (semi-natural habitat, forest, grassland, arable, urban, water). The map was created by combining three different land-cover maps (ATKIS 2019, IACS 2019, CORINE 2018).

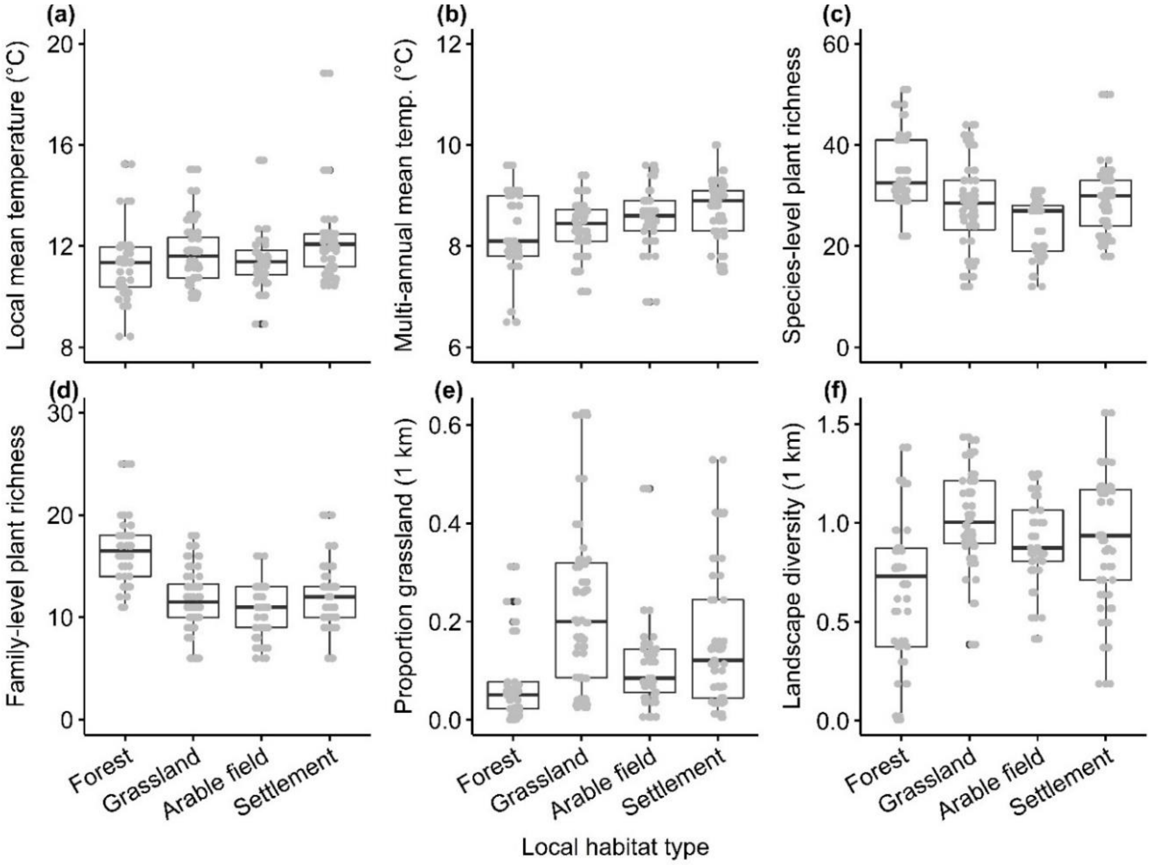

Figure S2 Visual evaluation of relationships between the categorical predictor variable (habitat type) and the continuous predictor variables used for analysis of herbivory by leaf-chewing invertebrates (80 plots). (a) Local mean temperature (1-month period prior to leaf sampling, exception: 78 plots), (b) Multi-annual mean temperature, (c) Species-level plant richness (= total plant species richness), (d) Family-level plant richness (= total plant familial richness), (e) Proportion managed grassland in 1-km surrounding, (f) Landscape diversity at 1-km scale

Figure S3 + Text: Multimodel averaging per plant functional group

Models on plot-average leaf area loss to leaf-chewing invertebrates with all possible predictor combinations at each spatial scale were created separately per plant functional group, including either plant richness at species or family level due to high correlation (Pearson's r: 0.76, **Table S3**). Only region was included as a random term, as plot-averaged data of a single plant functional group was modelled. Models with all possible predictor combinations were obtained using the dredge function in the MuMIn package (Barton 2020). Then, the sum of Akaike weights (Σwi, range: 0–low to 1–high) was calculated of each spatial scale and of each predictor at every spatial scale. This value indicates the relative importance of a spatial scale (compared to other scales) and of a predictor variable (compared to the other predictors) at a certain spatial scale, respectively (Burnham and Anderson 2002).

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Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach, 2nd edn. Springer

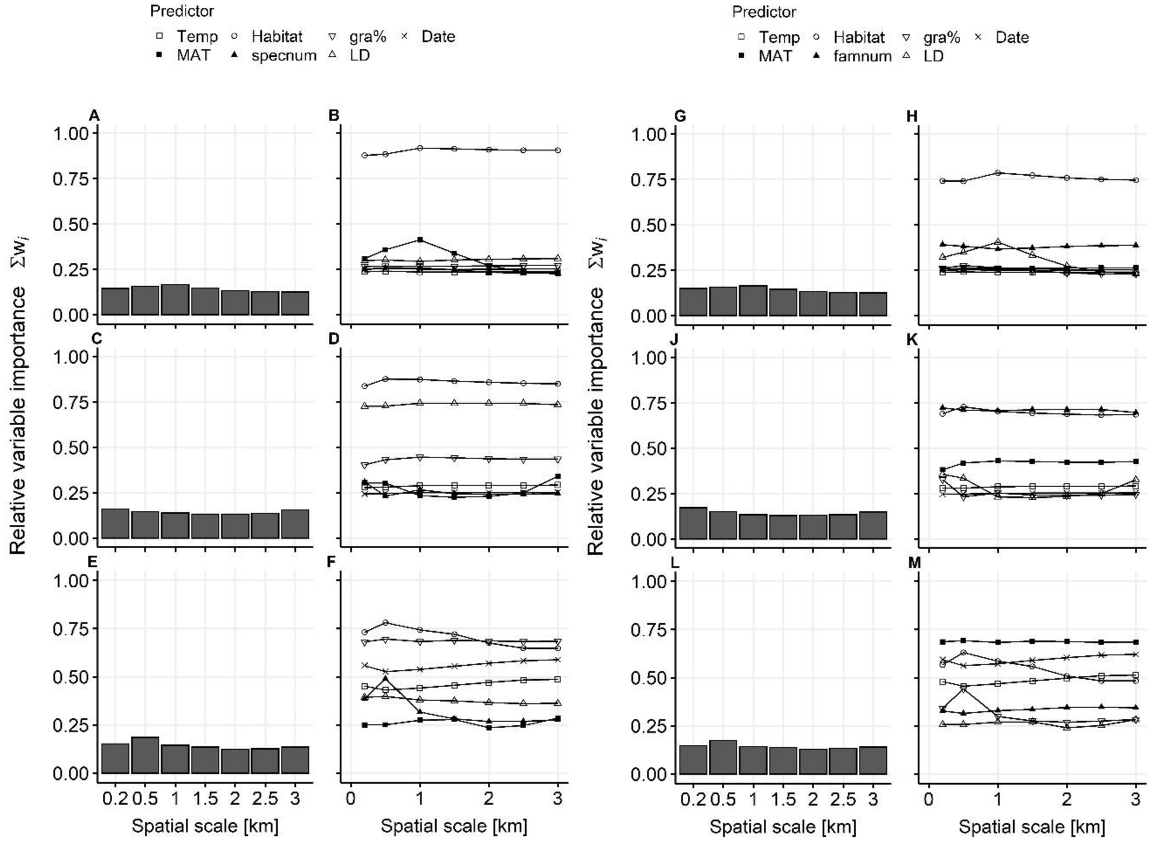

Figure S3 Effects of candidate predictors (and leaf sampling date, 'Date') on leaf-chewing herbivory among three plant functional groups (upper row: legumes, middle row: forbs, bottom row: grasses, 78 plots); Relative importance of each spatial scale (0.2–3.0 km, bar graphs) and each predictor (line graphs); Values range between zero (low) and one (high); A–F) including plant species richness ('specnum'), G–M) including plant richness at family-level ('famnum'); Temp: Local mean temperature, MAT: Multi-annual mean temperature, Habitat: Adjacent habitat type, gra%: Proportion grassland, LD: landscape diversity

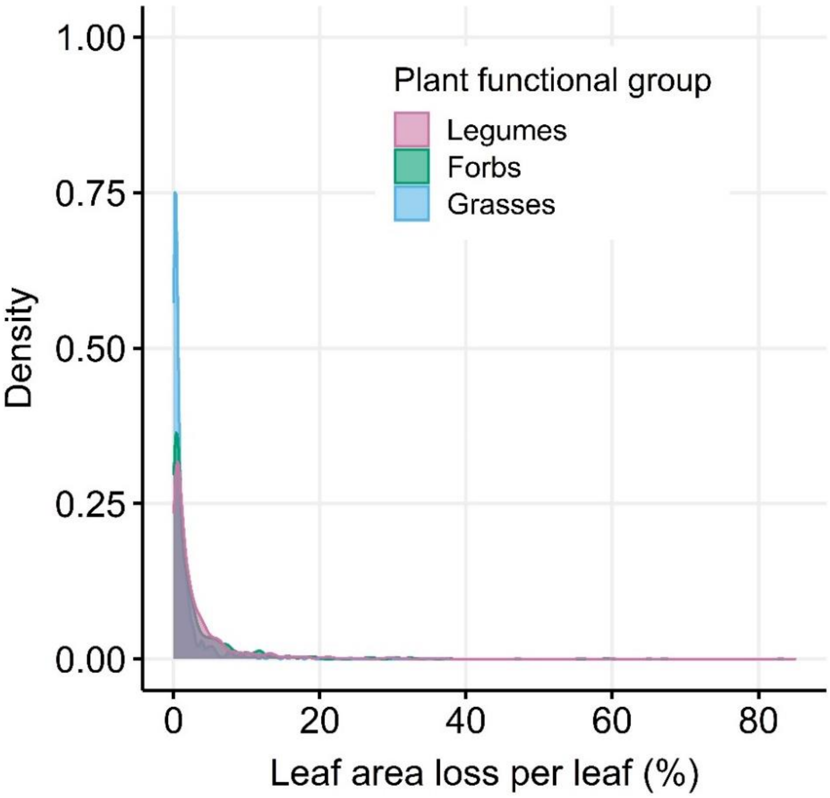

Figure S4 Density distribution of proportional leaf area loss to chewing invertebrates on individual leaves, on which damage is present (> 0%), per plant functional group (80 plots, 2737 leaves).

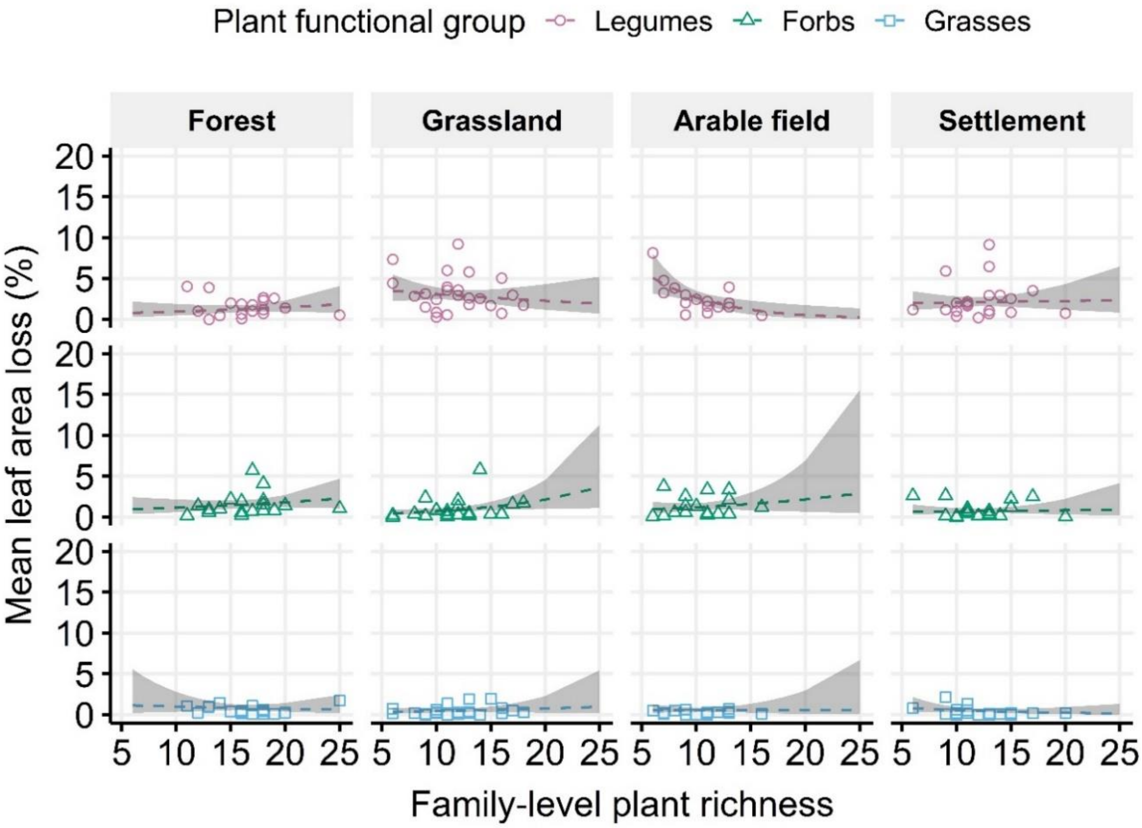

Figure S5 Interactive effects of plant richness at family-level and habitat type with plant functional group (legumes: pink circles, non-leguminous forbs: green triangles: grasses: blue squares) on plot-averaged leaf area loss to leaf-chewing invertebrates. Lines indicate predictions of the full beta mixed model based on the complete data set (80 plots). Grey shades indicate 95% confidence bands. Three-way-interaction with habitat type was not supported. Model selection was done using ΔAICc and parsimony.

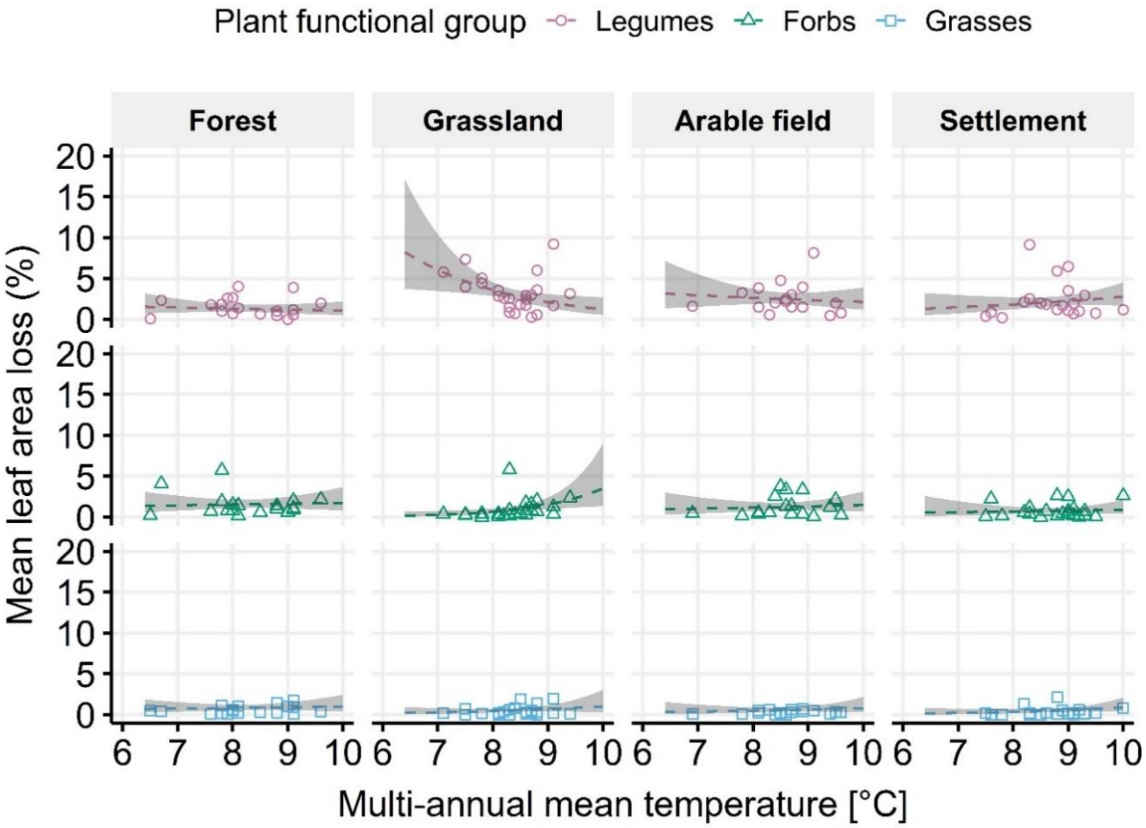

Figure S6 Interactive effects of multi-annual mean temperature and habitat type with plant functional group (legumes: pink circles, non-leguminous forbs: green triangles: grasses: blue squares) on plot-averaged leaf area loss to leaf-chewing invertebrates. Lines indicate predictions of the full beta mixed model based on the complete data set (80 plots). Grey shades indicate 95% confidence bands. Interactions of herbivory on plant functional groups with multi-annual mean temperature is only supported in grassland plots (24 plots). Model selection was done using ΔAICc and parsimony.

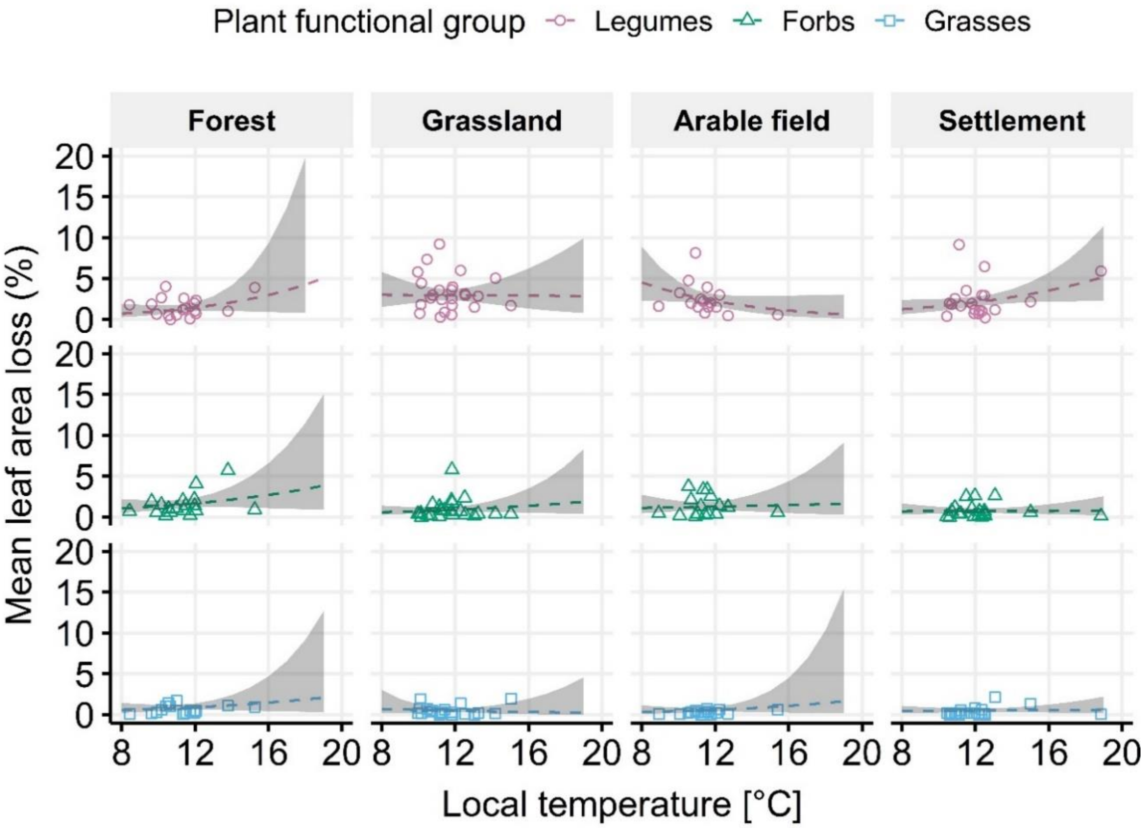

Figure S7 Interactive effects of local mean temperature and habitat type with plant functional group (legumes: pink circles, non-leguminous forbs: green triangles: grasses: blue squares) on plot-averaged leaf area loss to leaf-chewing invertebrates. Lines indicate predictions of the full beta mixed model based on the complete data set (78 plots). Grey shades indicate 95% confidence bands. Interactions with local mean temperature were not supported, also not in the grassland subset (24 plots). Model selection was done using ΔAICc and parsimony.

Table S1 + Text: Dominant invertebrate feeding guilds among plant functional groups and leaves of different age

The invertebrate feeding guild dominating leaf damage was determined for 6460 leaves on 138 plots under consideration of leaf position (estimate of leaf age) and plant functional group (**Table S1**). Chewing and mining damage, but not sucking damage, was more frequently observed on basal leaves than apical leaves, thus older than younger leaves, across plant functional groups. Among plant functional groups, chewing folivory dominated, but differed in frequency of occurrence; 69.7% of leaves from legumes were dominated by chewing folivory, whereas only 29% and 26% of leaves from non-leguminous forbs and grasses, respectively. In turn, more leaves without damage were recorded in the group ‘grasses’ (66.2%) and ‘forbs’ (58.5%) than ‘legumes’ (26.4%). Mining and sucking damage as the dominant cause of leaf damage occurred rarely (< 7%), but more frequently on forbs (mining and sucking) and grasses (sucking) than on legumes (**Table S1**).

Invertebrate chewing folivory was quantified and present (> 0%) on 4355 leaves on 167 plots (info on leaf position and dominant invertebrate feeding guild incomplete). Leaf area loss to chewing folivory on an individual leaf, when present, commonly fell below 4%, but was higher on legumes (median: 1.3%, mean: 3.4%, 3rd quantile: 3.6%, max: 82.9%) than forbs (median: 0.9%, mean: 3.1%, 3rd quantile: 3.0%, max: 59.3%) and grasses (median: 0.4%, mean: 1.4%, 3rd quantile: 1.3%, max: 36.5%).

Invertebrate chewing folivory data on all three plant functional groups (minimum 10 leaves per functional group and plot) were obtained for 80 plots, as not all plant functional groups were represented on each plot. These data were used as plot-averaged proportional leaf area loss values to address questions on differential effects of temperature, land use and plant richness on invertebrate chewing folivory – the dominant leaf damage type – among plant functional groups.

Table S1 Overview on dominant leaf damage (based on damaged leaf area) of leaves (number, percent) per plant functional group and leaf position (A: apical/top/young, M: middle/intermediate-old, B: basal/old) by invertebrate feeding guild (chewer, sucker, miner, unknown, none).

Plant functional group		**Legumes**				**Forbs**				**Grasses**			
													
Dominant invertebrate feeding guild	Leaf position	A	M	B	Σ	A	M	B	Σ	A	M	B	Σ
	Unit												
Chewer	-	333	369	374	1076	117	263	340	720	165	229	252	646
	%	63.5	74.2	74.8	70.7	14.3	32.3	41.6	29.4	19.6	27.9	30.6	26.0
Sucker	-	17	14	12	43	39	62	55	156	36	50	47	133
	%	3.2	2.8	2.4	2.8	4.8	7.6	6.7	6.4	4.3	6.1	5.7	5.3
Miner	-	0	2	2	4	15	35	41	91	2	3	7	12
	%	0.0	0.4	0.4	0.3	1.8	4.3	5.0	3.7	0.2	0.4	0.8	0.5
Unknown	-	0	2	2	4	8	9	5	22	2	11	16	29
	%	0.0	0.4	0.4	0.3	1.0	1.1	0.6	0.8	0.2	1.3	1.9	1.2
None (no damage)	-	174	110	110	394	642	445	377	1464	635	529	502	1666
	%	33.2	22.1	22.0	25.9	76.0	54.7	46.1	59.7	75.6	64.4	60.9	67.0
Σ	-	524	497	500	1521	821	814	818	2453	840	822	824	2486

Table S2 List of recorded plant species in vegetation survey and number of plots on which they occurred. Plant species list was used to derive plant richness measures (species and family level). Even though ferns, horsetails and woody plants are listed as part of the herb layer, they were not considered for herbivory assessment. No plant species occurred on all plots (= 179 plots).

Plant functional group	Family	Species	Number of plots
Forbs	Asteraceae	*Taraxacum* sect. *Ruderalia*	96
Forbs	Rubiaceae	*Galium album*	96
Forbs	Plantaginaceae	*Plantago lanceolata*	93
Forbs	Asteraceae	*Achillea millefolium* agg.	69
Forbs	Plantaginaceae	*Veronica chamaedrys*	65
Forbs	Ranunculaceae	*Ranunculus acris*	65
Forbs	Caryophyllaceae	*Cerastium holosteoides*	64
Forbs	Polygonaceae	*Rumex acetosa*	57
Forbs	Ranunculaceae	*Ranunculus repens*	56
Forbs	Urticaceae	*Urtica dioica*	50
Forbs	Lamiaceae	*Glechoma hederacea*	49
Forbs	Rosaceae	*Rubus* sect. *Rubus*	45
Forbs	Asteraceae	*Cirsium arvense*	43
Forbs	Rosaceae	*Potentilla reptans*	42
Forbs	Apiaceae	*Heracleum sphondylium*	39
Forbs	Convolvulaceae	*Convolvulus arvensis*	38
Forbs	Lamiaceae	*Ajuga reptans*	37
Forbs	Rubiaceae	*Galium aparine*	37
Forbs	Clusiaceae	*Hypericum perforatum*	36
Forbs	Rosaceae	*Rubus idaeus*	35
Forbs	Rosaceae	*Alchemilla vulgaris* agg.	34
Forbs	Caryophyllaceae	*Stellaria graminea*	33
Forbs	Lamiaceae	*Prunella vulgaris*	29
Forbs	Apiaceae	*Daucus carota*	28
Forbs	Primulaceae	*Lysimachia nummularia*	28
Forbs	Rosaceae	*Fragaria vesca*	28
Forbs	Rosaceae	*Geum urbanum*	26
Forbs	Lamiaceae	*Galeopsis tetrahit* agg.	25
Forbs	Asteraceae	*Crepis biennis*	23
Forbs	Polygonaceae	*Rumex obtusifolius*	23
Forbs	Juncaceae	*Juncus effusus*	22
Forbs	Asteraceae	*Leontodon hispidus*	21
Forbs	Asteraceae	*Centaurea jacea*	20
Forbs	Asteraceae	*Leucanthemum vulgare* agg.	20
Forbs	Campanulaceae	*Campanula patula*	18
Forbs	Dipsacaceae	*Knautia arvensis*	18
Forbs	Boraginaceae	*Myosotis arvensis*	17
Forbs	Plantaginaceae	*Veronica arvensis*	17
Forbs	Rosaceae	*Agrimonia eupatoria*	16
Forbs	Asteraceae	*Bellis perennis*	15

Forbs	Asteraceae	*Leontodon autumnalis*	15
Forbs	Rosaceae	*Sanguisorba minor*	15
Forbs	Rosaceae	*Sanguisorba officinalis*	15
Forbs	Apiaceae	*Aegopodium podagraria*	14
Forbs	Equisetaceae	*Equisetum arvense*	14
Forbs	Oxalidaceae	*Oxalis acetosella*	14
Forbs	Plantaginaceae	*Plantago major*	14
Forbs	Rubiaceae	*Galium verum*	14
Forbs	Asteraceae	*Hypochaeris radicata*	13
Forbs	Geraniaceae	*Geranium dissectum*	13
Forbs	Geraniaceae	*Geranium pratense*	13
Forbs	Apiaceae	*Pimpinella major*	12
Forbs	Juncaceae	*Luzula campestris*	12
Forbs	Onagraceae	*Epilobium angustifolium*	12
Forbs	Plantaginaceae	*Veronica officinalis*	12
Forbs	Scrophulariaceae	*Scrophularia nodosa*	12
Forbs	Violaceae	*Viola silvatica* agg.	12
Forbs	Asteraceae	*Tragopogon pratensis*	11
Forbs	Euphorbiaceae	*Euphorbia cyparissias*	11
Forbs	Orobanchaceae	*Rhinanthus minor*	11
Forbs	Plantaginaceae	*Plantago media*	11
Forbs	Polygonaceae	*Rumex crispus*	11
Forbs	Rosaceae	*Potentilla erecta*	11
Forbs	Asteraceae	*Tanacetum vulgare*	10
Forbs	Plantaginaceae	*Veronica persica*	10
Forbs	Valerianaceae	*Valerianella locusta*	10
Forbs	Caryophyllaceae	*Silene flos-cuculi*	9
Forbs	Dryopteridaceae	*Dryopteris carthusiana*	9
Forbs	Juncaceae	*Luzula multiflora*	9
Forbs	Lamiaceae	*Salvia pratensis*	9
Forbs	Violaceae	*Viola hirta*	9
Forbs	Asteraceae	*Cirsium palustre*	8
Forbs	Asteraceae	*Picris hieracioides*	8
Forbs	Asteraceae	*Tripleurospermum perforatum*	8
Forbs	Brassicaceae	*Capsella bursa-pastoris*	8
Forbs	Caryophyllaceae	*Stellaria holostea*	8
Forbs	Geraniaceae	*Geranium robertianum*	8
Forbs	Rosaceae	*Potentilla anserina*	8
Forbs	Asteraceae	*Erigeron annuus*	7
Forbs	Campanulaceae	*Campanula rotundifolia*	7
Forbs	Caryophyllaceae	*Moehringia trinervia*	7
Forbs	Caryophyllaceae	*Silene latifolia*	7
Forbs	Caryophyllaceae	*Stellaria media*	7
Forbs	Clusiaceae	*Hypericum maculatum*	7
Forbs	Dryopteridaceae	*Athyrium filix-femina*	7

Forbs	Lamiaceae	*Stachys sylvatica*	7
Forbs	Ranunculaceae	*Anemone nemorosa*	7
Forbs	Apiaceae	*Pimpinella saxifraga*	6
Forbs	Asteraceae	*Lactuca serriola*	6
Forbs	Asteraceae	*Lapsana communis*	6
Forbs	Balsaminaceae	*Impatiens parviflora*	6
Forbs	Brassicaceae	*Cardamine pratensis*	6
Forbs	Chenopodiaceae	*Chenopodium album*	6
Forbs	Colchicaceae	*Colchicum autumnale*	6
Forbs	-	Unidentified vascular plant species	6
Forbs	Geraniaceae	*Geranium pusillum*	6
Forbs	Lamiaceae	*Origanum vulgare*	6
Forbs	Plantaginaceae	*Veronica filiformis*	6
Forbs	Asteraceae	*Artemisia vulgaris*	5
Forbs	Balsaminaceae	*Impatiens glandulifera*	5
Forbs	Balsaminaceae	*Impatiens noli-tangere*	5
Forbs	Brassicaceae	*Thlaspi arvense*	5
Forbs	Caryophyllaceae	*Arenaria serpyllifolia*	5
Forbs	Caryophyllaceae	*Silene vulgaris*	5
Forbs	Juncaceae	*Juncus conglomeratus*	5
Forbs	Plantaginaceae	*Veronica serpyllifolia*	5
Forbs	Primulaceae	*Lysimachia nemorum*	5
Forbs	Saxifragaceae	*Saxifraga granulata*	5
Forbs	Violaceae	*Viola reichenbachiana*	5
Forbs	Apiaceae	*Chaerophyllum hirsutum*	4
Forbs	Asteraceae	*Cirsium oleraceum*	4
Forbs	Asteraceae	*Eupatorium cannabinum*	4
Forbs	Asteraceae	*Hieracium pilosella*	4
Forbs	Asteraceae	*Matricaria recutita*	4
Forbs	Asteraceae	*Solidago canadensis*	4
Forbs	Brassicaceae	*Alliaria petiolata*	4
Forbs	Convallariaceae	*Convallaria majalis*	4
Forbs	Geraniaceae	*Geranium molle*	4
Forbs	Lamiaceae	*Lamium purpureum*	4
Forbs	Lamiaceae	*Lycopus europaeus*	4
Forbs	Lamiaceae	*Thymus pulegioides*	4
Forbs	Onagraceae	*Circaea lutetiana*	4
Forbs	Onagraceae	*Epilobium* sp.	4
Forbs	Onagraceae	*Epilobium tetragonum*	4
Forbs	Plantaginaceae	*Linaria vulgaris*	4
Forbs	Polygonaceae	*Bistorta officinalis*	4
Forbs	Polygonaceae	*Polygonum aviculare*	4
Forbs	Polygonaceae	*Rumex acetosella*	4
Forbs	Ranunculaceae	*Ranunculus auricomus* agg.	4
Forbs	Rosaceae	*Filipendula ulmaria*	4

Forbs	Violaceae	*Viola arvensis*	4
Forbs	Asteraceae	*Arctium lappa*	3
Forbs	Asteraceae	*Cirsium vulgare*	3
Forbs	Asteraceae	*Tussilago farfara*	3
Forbs	Caryophyllaceae	*Cerastium glomeratum*	3
Forbs	Crassulaceae	*Sedum telephium*	3
Forbs	Dipsacaceae	*Knautia dipsacifolia*	3
Forbs	Dryopteridaceae	*Dryopteris dilatata*	3
Forbs	Equisetaceae	*Equisetum sylvaticum*	3
Forbs	Geraniaceae	*Geranium pyrenaicum*	3
Forbs	Juncaceae	*Luzula luzuloides*	3
Forbs	Lamiaceae	*Clinopodium vulgare*	3
Forbs	Plantaginaceae	*Veronica teucrium*	3
Forbs	Polygonaceae	*Rumex* sp.	3
Forbs	Polygonaceae	*Rumex conglomeratus*	3
Forbs	Primulaceae	*Lysimachia vulgaris*	3
Forbs	Primulaceae	*Primula veris*	3
Forbs	Ranunculaceae	*Ranunculus polyanthemos* agg.	3
Forbs	Rosaceae	*Potentilla argentea*	3
Forbs	Rubiaceae	*Galium boreale*	3
Forbs	Violaceae	*Viola canina*	3
Forbs	Alliaceae	*Allium* sp.	2
Forbs	Apiaceae	*Angelica sylvestris*	2
Forbs	Apiaceae	*Anthriscus sylvestris*	2
Forbs	Apiaceae	*Carum carvi*	2
Forbs	Apiaceae	*Chaerophyllum bulbosum*	2
Forbs	Apiaceae	*Falcaria vulgaris*	2
Forbs	Apiaceae	*Pastinaca sativa*	2
Forbs	Apiaceae	*Seseli libanotis*	2
Forbs	Apiaceae	*Silaum silaus*	2
Forbs	Asteraceae	*Aposeris foetida*	2
Forbs	Asteraceae	*Centaurea scabiosa*	2
Forbs	Asteraceae	*Cichorium intybus*	2
Forbs	Asteraceae	*Hieracium aurantiacum*	2
Forbs	Asteraceae	*Hieracium piloselloides*	2
Forbs	Asteraceae	*Hieracium sabaudum*	2
Forbs	Asteraceae	*Prenanthes purpurea*	2
Forbs	Asteraceae	*Senecio ovatus*	2
Forbs	Asteraceae	*Senecio sylvaticus*	2
Forbs	Asteraceae	*Senecio vulgaris*	2
Forbs	Boraginaceae	*Symphytum officinale*	2
Forbs	Brassicaceae	*Barbarea vulgaris*	2
Forbs	Campanulaceae	*Phyteuma orbiculare*	2
Forbs	Campanulaceae	*Phyteuma spicatum*	2
Forbs	Caryophyllaceae	Unidentified species	2

Forbs	Caryophyllaceae	*Cerastium arvense*	2
Forbs	Caryophyllaceae	*Stellaria alsine*	2
Forbs	Caryophyllaceae	*Stellaria aquatica*	2
Forbs	Clusiaceae	*Hypericum pulchrum*	2
Forbs	Clusiaceae	*Hypericum tetrapterum*	2
Forbs	Convallariaceae	*Polygonatum verticillatum*	2
Forbs	Convolvulaceae	*Calystegia sepium*	2
Forbs	Dipsacaceae	*Dipsacus fullonum*	2
Forbs	Dipsacaceae	*Scabiosa columbaria*	2
Forbs	Euphorbiaceae	*Mercurialis perennis*	2
Forbs	Juncaceae	*Luzula sylvatica*	2
Forbs	Lamiaceae	*Betonica officinalis*	2
Forbs	Lamiaceae	*Lamium galeobdolon* agg.	2
Forbs	Lamiaceae	*Lamium maculatum*	2
Forbs	Lamiaceae	*Mentha longifolia*	2
Forbs	Lamiaceae	*Salvia glutinosa*	2
Forbs	Lythraceae	*Lythrum salicaria*	2
Forbs	Malvaceae	*Malva moschata*	2
Forbs	Onagraceae	*Epilobium hirsutum*	2
Forbs	Onagraceae	*Epilobium tetragonum* ssp. *lamyi*	2
Forbs	Orobanchaceae	*Rhinanthus alectorolophus*	2
Forbs	Papaveraceae	*Papaver rhoeas*	2
Forbs	Plantaginaceae	*Veronica montana*	2
Forbs	Polygonaceae	*Persicaria amphibia*	2
Forbs	Polygonaceae	Unidentified species	2
Forbs	Ranunculaceae	*Clematis vitalba*	2
Forbs	Ranunculaceae	*Ranunculus ficaria*	2
Forbs	Ranunculaceae	*Ranunculus lanuginosus*	2
Forbs	Rosaceae	*Potentilla* sp.	2
Forbs	Rubiaceae	*Galium saxatile*	2
Forbs	Scrophulariaceae	*Verbascum nigrum*	2
Forbs	Solanaceae	*Atropa bella-donna*	2
Forbs	Valerianaceae	*Valeriana officinalis*	2
Forbs	Violaceae	*Viola* sp.	2
Forbs	Violaceae	*Viola odorata*	2
Forbs	Alliaceae	*Allium carinatum*	1
Forbs	Alliaceae	*Allium schoenoprasum*	1
Forbs	Anthericaceae	*Anthericum ramosum*	1
Forbs	Apiaceae	*Astrantia major*	1
Forbs	Apiaceae	*Bupleurum falcatum*	1
Forbs	Apiaceae	*Chaerophyllum aureum*	1
Forbs	Apiaceae	*Chaerophyllum temulum*	1
Forbs	Apiaceae	*Eryngium campestre*	1
Forbs	Apiaceae	*Sanicula europaea*	1
Forbs	Apiaceae	*Torilis arvensis*	1

Forbs	Araliaceae	*Hedera helix*	1
Forbs	Asparagaceae	*Asparagus officinalis*	1
Forbs	Asteraceae	*Anthemis tinctoria*	1
Forbs	Asteraceae	*Arctium* sp.	1
Forbs	Asteraceae	Unidentified species	1
Forbs	Asteraceae	*Buphthalmum salicifolium*	1
Forbs	Asteraceae	*Centaurea cyanus*	1
Forbs	Asteraceae	*Cichorium endivia*	1
Forbs	Asteraceae	*Cirsium* sp.	1
Forbs	Asteraceae	*Cirsium eriophorum*	1
Forbs	Asteraceae	*Cirsium heterophyllum*	1
Forbs	Asteraceae	*Crepis* sp.	1
Forbs	Asteraceae	*Hieracium* sp.	1
Forbs	Asteraceae	*Matricaria discoidea*	1
Forbs	Asteraceae	*Mycelis muralis*	1
Forbs	Asteraceae	*Petasites albus*	1
Forbs	Asteraceae	*Solidago virgaurea*	1
Forbs	Asteraceae	*Sonchus asper*	1
Forbs	Asteraceae	*Sonchus oleraceus*	1
Forbs	Boraginaceae	*Myosotis* sp.	1
Forbs	Boraginaceae	*Myosotis scorpioides*	1
Forbs	Boraginaceae	*Myosotis sylvatica*	1
Forbs	Brassicaceae	*Arabis glabra*	1
Forbs	Brassicaceae	*Brassica napus*	1
Forbs	Brassicaceae	*Brassicaceae*	1
Forbs	Brassicaceae	*Bunias orientalis*	1
Forbs	Brassicaceae	*Cardaria draba*	1
Forbs	Brassicaceae	*Hesperis matronalis*	1
Forbs	Brassicaceae	*Lepidium campestre*	1
Forbs	Brassicaceae	*Rorippa austriaca*	1
Forbs	Brassicaceae	*Sisymbrium officinale*	1
Forbs	Campanulaceae	*Campanula* sp.	1
Forbs	Campanulaceae	*Campanula persicifolia*	1
Forbs	Campanulaceae	*Campanula trachelium*	1
Forbs	Caryophyllaceae	*Cerastium* sp.	1
Forbs	Caryophyllaceae	*Cerastium lucorum*	1
Forbs	Caryophyllaceae	*Dianthus deltoides*	1
Forbs	Caryophyllaceae	*Herniaria glabra*	1
Forbs	Caryophyllaceae	*Silene dioica*	1
Forbs	Caryophyllaceae	*Silene nutans*	1
Forbs	Caryophyllaceae	*Stellaria nemorum*	1
Forbs	Clusiaceae	*Hypericum hirsutum*	1
Forbs	Crassulaceae	*Sedum acre*	1
Forbs	Dennstaedtiaceae	*Pteridium aquilinum*	1
Forbs	Dipsacaceae	*Knautia* sp.	1

Forbs	Dipsacaceae	*Scabiosa columbaria* agg.	1
Forbs	Dipsacaceae	*Succisa pratensis*	1
Forbs	Dryopteridaceae	*Dryopteris expansa*	1
Forbs	Dryopteridaceae	*Dryopteris filix-mas*	1
Forbs	Equisetaceae	*Equisetum palustre*	1
Forbs	Euphorbiaceae	*Euphorbia amygdaloides*	1
Forbs	Euphorbiaceae	*Euphorbia seguieriana*	1
Forbs	Euphorbiaceae	*Mercurialis ovata*	1
Forbs	Gentianaceae	*Centaurium erythraea*	1
Forbs	Geraniaceae	*Geranium columbinum*	1
Forbs	Lamiaceae	*Acinos alpinus*	1
Forbs	Lamiaceae	*Ajuga genevensis*	1
Forbs	Lamiaceae	*Galeopsis speciosa*	1
Forbs	Lamiaceae	Unidentified species	1
Forbs	Lamiaceae	*Lamium album*	1
Forbs	Lamiaceae	*Lamium montanum*	1
Forbs	Lamiaceae	*Mentha arvensis*	1
Forbs	Lamiaceae	*Mentha spicata* agg.	1
Forbs	Lamiaceae	*Scutellaria galericulata*	1
Forbs	Lamiaceae	*Stachys palustris*	1
Forbs	Lamiaceae	*Teucrium chamaedrys*	1
Forbs	Lamiaceae	*Teucrium scorodonia*	1
Forbs	Lamiaceae	*Thymus praecox*	1
Forbs	Linaceae	*Linum catharticum*	1
Forbs	Onagraceae	*Epilobium collinum*	1
Forbs	Onagraceae	*Epilobium montanum*	1
Forbs	Onagraceae	*Epilobium obscurum*	1
Forbs	Onagraceae	*Epilobium palustre*	1
Forbs	Onagraceae	*Epilobium parviflorum*	1
Forbs	Orchidaceae	*Cephalanthera rubra*	1
Forbs	Orobanchaceae	*Euphrasia* sp.	1
Forbs	Orobanchaceae	*Melampyrum arvense*	1
Forbs	Orobanchaceae	*Melampyrum pratense*	1
Forbs	Orobanchaceae	*Melampyrum sylvaticum*	1
Forbs	Orobanchaceae	*Orobanche gracilis*	1
Forbs	Oxalidaceae	*Oxalis stricta*	1
Forbs	Papaveraceae	*Chelidonium majus*	1
Forbs	Papaveraceae	*Papaver dubium*	1
Forbs	Plantaginaceae	*Chaenorhinum minus*	1
Forbs	Plantaginaceae	*Digitalis purpurea*	1
Forbs	Plantaginaceae	*Veronica agrestis*	1
Forbs	Plantaginaceae	*Veronica hederifolia*	1
Forbs	Polygalaceae	*Polygala chamaebuxus*	1
Forbs	Polygalaceae	*Polygala comosa*	1
Forbs	Polygonaceae	*Persicaria* sp.	1

Forbs	Polygonaceae	*Persicaria maculosa*	1
Forbs	Polygonaceae	*Polygonum* sp.	1
Forbs	Primulaceae	*Lysimachia punctata*	1
Forbs	Primulaceae	*Primula* sp.	1
Forbs	Primulaceae	*Primula elatior*	1
Forbs	Ranunculaceae	*Aquilegia vulgaris*	1
Forbs	Rosaceae	*Alchemilla mollis*	1
Forbs	Rosaceae	*Geum rivale*	1
Forbs	Rubiaceae	*Cruciata laevipes*	1
Forbs	Rubiaceae	*Galium odoratum*	1
Forbs	Rubiaceae	*Galium pumilum*	1
Forbs	Rubiaceae	*Galium rotundifolium*	1
Forbs	Rubiaceae	*Galium uliginosum*	1
Forbs	Rubiaceae	*Sherardia arvensis*	1
Forbs	Scrophulariaceae	*Verbascum* sp.	1
Forbs	Thelypteridaceae	*Oreopteris limbosperma*	1
Forbs	Thelypteridaceae	*Phegopteris connectilis*	1
Forbs	Trilliaceae	*Paris quadrifolia*	1
Forbs	Valerianaceae	*Valeriana officinalis* agg.	1
Forbs	Violaceae	*Viola mirabilis*	1
Forbs	Violaceae	*Viola riviniana*	1
Grasses	Poaceae	*Dactylis glomerata*	129
Grasses	Poaceae	*Poa pratensis*	98
Grasses	Poaceae	*Arrhenatherum elatius*	95
Grasses	Poaceae	*Poa trivialis*	84
Grasses	Poaceae	*Alopecurus pratensis*	69
Grasses	Poaceae	*Elymus repens*	68
Grasses	Poaceae	*Festuca pratensis*	65
Grasses	Poaceae	*Festuca rubra* agg.	65
Grasses	Poaceae	*Lolium perenne*	59
Grasses	Poaceae	*Holcus lanatus*	58
Grasses	Poaceae	*Phleum pratense*	52
Grasses	Poaceae	*Trisetum flavescens*	50
Grasses	Poaceae	*Agrostis capillaris*	48
Grasses	Poaceae	*Anthoxanthum odoratum*	35
Grasses	Cyperaceae	*Carex hirta*	25
Grasses	Poaceae	*Agrostis gigantea*	22
Grasses	Poaceae	*Cynosurus cristatus*	19
Grasses	Cyperaceae	*Carex muricata* agg.	18
Grasses	Poaceae	*Calamagrostis epigejos*	18
Grasses	Poaceae	*Deschampsia cespitosa*	18
Grasses	Cyperaceae	*Carex brizoides*	17
Grasses	Poaceae	*Bromus hordeaceus*	17
Grasses	Cyperaceae	*Carex sylvatica*	15
Grasses	Poaceae	*Holcus mollis*	15

Grasses	Cyperaceae	*Carex flacca*	14
Grasses	Poaceae	*Brachypodium sylvaticum*	14
Grasses	Cyperaceae	*Carex ovalis*	13
Grasses	Poaceae	*Poa angustifolia*	12
Grasses	Poaceae	*Bromus sterilis*	11
Grasses	Poaceae	*Lolium multiflorum*	11
Grasses	Poaceae	*Brachypodium pinnatum*	10
Grasses	Poaceae	*Festuca ovina* agg.	10
Grasses	Poaceae	*Helictotrichon pubescens*	9
Grasses	Poaceae	*Triticum aestivum*	9
Grasses	Cyperaceae	*Carex pallescens*	8
Grasses	Cyperaceae	*Carex remota*	7
Grasses	Poaceae	*Brachypodium rupestre*	7
Grasses	Poaceae	*Bromus erectus*	7
Grasses	Poaceae	*Poa nemoralis*	7
Grasses	Poaceae	*Briza media*	6
Grasses	Poaceae	*Bromus inermis*	6
Grasses	Poaceae	*Poa annua*	6
Grasses	Cyperaceae	*Carex pilulifera*	5
Grasses	Poaceae	*Deschampsia flexuosa*	5
Grasses	Poaceae	*Danthonia decumbens*	4
Grasses	Poaceae	*Festuca arundinacea*	4
Grasses	Poaceae	*Phragmites australis*	4
Grasses	Cyperaceae	*Carex flava*	3
Grasses	Poaceae	*Alopecurus myosuroides*	3
Grasses	Poaceae	*Elymus caninus*	3
Grasses	Poaceae	*Festuca* sp.	3
Grasses	Poaceae	*Melica uniflora*	3
Grasses	Poaceae	*Milium effusum*	3
Grasses	Poaceae	*Phalaris arundinacea*	3
Grasses	Poaceae	*Poa* sp.	3
Grasses	Cyperaceae	*Carex* sp.	2
Grasses	Cyperaceae	*Carex caryophyllea*	2
Grasses	Cyperaceae	*Carex montana*	2
Grasses	Cyperaceae	*Scirpus sylvaticus*	2
Grasses	Poaceae	*Agrostis stolonifera* agg.	2
Grasses	Poaceae	*Calamagrostis arundinacea*	2
Grasses	Poaceae	*Calamagrostis varia*	2
Grasses	Poaceae	*Festuca gigantea*	2
Grasses	Poaceae	*Hordeum vulgare*	2
Grasses	Poaceae	*Molinia caerulea*	2
Grasses	Poaceae	*Secale cereale*	2
Grasses	Poaceae	*Sesleria albicans*	2
Grasses	Cyperaceae	*Carex alba*	1
Grasses	Cyperaceae	*Carex digitata*	1

Grasses	Cyperaceae	*Carex humilis*	1
Grasses	Cyperaceae	*Carex nigra*	1
Grasses	Cyperaceae	*Carex panicea*	1
Grasses	Cyperaceae	*Carex vulpina*	1
Grasses	Poaceae	*Apera spica-venti*	1
Grasses	Poaceae	*Bromus arvensis*	1
Grasses	Poaceae	*Bromus benekenii*	1
Grasses	Poaceae	*Bromus secalinus*	1
Grasses	Poaceae	*Festuca heterophylla*	1
Grasses	Poaceae	*Glyceria notata*	1
Grasses	Poaceae	*Hordelymus europaeus*	1
Grasses	Poaceae	*Koeleria pyramidata*	1
Grasses	Poaceae	*Melica nutans*	1
Grasses	Poaceae	*Molinia arundinacea*	1
Grasses	Poaceae	Unidentified species	1
Grasses	Poaceae	*Stipa pennata*	1
Legumes	Fabaceae	*Trifolium repens*	76
Legumes	Fabaceae	*Trifolium pratense*	63
Legumes	Fabaceae	*Lotus corniculatus*	49
Legumes	Fabaceae	*Lathyrus pratensis*	48
Legumes	Fabaceae	*Vicia sepium*	44
Legumes	Fabaceae	*Vicia cracca*	32
Legumes	Fabaceae	*Trifolium dubium*	24
Legumes	Fabaceae	*Vicia hirsuta*	22
Legumes	Fabaceae	*Medicago lupulina*	20
Legumes	Fabaceae	*Vicia angustifolia*	17
Legumes	Fabaceae	*Trifolium medium*	9
Legumes	Fabaceae	*Vicia sativa*	9
Legumes	Fabaceae	*Vicia tetrasperma*	9
Legumes	Fabaceae	*Securigera varia*	6
Legumes	Fabaceae	*Lathyrus tuberosus*	5
Legumes	Fabaceae	*Medicago* x *varia*	5
Legumes	Fabaceae	*Anthyllis vulneraria*	4
Legumes	Fabaceae	*Medicago falcata*	3
Legumes	Fabaceae	*Melilotus officinalis*	3
Legumes	Fabaceae	*Onobrychis viciifolia*	3
Legumes	Fabaceae	*Astragalus glycyphyllos*	2
Legumes	Fabaceae	*Lathyrus linifolius*	2
Legumes	Fabaceae	*Lupinus polyphyllus*	2
Legumes	Fabaceae	*Ononis repens*	2
Legumes	Fabaceae	*Ononis spinosa* agg.	2
Legumes	Fabaceae	Unidentified species	1
Legumes	Fabaceae	*Hippocrepis comosa*	1
Legumes	Fabaceae	*Lathyrus sylvestris*	1
Legumes	Fabaceae	*Lathyrus vernus*	1

Legumes	Fabaceae	*Lotus pedunculatus*	1
Legumes	Fabaceae	*Medicago minima*	1
Legumes	Fabaceae	*Melilotus albus*	1
Legumes	Fabaceae	*Trifolium alpestre*	1
Legumes	Fabaceae	*Trifolium hybridum*	1
Legumes	Fabaceae	*Trifolium incarnatum*	1
Legumes	Fabaceae	*Vicia pannonica*	1
Woody plants	Fagaceae	*Quercus robur*	17
Woody plants	Rosaceae	*Prunus* sp.	17
Woody plants	Aceraceae	*Acer pseudoplatanus*	14
Woody plants	Cornaceae	*Cornus sanguinea*	13
Woody plants	Aceraceae	*Acer platanoides*	11
Woody plants	Pinaceae	*Picea abies*	11
Woody plants	Fagaceae	*Fagus sylvatica*	9
Woody plants	Oleaceae	*Fraxinus excelsior*	9
Woody plants	Rosaceae	*Crataegus monogyna*	9
Woody plants	Rosaceae	*Sorbus aucuparia*	9
Woody plants	Betulaceae	*Betula pendula*	8
Woody plants	Ericaceae	*Vaccinium myrtillus*	7
Woody plants	Aceraceae	*Acer campestre*	6
Woody plants	Pinaceae	*Pinus sylvestris*	6
Woody plants	Rosaceae	*Rosa* sp.	6
Woody plants	Betulaceae	*Carpinus betulus*	5
Woody plants	Rosaceae	*Rosa canina*	5
Woody plants	Salicaceae	*Salix caprea*	5
Woody plants	Caprifoliaceae	*Sambucus nigra*	4
Woody plants	Celastraceae	*Euonymus europaea*	4
Woody plants	Pinaceae	*Abies alba*	4
Woody plants	Rosaceae	*Prunus spinosa*	4
Woody plants	Salicaceae	*Populus nigra*	4
Woody plants	Salicaceae	*Salix* sp.	4
Woody plants	Betulaceae	*Corylus avellana*	3
Woody plants	Ericaceae	*Calluna vulgaris*	3
Woody plants	Aceraceae	*Acer* sp.	2
Woody plants	Caprifoliaceae	*Lonicera xylosteum*	2
Woody plants	Ericaceae	*Vaccinium vitis-idaea*	2
Woody plants	Fagaceae	*Quercus* sp.	2
Woody plants	Oleaceae	*Ligustrum vulgare*	2
Woody plants	Rhamnaceae	*Frangula alnus*	2
Woody plants	Salicaceae	*Populus tremula*	2
Woody plants	Berberidaceae	*Mahonia aquifolium*	1
Woody plants	Cornaceae	*Cornus sanguinea* ssp. *sanguinea*	1
Woody plants	Fagaceae	*Quercus petraea*	1
Woody plants	Fagaceae	*Quercus rubra*	1
Woody plants	Grossulariaceae	*Ribes rubrum*	1

Woody plants	Pinaceae	*Larix decidua*	1
Woody plants	Rosaceae	*Prunus avium*	1
Woody plants	Rosaceae	*Sorbus* sp.	1
Woody plants	Rosaceae	*Sorbus torminalis*	1

Table S3 Pearson correlation coefficients for all continuous variables included in model selection processes on herbivory data (80 plots, 78 plots when including local mean temperature). Significant correlations based on α = 0.05 are indicated as following: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$

		Pearson correlation coefficients				
Scale [km]	Variable	Temp (1)	MAT (2)	specnum (3)	famnum (4)	Gra% (5)
-	Local mean temperature (1)					
-	Multi-annual mean temperature (2)	0.23***				
-	Species-level plant richness (3)	-0.03	-0.02			
-	Family-level plant richness (4)	-0.09	-0.05	0.76***		
0.2	Grassland percentage (5)	-0.04	-0.09	-0.15*	-0.23***	
0.5	Grassland percentage	0.10	-0.16*	-0.17*	-0.21***	
1.0	Grassland percentage	0.09	-0.29***	-0.14*	-0.14*	
1.5	Grassland percentage	0.07	-0.42***	-0.11	-0.13*	
2.0	Grassland percentage	0.06	-0.47***	-0.09	-0.11	
2.5	Grassland percentage	0.06	-0.51***	-0.07	-0.10	
3.0	Grassland percentage	0.07	-0.52***	-0.06	-0.09	
0.2	Landscape diversity	0.12	0.19**	-0.22***	-0.40***	0.39***
0.5	Landscape diversity	0.29***	0.13	-0.14*	-0.29***	0.44***
1.0	Landscape diversity	0.17**	0.05	-0.18**	-0.18**	0.51***
1.5	Landscape diversity	0.10	0.03	-0.18**	-0.19**	0.49***
2.0	Landscape diversity	0.07	0.00	-0.16*	-0.17**	0.44***
2.5	Landscape diversity	0.10	-0.00	-0.14*	-0.18**	0.39***
3.0	Landscape diversity	0.12	-0.04	-0.14*	-0.19**	0.37***

Table S4 Null, “full” and best beta mixed models on mean leaf area loss by chewing invertebrates per plant functional group and plot (80 plots). “Full” models include different sets of fixed effects but always include plant functional group, one climatic environmental variable, one land-use or plant-richness variable and their interaction terms. Fixed effects encompass: Plant functional group (Plant guild), multi-annual mean temperature (MAT), habitat type (habitat), species-level plant richness (specnum) and family-level plant richness (famnum), and proportion grassland (Gra) and landscape diversity (LD) at multiple spatial scales. Continuous predictor variables were z-transformed (s-Fixed effect) prior to modelling. To account for study design, plot nested in region was added as random term. Asterisks (*) between fixed effects indicate that both, all main effects and all interaction terms were included. Bold font indicates the best model based on relative goodness of model fit (lowest AICc).

Spatial scale [km]	Model	Fixed effects	Random effects	df	AICc
-	NULL	-	Region/Plot	4	-1606.3
-	“full”	Plant guild*sMAT*habitat	Region/Plot	27	-1686.6
	best	**Plant guild*habitat**	**Region/Plot**	**15**	**-1697.6**
-	“full”	Plant guild*sMAT*sspecnum	Region/Plot	15	-1685.2
-	best	Plant guild	Region/Plot	6	-1688.5
-	“full”	Plant guild*sMAT*sfamnum	Region/Plot	15	-1698.0
-	**best**	**Plant guild*sfamnum**	**Region/Plot**	**9**	**-1698.9**
0.2	“full”	Plant guild*sMAT*sGra	Region/Plot	15	-1684.5
0.2	best	Plant guild	Region/Plot	6	-1688.5
0.5	“full”	Plant guild*sMAT*sGra	Region/Plot	15	-1676.3
0.5	best	Plant guild	Region/Plot	6	-1688.5
1.0	“full”	Plant guild*sMAT*sGra	Region/Plot	15	-1673.5
1.0	best	Plant guild	Region/Plot	6	-1688.5
1.5	“full”	Plant guild*sMAT*sGra	Region/Plot	15	-1672.8
1.5	best	Plant guild	Region/Plot	6	-1688.5
2.0	“full”	Plant guild*sMAT*sGra	Region/Plot	15	-1673.1
2.0	best	Plant guild	Region/Plot	6	-1688.5
2.5	“full”	Plant guild*sMAT*sGra	Region/Plot	15	-1674.3
2.5	best	Plant guild	Region/Plot	6	-1688.5
3.0	“full”	Plant guild*sMAT*sGra	Region/Plot	15	-1675.3
3.0	best	Plant guild	Region/Plot	6	-1688.5
0.2	“full”	Plant guild*sMAT*sLD	Region/Plot	15	-1683.9
0.2	best	Plant guild	Region/Plot	6	-1688.5
0.5	“full”	Plant guild*sMAT*sLD	Region/Plot	15	-1675.5
0.5	best	Plant guild	Region/Plot	6	-1688.5
1.0	“full”	Plant guild*sMAT*sLD	Region/Plot	15	-1673.2
1.0	best	Plant guild	Region/Plot	6	-1688.5
1.5	“full”	Plant guild*sMAT*sLD	Region/Plot	15	-1673.6
1.5	best	Plant guild	Region/Plot	6	-1688.5
2.0	“full”	Plant guild*sMAT*sLD	Region/Plot	15	-1674.4
2.0	best	Plant guild	Region/Plot	6	-1688.5
2.5	“full”	Plant guild*sMAT*sLD	Region/Plot	15	-1675.9
2.5	best	Plant guild	Region/Plot	6	-1688.5
3.0	“full”	Plant guild*sMAT*sLD	Region/Plot	15	-1676.8
3.0	best	Plant guild	Region/Plot	6	-1688.5

Table S5 Null, “full” and best beta mixed models on mean leaf area loss by chewing invertebrates per plant functional group and plot (78 plots). “Full” models include different sets of fixed effects but always include plant functional group, one climatic environmental variable, one land-use or plant-richness variable and their interaction terms. Fixed effects encompass: Plant functional group (Plant guild), local mean temperature of the 1-month period prior to leaf sampling (Temp), habitat type (habitat), species-level plant richness (specnum) and family-level plant richness (famnum), and proportion grassland (Gra) and landscape diversity (LD) at multiple spatial scales. Continuous predictor variables were z-transformed (s-Fixed effect) prior to modelling. To account for study design, plot nested in region was added as random term. Asterisks (*) between fixed effects indicate that both, all main effects and all interaction terms were included. Bold font indicates the best model based on relative goodness of model fit (lowest AICc).

Spatial scale [km]	Model	Fixed effects	Random effects	df	AICc
-	NULL	-	Region/Plot	4	-1606.2
-	“full”	Plant guild*sTemp*habitat	Region/Plot	27	-1635.1
	best	**Plant guild*habitat**	**Region/Plot**	**15**	**-1697.6**
-	“full”	Plant guild*sTemp*sspecnum	Region/Plot	15	-1635.4
-	best	Plant guild	Region/Plot	6	-1688.5
-	“full”	Plant guild*sTemp*sfamnum	Region/Plot	15	-1641.6
-	**best**	**Plant guild*sfamnum**	**Region/Plot**	**9**	**-1698.9**
0.2	“full”	Plant guild*sTemp*sGra	Region/Plot	15	-1633.1
0.2	best	Plant guild	Region/Plot	6	-1688.5
0.5	“full”	Plant guild*sTemp*sGra	Region/Plot	15	-1630.2
0.5	best	Plant guild	Region/Plot	6	-1688.5
1.0	“full”	Plant guild*sTemp*sGra	Region/Plot	15	-1628.6
1.0	best	Plant guild	Region/Plot	6	-1688.5
1.5	“full”	Plant guild*sTemp*sGra	Region/Plot	15	-1630.3
1.5	best	Plant guild	Region/Plot	6	-1688.5
2.0	“full”	Plant guild*sTemp*sGra	Region/Plot	15	-1630.7
2.0	best	Plant guild	Region/Plot	6	-1688.5
2.5	“full”	Plant guild*sTemp*sGra	Region/Plot	15	-1630.8
2.5	best	Plant guild	Region/Plot	6	-1688.5
3.0	“full”	Plant guild*sTemp*sGra	Region/Plot	15	-1630.7
3.0	best	Plant guild	Region/Plot	6	-1688.5
0.2	“full”	Plant guild*sTemp*sLD	Region/Plot	15	-1630.8
0.2	best	Plant guild	Region/Plot	6	-1688.5
0.5	“full”	Plant guild*sTemp*sLD	Region/Plot	15	-1629.6
0.5	best	Plant guild	Region/Plot	6	-1688.5
1.0	“full”	Plant guild*sTemp*sLD	Region/Plot	15	-1627.6
1.0	best	Plant guild	Region/Plot	6	-1688.5
1.5	“full”	Plant guild*sTemp*sLD	Region/Plot	15	-1628.2
1.5	best	Plant guild	Region/Plot	6	-1688.5
2.0	“full”	Plant guild*sTemp*sLD	Region/Plot	15	-1628.8
2.0	best	Plant guild	Region/Plot	6	-1688.5
2.5	“full”	Plant guild*sTemp*sLD	Region/Plot	15	-1628.6
2.5	best	Plant guild	Region/Plot	6	-1688.5
3.0	“full”	Plant guild*sTemp*sLD	Region/Plot	15	-1629.0
3.0	best	Plant guild	Region/Plot	6	-1688.5

Table S6 Selection process of beta mixed models on plot-averaged leaf area loss by chewing invertebrates per plant functional group on data from grassland habitats only (24 plots). Fixed effects encompass plant functional group (Plant guild) and z-transformed multi-annual mean temperature (sMAT) or local mean temperature 1-month prior to leaf sampling (sTemp). As a single habitat type was subsetted, no random term was added. Asterisks (*) between fixed effects indicate that both, main effects and all interaction terms were included. Relative goodness of model fit is indicated by Akaike's information criterion corrected for small sample size (AICc). Bold font highlights the best model based on ΔAICc < 2.

Fixed effects	Random effects	df	AICc	ΔAICc
Plant guild*sMAT	**Plot**	**8**	**-511.6**	**0.00**
Plant guild+sMAT	Plot	6	-504.5	7.14
Plant guild	Plot	5	-506.6	5.05
sMAT	Plot	4	-468.4	43.20
- (Null model)	Plot	3	-468.1	43.48
Plant guild*sTemp	Plot	8	-500.2	6.41
Plant guild+sTemp	Plot	6	-504.3	2.27
Plant guild	**Plot**	**5**	**-506.6**	**0.00**
sTemp	Plot	4	-466.0	40.61
- (Null model)	Plot	3	-468.1	38.43

Chapter 3

Landscape diversity and local temperature, but not climate, affect arthropod predation among habitat types

Ute Fricke, Ingolf Steffan-Dewenter, Jie Zhang, Cynthia Tobisch, Sandra Rojas-Botero, Caryl S. Benjamin, Jana Englmeier, Cristina Ganuza, Maria Haensel, Rebekka Riebl, Johannes Uhler, Lars Uphus, Jörg Ewald, Johannes Kollmann, Sarah Redlich

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Abstract

Arthropod predators are important for ecosystem functioning by providing top-down regulation of insect herbivores. As predator communities and activity are influenced by biotic and abiotic factors on different spatial scales, the strength of top-down regulation (‘arthropod predation’) is also likely to vary. Understanding the combined effects of potential drivers on arthropod predation is urgently needed with regard to anthropogenic climate and land-use change. In a large-scale study, we recorded arthropod predation rates using artificial caterpillars on 113 plots of open herbaceous vegetation embedded in contrasting habitat types (forest, grassland, arable field, settlement) along climate and land-use gradients in Bavaria, Germany. As potential drivers we included habitat characteristics (habitat type, plant species richness, local mean temperature and mean relative humidity during artificial caterpillar exposure), landscape diversity (0.5–3.0-km, six scales), climate (multi-annual mean temperature, ‘MAT’) and interactive effects of habitat type with other drivers. We observed no substantial differences in arthropod predation rates between the studied habitat types, related to plant species richness and across the Bavarian-wide climatic gradient, but predation was limited when local mean temperatures were low and tended to decrease towards higher relative humidity. Arthropod predation rates increased towards more diverse landscapes at a 2-km scale. Interactive effects of habitat type with local weather conditions, plant species richness, landscape diversity and MAT were not observed. We conclude that landscape diversity favours high arthropod predation rates in open herbaceous vegetation independent of the dominant habitat in the vicinity. This finding may be harnessed to improve top-down control of herbivores, e.g. agricultural pests, but further research is needed for more specific recommendations on landscape management. The absence of MAT effects suggests that high predation rates may occur independent of moderate increases of MAT in the near future.

Introduction

Predation and parasitism are frequent causes of mortality to many herbivorous insect species (Hawkins et al. 1997) and hence can exert strong impact on herbivore communities (Schmitz et al. 2000; Halaj and Wise 2001). Through their impact on herbivores, natural enemies can also indirectly affect plant damage, vegetation structure and composition, and nutrient cycling (Schmitz et al. 2000; Halaj and Wise 2001; Schowalter 2016). This renders natural enemies and their biotic interactions essential to ecosystem functioning. Important natural enemies for the regulation of herbivorous insects are arthropod predators (Haan et al. 2021). Predation intensity can differ between habitat types (Ferrante et al. 2014, 2017b), albeit direct comparisons among typical habitat types in temperate regions (forest, grassland, arable fields and settlements) are lacking. Besides, arthropod activity is influenced by local weather conditions (Nève 1994), while plant species richness (Schuldt et al. 2019), climate (Bale et al. 2002) and regional land use (Martin et al. 2019) affect arthropod communities, with potential consequences for top-down suppression of herbivores (Griffin et al. 2013; Alhadidi et al. 2018). However, the combined effects of these drivers on arthropod predation in different habitats are largely unknown, albeit urgently needed with regard to anthropogenic climate and land-use change.

Local habitat characteristics such as habitat type, plant species richness and weather conditions affect predator richness, activity or both with possible implications on predation rates. With respect to habitat type, Ferrante et al. (2017b) observed higher predation rates in forests than in maize fields. This may be related to on average higher natural enemy richness in natural than agricultural ecosystems (Letourneau et al. 2009), which possibly translates into higher and lower predation rates, respectively (Griffin et al. 2013). Plant species richness was described both to benefit natural enemies (Barnes et al. 2020) and predation rates (Hertzog et al. 2017), whereby predation rates may be affected directly or indirectly, via changes in the composition of the natural enemy community (Letourneau et al. 2009; Griffin et al. 2013). Besides, higher plant species richness can also lead to higher structural complexity of the vegetation (Schuldt et al. 2019), which may alter predator behaviour with positive effects on predation rates, e.g. reduced intraguild predation (Finke and Denno 2002). However, knowledge of plant richness effects on natural enemies and their services originate almost exclusively from plant diversity experiments (Hertzog et al. 2017; e.g. Schuldt et al. 2019; Barnes et al. 2020), while complementing field studies are lacking. Similar applies to weather conditions. Temperature and humidity modify arthropod activity in terms of catchability by traps (Nève 1994), but little is known about their effects on predation rates. For instance, activity of predatory carabid beetles increases with temperature (Nève 1994; Honěk 1997), and, depending on species traits, decreases towards higher relative humidity (Nève 1994), while too low temperatures can restrict carabid activity (Holland 2002). Thus, the richness and activity of predators are affected through habitat characteristics, yet the consequences for predation rates are much less clear.

At a regional scale, landscape complexity and climatic factors impact predators. In complex landscapes, both species richness and abundance of generalist enemies are higher, and top-down control of herbivorous arthropods is commonly increased (Bianchi et al. 2006; Chaplin-Kramer et al. 2011; Martin et al. 2019). Considering landscape diversity as an aspect of landscape complexity (Chaplin-Kramer et al. 2011), diverse landscapes can provide complementary or supplementary resources to organisms moving between habitat patches with beneficial effects on their population size (Dunning et al. 1992). Thus, predation rates may increase towards more diverse landscapes. In addition, climate change, and in particular a warmer climate, is expected to affect arthropods in many aspects, for instance, in their geographic distribution and life history traits (Bale et al. 2002; Rall et al. 2010). Consequently, this may impact predation rates. Indeed, the efficacy of predators to suppress herbivores can increase with mean annual temperatures (Michalko et al. 2019) as well as predation rates increase towards lower altitudes and latitudes (Roslin et al. 2017). Thus, both diverse landscapes and warm climates may favour higher predation rates.

Here we use arthropod attack marks on artificial caterpillars, facilitating standardized estimates of predation rates over large spatial scales, to study the combined effects of local habitat type, plant species richness, weather, landscape diversity and multi-annual mean temperature on arthropod predation, and ask whether effects differ among habitat types. This study advances the understanding of top-down regulation of herbivores and natural pest control services in the context of climate and land use.

Material and Methods

Study area and plot selection

This study was conducted within the LandKlif project in Bavaria, Germany, which used a novel multi-scale study design to disentangle the combined effects of climate and land use on biodiversity and ecosystem functions (Redlich et al. 2021), here on arthropod predation rates. From grid cells (5.8 km x 5.8 km) covering Bavaria (Germany), 60 grid cells (= 60 'regions') were selected encompassing four replicates of 15 combinations of climate zones (multi-annual mean temperature between 1981–2010; < 7.5 °C, in 0.5 °C steps until 9 °C, > 9 °C) and landscape-scale land-use types (near-natural, agriculture and urban) (**Fig. S1**). Regional land-use types were defined as near-natural when > 85% of the region were covered by near-natural vegetation with a minimum of 50% forest, as agriculture when > 40% were covered by arable land and managed grassland, and as urban when > 14% were covered by housing, industry and traffic infrastructure. In each selected region, plots were established in the three habitat types dominating in the respective region (out of four possible types: forest, grassland, arable field or settlement), while avoiding overlap of 1-km ‘buffer zones’ among plots. When habitat types happened to be similarly represented in a region, the more contrasting habitat type was chosen. This means, if arable field and settlement had been selected by dominance, forest rather than grassland was chosen as third habitat type. Plots were installed as 30 m x 3 m experimental strips on open herbaceous vegetation – e.g. forest glades, grassland, field margins, parks – with at least 50 m distance to larger roads and other habitat types (e.g. between forest and an experimental strip on a field margin). Land owners (e.g. private individuals) or their official representatives (i.e. in case of ownership through municipalities, church, the Bavarian State Forest and the National Park Bavarian Forest) approved access to their land and the conduct of experiments, as well as the leaseholders, where applicable. Research on predation rates was realised on 147 out of 179 LandKlif plots, yet complete data sets were acquired for 113 plots (data exclusion criteria, see below).

Predation rate assessment

Arthropod predation rates were assessed using standardised green artificial caterpillars (diameter 3 mm; length 20 mm) made from plasticine (Weible Fantasia KNET grün, Weible GmbH & Co. KG, Germany), as suggested for rapid ecosystem function assessment with large geographic extent (Meyer et al. 2015). Brown pieces of paper (size 40 x 19 mm; 100 g m^{-2}, hazelnut brown, paper type “Paperado”, Rössler Papier GmbH & Co. KG, Germany) served as carrier onto which the artificial caterpillars were glued (UHU Alleskleber extra tropffrei gel, UHU GmbH & Co. KG, Germany); 20 artificial caterpillars were placed on every plot at ground level below vegetation but above litter to standardize position. The artificial caterpillars were spread across the 30 m x 3 m experimental strip with at least 1-m spacing between two caterpillars and other experimental items (e.g. Malaise trap). Bamboo sticks with a red tip were punched through a hole in the paper carrier to fix and mark the position of each artificial caterpillar. The collection of the caterpillars started after 48 ± 6 hours (range: 42–54 hours). The presence or absence of arthropod attack marks was assessed in the field using reference images provided by Low et al. (2014). Arthropod attack marks were not further differentiated into finer taxonomic level as this is error prone and hence not recommended (Low et al. 2014). We calculated predation rates per plot as the proportion of artificial caterpillars with arthropod attack marks after 2-d exposure relative to the total number of caterpillars per site. We call the obtained measure ‘predation rate’, as ground-active arthropods, particularly carabids (Coleoptera: Carabidae), are among the most frequent attackers of artificial caterpillars at ground-level and as attack marks of parasitoids are rare (Hertzog et al. 2017, Personal observation UF). Arthropod predation rates were assessed once per plot in May (starting dates between 10th and 25th May 2019).

Measures of habitat characteristics

Plots were established in different local habitat types (forest, grassland, arable field and settlement). Through establishing plots in forest glades, extensive grasslands, crop field margins and green areas in settlements within the different local habitat types, exposure of artificial caterpillars was standardized to open herbaceous vegetation.

Plant species richness per plot was derived between May and July 2019 from plant species records in seven subplots (10 m^2 total sampling area). Further details and a species list are provided in Fricke et al. (2021).

Local weather conditions during caterpillar exposure were derived from thermologgers (ibutton, type DS1923). Those were attached north-facing to a wooden pole, at 1.1 m above ground and roughly 0.15 m below a wooden roof, which prevented direct solar radiation. One thermologger was established per plot. We extracted mean temperature and mean relative humidity (in the following referred to as 'local mean temperature' and 'mean relative humidity') during the study-site specific exposure period of the artificial caterpillars from hourly measurements of the thermologgers.

Measures of regional land use and climate

Landscape diversity was calculated as Shannon Index from detailed land-cover maps (combination of ATKIS 2019, CORINE 2018 and IACS 2019, see (Fricke et al. 2021)) based on six main land-cover types (semi-natural habitat, forest, grassland, arable, urban, water). Thus, high landscape diversity indicates more different land-cover classes, more similar proportions of them or both. Landscape diversity was calculated in radii around the centre point of the plots at six spatial scales (0.5–3.0 km, in 500-m steps). At 2-km scale, low landscape diversity equated a dominance of forest or arable land, and the land-cover proportions of semi-natural habitat and water were below 7.5% and 10.2%, respectively.

We retrieved 30-year multi-annual mean temperatures (1981–2010, MAT) per plot based on gridded (1-km resolution) monthly averaged mean daily air temperatures (Deutscher Wetterdienst 2020).

Data analysis

Prior to data analysis, data exclusion criteria were applied to standardize data. We excluded artificial caterpillars exposed to attack for more than 54 hours (exceeding 48 ± 6 h limit), 'released' later than 25th May, and recovered incomplete with a loss of more than 20% (<16 artificial caterpillars per plot). In total, we achieved standardized data on 113 plots. Artificial caterpillars from 58 of these plots (51%) were transported to the lab to double-check the assessments done in the field.

Field and lab assessments of arthropod predation rates were positively correlated (Pearson's r = 0.79; **Fig. S2**). In the following, arthropod predation rates refer to the field observations (113 plots).

Arthropod predation rate data were analysed with binomial generalized mixed effect models to cope with proportional data (derived from absence-presence data) using the R-package 'glmmTMB' (Brooks et al. 2017) with R version 4.0.3 (R Core Team 2020). Region was included as a random term to account for the nested study design and was retrieved throughout the model selection process (Bolker et al. 2008). Due to zero-inflation (complete absence of attack from 17% of plots), confirmed using the R-package 'DHARMa' (Hartig 2020), we added a zero-inflation term. We did not account for exposure duration of the artificial caterpillars in the models, since data were standardized by exposure duration (48 ± 6 h limit) and similar exposure durations of 48.2 ± 1.7 h (mean ± SD) were realized among plots.

As candidate predictors (fixed effects) of arthropod predation rates, we included habitat type, plant species richness, local mean temperature and mean relative humidity (during artificial caterpillar exposure), landscape diversity and MAT. Candidate predictors were z-transformed prior to analysis, while presented models contain untransformed predictor variables.

To parametrize the zero-inflation term, we considered factors which might explain absence of attack on plot level, e.g. arthropod activity limited by low temperatures (Holland 2002). Besides, we visually screened the candidate predictors for accumulation of absence-of-attack events (predation rate = 0) at the extremes of the predictor ranges. Local mean temperature was the only candidate predictor in which absence of attack marks was frequently observed at the lower range on a per plot basis. Therefore, local mean temperature was included as a single candidate predictor in the zero-inflation term. Additionally, we run a separate analysis on presence-absence of attack on plot level (data extracted from predation rate data; predation rate > 0 replaced by 1) to investigate how the probability of attack on plot level was affected through local mean temperature using binomial generalized linear mixed effect models including region as random term (see **Table S1**).

When analysing the data, we first conducted multi-model averaging to identify the most relevant predictors and spatial scales. Models with all possible predictor combinations were created separately for each spatial scale (0.5–3.0 km, six scales). Akaike weights were computed using the dredge-function from the 'MuMin' R-package (Barton 2020). Achieved Akaike weights (w_i) were summed per predictor and spatial scale, whereby high summed Akaike weights (Σw_i; range: 0 (low) – 1 (high)) indicate a high relative importance of a predictor, corresponding to high cumulative probability that a predictor occurs in the best model at the respective spatial scale (Burnham and Anderson 2002).

In a second step, we analysed potential interactive effects of habitat type with plant species richness, weather conditions during artificial caterpillar exposure (local mean temperature, mean relative humidity), landscape diversity and MAT. Therefore, we added single interaction terms (e.g. local habitat type * plant species richness) to the best model at the most relevant spatial scale derived from multi-model averaging. Model selection was done based on Akaike's information criterion corrected for small sample size (AICc). Thereby, models with lower AICc were considered better, and models with ΔAICc < 2 were considered equal and the more parsimonious model was chosen.

Pearson correlations between continuous candidate predictor variables were rather low ≤ 0.33 (**Table S2**) with two exceptions. MAT was positively correlated with local mean temperature (Pearson's $r = 0.59$) and negatively correlated with mean relative humidity (Pearson's $r = -0.51$). However, all variance inflation factors (VIF) fell below the commonly applied threshold for collinearity of variance inflation factor >10 (30, see **Table S3**), unless interactions with the only categorical variable habitat type were included (**Table S4**), which commonly inflates VIF; the latter were calculated using the R-package 'performance' (Lüdecke et al. 2020). Local mean temperature (Kruskal Wallis, $P = 0.070$), mean relative humidity (Kruskal Wallis, $P = 0.219$) and landscape diversity (2-km scale, Kruskal Wallis, $P = 0.187$) were similar among habitat types whereas plant species richness was higher in grasslands than arable plots and intermediate in forests and settlements (Kruskal Wallis, $P = 0.022$; Bonferroni-corrected Wilcoxon test), and MAT was higher in settlements than forests and grasslands, and intermediate in arable plots (Kruskal Wallis, $P = 0.008$; Bonferroni-corrected Wilcoxon test) (**Fig. S3**).

Results

Artificial caterpillars encountered arthropod attack on 83% of the plots. At plot level, absence of arthropod attack occurred mainly at low local temperatures, while attack (predation rates > 0) was observed with 80% probability when local mean temperatures were above 7°C (**Fig. 1, Table S1**). On plots with arthropod attack, on average 26% (mean; ± 19% SD) of the artificial caterpillars were attacked per plot within 2-d exposure; across all plots, the average predation rate was 21% (mean± 20% SD).

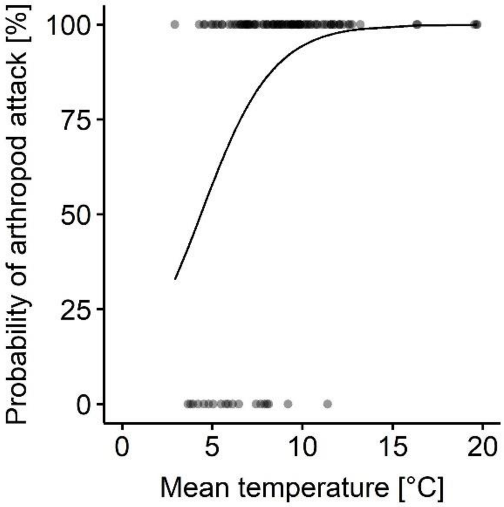

Figure 1. Probability of arthropod attack relative to local mean temperature during artificial caterpillar exposure. Logistic regression curve and dots indicate absence (0) and presence (1) of arthropod attack on artificial caterpillars at plot level.

Due to landscape diversity as landscape parameter, models at intermediate scales (1.5, 2.0 or 2.5-km) – particularly at 2-km scale – were more important for explaining arthropod predation rates than models at smaller (0.5 km, 1.0 km) or larger scales (3.0 km), as shown by sum of Akaike weights (Σw_i, **Fig 2A**). The relative importance of candidate predictors for explaining arthropod predation rates revealed a similar pattern across all spatial scales, with high relative importance of landscape diversity and local mean temperature as zero-inflation term, intermediate relative importance of mean relative humidity, and low relative importance of MAT, plant species richness, local mean temperature (as fixed effect) and habitat type (**Figs 2B and 3**). Thus, landscape diversity and – as a zero-inflation term – local mean temperature have a high probability to appear in the best fitting model across spatial scales (**Fig. 2B**), with the most substantial contribution in models including landscape diversity at the intermediate 2-km scale (**Fig. 2A**, see also **Table S3**).

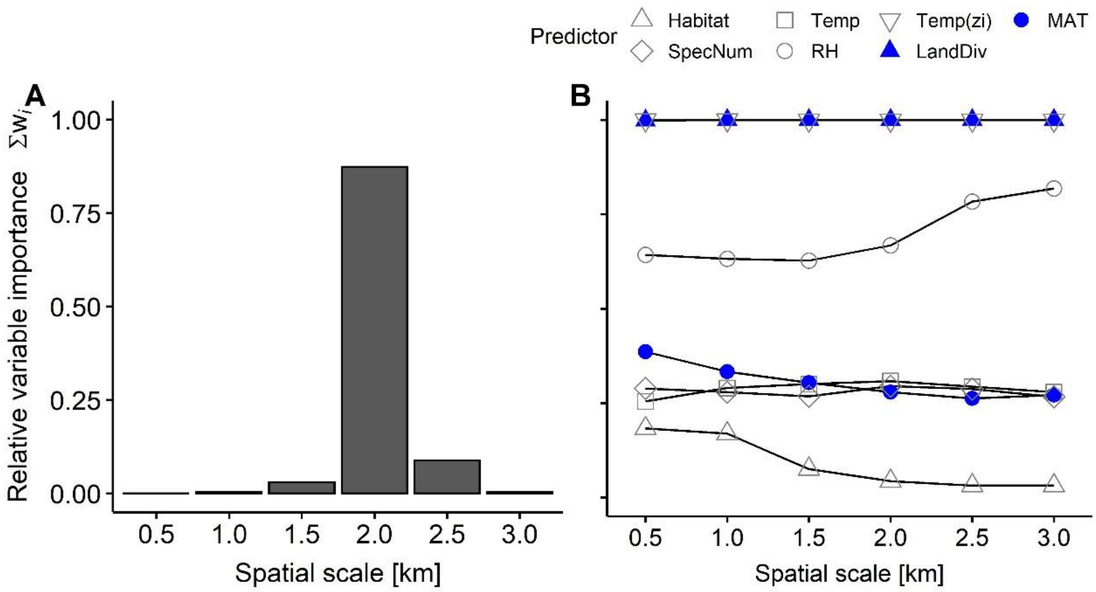

Figure 2. Relative importance (sum of Akaike weights) for explaining arthropod predation rates of A) spatial scale (i.e. models with all possible predictor combinations at one scale relative to the others) and of B) each candidate predictor per spatial scale. White symbols refer to habitat characteristics (Habitat: habitat type, SpecNum: plant species richness, Temp or RH: local mean temperature or mean relative humidity during artificial caterpillar exposure, zi: included as zero-inflation term) and filled blue symbols to regional factors (LandDiv: landscape diversity, MAT: multi-annual mean temperature). Landscape diversity is the only landscape parameter (value changes with spatial scale).

Multi-model averaging revealed that, arthropod predation rates were similar among habitat types (**Fig. 3A**; mean ± SD, forests 0.20 ± 0.20, grasslands 0.22 ± 0.20, arable fields 0.21 ± 0.20, settlements 0.21 ± 0.20), and across the observed range of plant species richness (**Fig. 3B**) and local mean temperature (**Fig. 3C**), while higher relative humidity tended to decrease arthropod predation rates (**Fig. 3D; Table S3**). Local mean temperature as zero-inflation term equals a higher probability of arthropod attack at plot level with higher local mean temperatures (**Fig 1**). Particularly at 2-km scale (**Fig. 2A**), arthropod predation rates increased towards diverse landscapes (**Fig. 3E**). Higher maximum predation rates and more frequently high predation rates were observed in more diverse landscapes than landscapes dominated by a single land cover type (**Fig. 3E**, e.g. compare landscape diversity < 0.69 and ≥ 0.69, landscape diversity value of 0.69 equals an effective number of two land-cover types). MAT did not substantially affect arthropod predation rates (**Fig. 3F**). We observed no interaction effects of any predictor on arthropod predation rates depending on habitat type (**Table S4**).

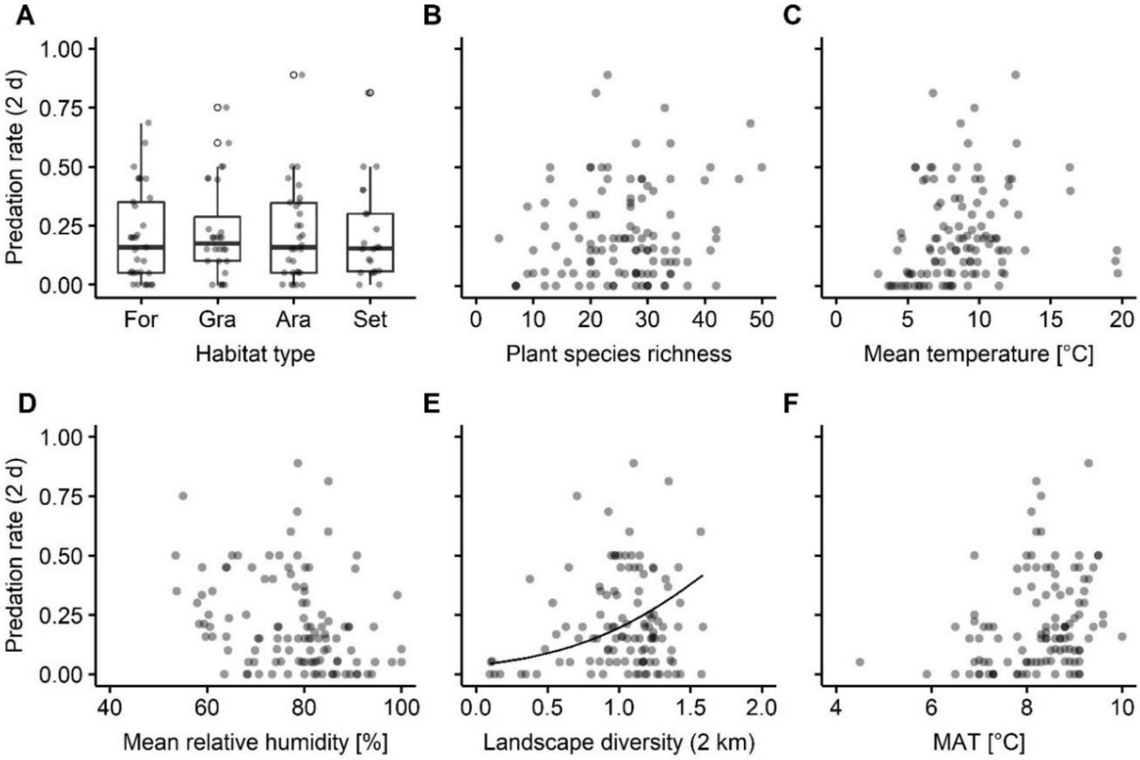

Figure 3. Relationship between arthropod predation rates and candidate predictors: A) Habitat type (For: forest, Gra: grassland, Ara: arable field, Set: Settlement), B) plant species richness, C+D) local mean temperature and mean relative humidity during artificial caterpillar exposure, E) landscape diversity at 2-km scale and F) multi-annual mean temperature (MAT). Light grey dots present values per plot; overlapping dots appear darker. In A) circles indicate outliers. In B-F) solid lines indicate model predictions of the best model derived through multimodel averaging.

Discussion

In this study, we assessed drivers of arthropod predation in open herbaceous vegetation in typical habitat types of the temperate region. Arthropod predation rates in different habitat types were similar and responded similarly to both local and regional drivers. Towards diverse landscapes, particularly at 2-km scale, arthropod predation rates increased, whereas they tended to decrease towards higher mean relative humidity and were frequently absent from plots with low local mean temperatures. Plant species richness and MAT did not substantially affect arthropod predation rates.

The observed average arthropod predation rate of 21% (in 2 days) in May was in the same order of magnitude as reported in other studies on artificial caterpillars at ground-level in temperate regions, when assuming that arthropod predation rates scale linearly with exposure time (see Meyer et al. 2019) and tend to increase from spring towards summer (Ferrante et al. 2014; Hertzog et al. 2017). In open herbaceous vegetation, Hertzog et al. (2017) obtained average arthropod predation rates of 15% (per day) in May, and Meyer et al. (2019) determined arthropod attack marks on 51% of the recovered artificial caterpillars (after 3 days) in summer.

Among local habitat types (forest, grassland, arable field, settlement) arthropod predation rates were not substantially different and high arthropod predation rates were observed in all habitat types. However, large variation in predation rates among plots of the same habitat type may result from largely different natural enemy communities due to a selective permeability of habitat edges. This permeability depends both on characteristics of the habitat edge – e.g. of natural or anthropogenic origin (Magura et al. 2017) – and on the behaviour of a predator – e.g. habitat and trophic specialist or generalist (Denno et al. 2005; Rand et al. 2006). Thus, large variation in spill-over from adjoining habitat into open herbaceous vegetation possibly masked differential effects of local habitat types on arthropod predation rates. This assumption of variation in spill-over from adjoining habitat is supported by the significant impact of landscape diversity on local predation rates.

Towards higher landscape diversity (particularly at 2-km scale), arthropod predation rates increased. Thus, in more diverse landscapes natural enemy communities were likely denser (Denno et al. 2005, p. 218), richer in the number of species (Griffin et al. 2013) or more frequently included effective predators (Griffin et al. 2013; Alhadidi et al. 2018). However, among plots in diverse landscapes we also observed large variability in predation rates, which may have several reasons. First, natural enemies may respond variably to diverse landscapes depending on i) the presence, proportion and combination of certain land-cover types – which may differ in their supply of complementing or supplementing resources (Dunning et al. 1992; Rand et al. 2006) –, ii) the permeability of boundaries between land-cover types – but also at finer scales – (Denno et al. 2005; Rand et al. 2006), and therefore iii) the configuration of land-cover types (Fahrig 2017). Second, changes in natural enemy communities likely mediate landscape-diversity effects on predation rates, but it is not yet fully understood which changes landscape diversity elicits in natural enemy communities (see Denno et al. 2005, p. 218), and how and under which conditions this links to altered predation functions (Griffin et al. 2013; Alhadidi et al. 2018; Ostandie et al. 2021). Thus, landscape diversity promotes predation rates, but variability in predation rates in diverse landscapes – and elucidated potential sources of this – point out future research directions to derive more specific recommendations for landscape management aiming to promote top-down regulation of herbivores and potentially also of agricultural pests.

The absence of habitat type effects but increasing predation rates towards higher landscape diversity does not mean that directly adjoining habitat type is less important to arthropod predation than general landscape diversity, yet it suggests that the landscape composition of the intermediate surrounding (i.e. 2-km radius) impacts natural enemy communities in a way that can alter predation rates independent of the dominant habitat in the vicinity. Thus, our results provide first evidence that landscape diversity favours high predation services (in open herbaceous vegetation) across typical habitat types in the temperate region.

Local weather conditions during artificial caterpillar exposure partially shaped arthropod predation. In our study, higher local mean temperatures made it more likely to observe predation (predation rates > 0), but did not substantially increase predation rates. This seems to be in contrast to observations from pitfall trap catches, where numbers of many ground-active arthropod species in the catches increased with temperature (Saska et al. 2013), which similarly could have increased the likelihood of encounter with an artificial caterpillar. However, as we did not study predation rates as time-series but on different plots, natural enemy communities possibly differed between plots and entailed arthropod species with different temperature preferences (Holland 2002) and sensitivities (see Saska et al. 2013), which can explain the absence of a clear temperature relationship in our study. Furthermore, local mean temperatures measured 1-m above ground possibly reflected the conditions experienced by a predator differently depending on the effects of vegetation structure on microclimate and the daily activity pattern. Thus, local weather conditions may influence predation rates but this effect might be masked in our study, possibly through differences in natural enemy communities among plots and a discrepancy between the measured and experienced temperature by ground-active arthropods. However, we more frequently observed the absence of attack (predation rates = 0) at low local mean temperatures. Accordingly, temperature thresholds may apply more broadly to arthropod predation, at least in spring. Both, because emergence after overwintering is temperature-dependent (Denlinger 2002) and temperature thresholds of relevant predators may not have been reached in colder areas of our study region or not long enough for relevant predators to move onto the plots, and – maybe even more importantly– because initiation of daily activity seems to depend on certain temperatures (Holland 2002, p. 13). Thus far only few studies, which quantified predation, have reported on local weather conditions (Ambarlı et al. 2021). Our results provide further evidence that local temperature impacts predation and thus should be considered when interpreting predation functions.

MAT did not substantially affect arthropod predation rates. This may have several reasons. First, natural enemy communities were not substantially altered along the observed MAT gradient, or second, different natural enemy communities can provide similar predation rates. Although we cannot test the first reason, studies reporting on increased predation rates towards lower latitudes and altitude (Roslin et al. 2017) or towards higher mean annual temperatures (Michalko et al. 2019) were conducted at a global scale. Thus, various factors may obscure a (weak) climate effect in studies covering a fraction of the global temperature range, such as our study. Indeed, we observed large variation in predation rates among plots of similar MAT, which may suggest that other factors impact natural enemy communities more strongly than MAT. However, even if natural enemy communities change along the MAT gradient, this may not have led to differences in predation rates. This is supported by the observation that several independent studies using artificial caterpillars in temperate regions reported predation rates in the same order of magnitude (see above)

– which likely encompasses large differences in natural enemy communities –, but also by the marked relevance of key predators for predation functions, e.g. compared to natural enemy richness (Griffin et al. 2013). Key predators can be, for instance, particular voracious predator species (Işikber and Copland 2001) and predators with specific feeding traits matching the ‘vulnerability trait’ of the prey (Brousseau et al. 2018). Thus, high predation rates across the covered MAT gradient illustrate the potential to increase predation rates (e.g. through landscape management) independent of a potential moderate increase of MAT in the near future.

Plant species richness did not substantially affect arthropod predation rates in our study, whereas Barnes et al. (2020) reported increasing top-down control and Hertzog et al. (2017) increasing invertebrate predation rates towards higher plant species richness. However, these positive effects of plant species richness on predation rates were reported from grassland experiments (Hertzog et al. 2017; Barnes et al. 2020), whereas we report from a multi-scale field experiment. This likely included much more variation in natural enemy communities and also considerable differences in plant species pools between plots. Thus, plant species richness may indirectly affect arthropod predation rates depending on the natural enemy community composition and the plant species pool, but our data suggests that this is not a ubiquitous or dominant pattern.

Our results provide insights into herbivore regulation through arthropod predators, but are limited by the method of artificial caterpillars as sentinel prey. Common predators on artificial caterpillars at ground-level are chewing insects, especially carabids (Ferrante et al. 2014). Properties of the artificial caterpillars such as length (Lövei and Ferrante 2017) and colour (Ferrante et al. 2017a) act as a filter – with yet unknown specificity – on the interacting predators. Furthermore, predation rates on artificial caterpillars do not directly translate into successful predation attempts as the complexity of predator-prey interactions is reduced by e.g. prey mobility (Öhlund et al. 2014) and defensive traits such as cuticular toughness (Brousseau et al. 2018). However, predation rates on artificial caterpillars are widely recognised for their standardisable estimate (Howe et al. 2009; Meyer et al. 2015) and can provide unique insights into drivers of predation functions through generalist predators, which are otherwise impossible to obtain.

Conclusion

We conclude that landscape diversity favours high arthropod predation rates in open herbaceous vegetation across typical habitat types in the temperate region, while adjoining habitat type and plant species richness are of minor importance when studying a large spatial extent with possibly vastly different natural enemy communities. However, more research is needed on the underlying mechanisms of the landscape diversity effect to deduce more specific management options for improved top-down control of herbivores, and for enhanced natural pest control in agricultural ecosystems. Besides, local weather conditions impact predation, e.g. low local mean temperatures can limit predation, and hence should be considered when interpreting predation rates. With respect to MAT, arthropod predation rates did not substantially change and high rates were observed across the covered climatic gradient, which highlights the potential to increase predation rates (e.g. through landscape management) independent of potential moderate temperature increases in the near future.

Acknowledgements

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Supplement

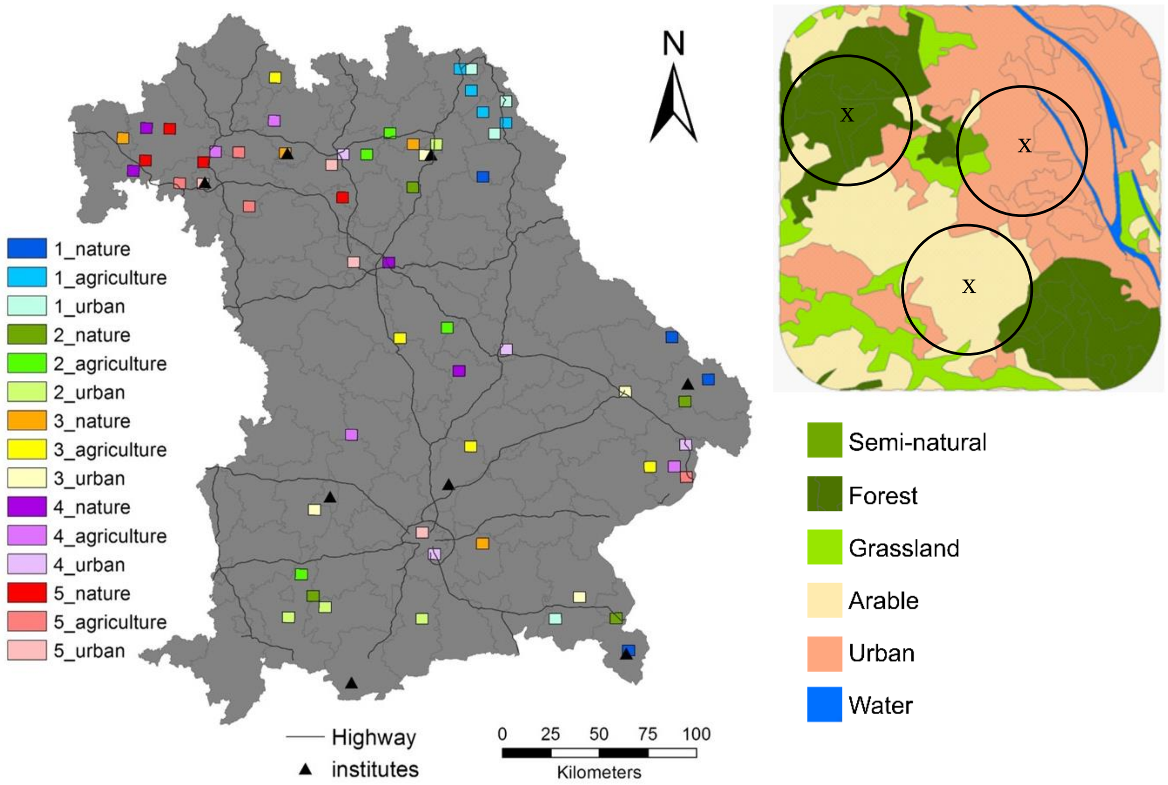

Figure S1 Maps showing study regions within Bavaria, Germany (left), and plots within an example region (right). Squares indicate locations of study regions. Different colours represent the 15 combinations of climate zones (1–5: multi-annual mean temperature from 1981–2010; < 7 °C, in 0.5 °C steps to 9°C, > 9°C) and regional land-use types (nature = near-natural, agriculture and urban), in four replicates. Regional land-use types were defined as near-natural when > 85% of the region were covered by near-natural vegetation with a minimum of 50% forest, as agriculture when > 40% were covered by arable land and managed grassland, and as urban when > 14% were covered by housing, industry and traffic infrastructure. The land cover map, to the right, shows six main land use types (different colours), three plot locations marked by “x” within the dominating land use types of the region, and 1-km “buffer zones” around the plots.

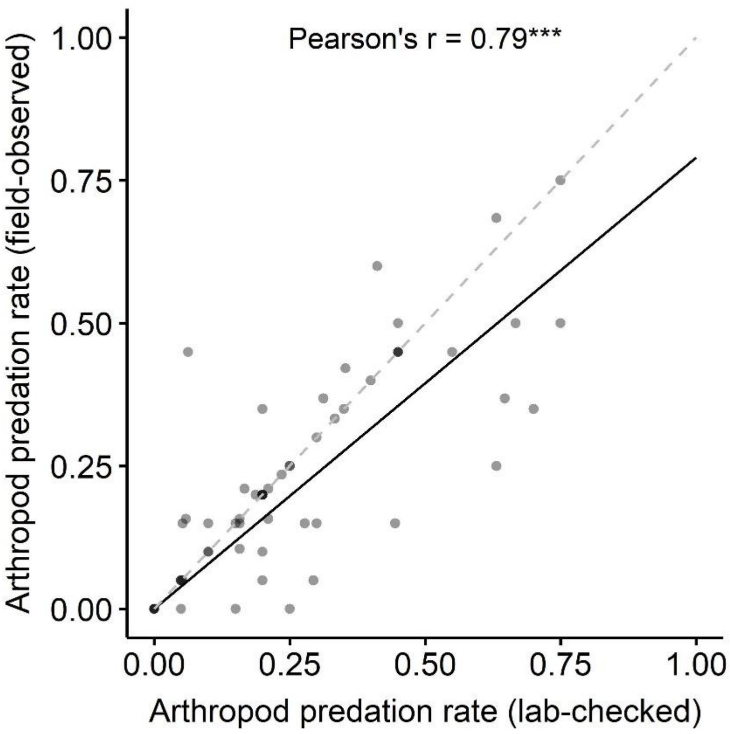

Figure S2 Pearson correlation between arthropod predation rates assessed in the field and in the lab. Dots indicate values per plot; overlapping dots appear darker. The dashed grey line presents a hypothetically perfect correlation (r = 1) and the solid black line, the observed correlation based on α = 0.05, P < 0.001***.

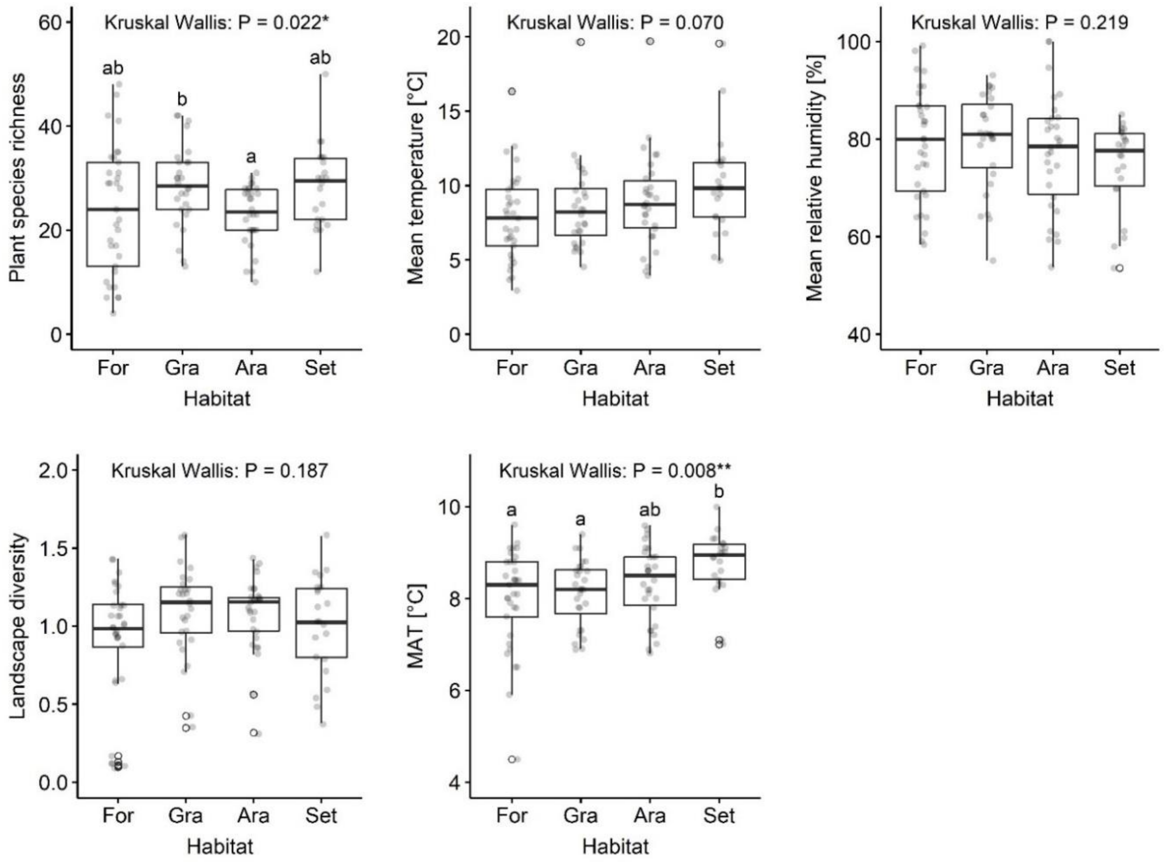

Figure S3 Relationship between habitat type and other candidate predictors of arthropod predation rates. Dots indicate values per plot; overlapping dots appear darker. Asterisks highlight significance levels of P < 0.05* and P < 0.01**. Letters indicate significant differences between habitat types based on Bonferroni-corrected pairwise comparisons using Wilcoxon rank sum test.

Table S1 Model output on the probability of arthropod attack on plot level (presence-absence of attack from a plot, binomial generalized linear mixed model) including local mean temperature during artificial caterpillar exposure as predictor compared to an empty model (null, null model). Bold font highlights the best model based on ΔAICc < 2 and parsimony.

Model	Estimate	df	AICc	ΔAICc
incl. mean temperature	1.58	3	89.4	0.00
(null)		2	106.5	17.02

Table S2 Predictor variable details and Pearson's correlation coefficients included in multimodel averaging on arthropod predation rate models based on 113 study sites. Significant correlations based on α = 0.05 are indicated as following: *P* < 0.05*, *P* < 0.01**, *P* < 0.001***.

								Pearson's correlation coefficients			
Scale [km]	Predictor	Min	1st Qu	Median	Mean	3rd Qu	Max	SpecNum	Temp	RH	MAT
	SpecNum	4	20	27	25.7	31	50				
	Temp	2.9	6.6	8.6	8.7	10.3	19.7	0.32***			
	RH	53.6	70.5	79.8	77.7	84.8	100.0	-0.28**	-0.24*		
	MAT	4.5	7.8	8.4	8.3	8.9	10.0	0.33***	0.59***	-0.51***	
0.5	LandDiv	0.0	0.5	0.9	0.8	1.1	1.4	0.13	-0.07	0.05	0.02
1.0	LandDiv	0.0	0.7	0.9	0.9	1.2	1.6	0.09	-0.13	0.08	0.00
1.5	LandDiv	0.0	0.8	1.1	1.0	1.2	1.6	0.06	-0.09	0.07	0.06
2.0	LandDiv	0.1	0.9	1.1	1.0	1.2	1.6	0.03	-0.07	0.09	0.07
2.5	LandDiv	0.1	0.9	1.1	1.1	1.2	1.6	-0.00	-0.06	0.11	0.07
3.0	LandDiv	0.1	1.0	1.1	1.1	1.3	1.6	-0.03	-0.06	0.14	0.03

Min: Minimum, Max.: Maximum, Qu: Quantile, SpecNum: plant species richness, Temp or RH: local mean temperature [°C] or mean relative humidity [%] during artificial caterpillar exposure, LandDiv: landscape diversity (Shannon index), MAT: Multi-annual mean temperature

Table S3 Model output of arthropod predation rate models (zero-inflated binomial generalized linear mixed model) with different parametrization (best: best model based on ΔAICc < 2 and parsimony; ΔAICc < 4; full: model containing all candidate predictors; null: null model with or without temperature as zero-inflation term) at the best spatial scale identified by multimodel averaging (2-km scale). Best model is highlighted in bold font.

	Candidate predictors												
Model	Habitat	Spec Num	Temp	RH	Temp(zi)	LandDiv	MAT	df	AICc	ΔAICc	Pseudo R^2_m	Pseudo R^2_c	VIF_{max}
best					**-2.44**	**0.59**		5	591.4	1.81	0.08	0.25	-
ΔAICc<4				-0.27	-2.40	0.58		6	589.6	0.00	0.09	0.23	1.00
ΔAICc<4		-0.06		-0.28	-2.41	0.59		7	591.3	1.73	0.09	0.24	1.05
ΔAICc<4			0.10	-0.25	-2.39	0.58		7	591.4	1.78	0.09	0.23	1.05
ΔAICc<4				-0.24	-2.39	0.57	0.07	7	591.7	2.11	0.09	0.23	1.18
ΔAICc<4			0.15		-2.43	0.60		6	592.5	2.90	0.08	0.25	1.01
ΔAICc<4					-2.41	0.58	0.16	6	592.5	2.91	0.09	0.24	1.01
ΔAICc<4		-0.07	0.12	-0.26	-2.41	0.60		8	592.9	3.32	0.09	0.24	1.10
ΔAICc<4		-0.04			-2.46	0.60		6	593.4	3.77	0.08	0.26	1.03
ΔAICc<4		-0.06		-0.26	-2.40	0.59	0.07	8	593.4	3.84	0.09	0.24	1.19
full	+	-0.08	0.13	-0.27	-2.42	0.62	0.01	12	601.8	12.18	0.10	0.24	1.55
null+ Temp(zi)					-2.07			4	625.1	35.48	0.00	0.14	-
null								3	638.7	49.15	0.00	0.16	-

SpecNum: plant species richness, Temp or RH: local mean temperature [°C] or mean relative humidity [%] during artificial caterpillar exposure, LandDiv: landscape diversity (Shannon index), MAT: Multi-annual mean temperature [°C], zi: included as zero-inflation term, df: Degrees of freedom, AICc: Akaike's information criterion corrected for small sample size, ΔAICc: Difference in AICc relative to minimum value, Pseudo R^2: marginal (only fixed effects) and conditional (fixed + random effects) Nakagawa R^2 values, VIF_{max}: Highest variance inflation factor

Table S4 Model output of arthropod predation rate models including interactive effects with habitat type (zero-inflated binomial generalized linear mixed model) at the best spatial scales identified by multimodel averaging (2-km scale). Interaction terms are added to the original best model and to null models containing only temperature during exposure as zero-inflation term. Asterisks between candidate predictors indicate that both main effects and their interaction term is included. Best model parametrization is derived based on ΔAICc < 2 and parsimony. Best models are highlighted in bold font.

Interaction term Model	Candidate predictors	df	AICc	ΔAICc	Pseudo R^2_m	Pseudo R^2_c	VIF_{max}
*Habitat*SpecNum*							
original.best + interaction	Habitat*SpecNum + LandDiv + Temp(zi)	12	599.8	8.45	0.09	0.27	13.98
interaction	Habitat*SpecNum + Temp(zi)	11	631.4	40.01	0.01	0.15	11.08
best	**LandDiv + Temp(zi)**	5	591.4	0.00	0.08	0.25	-
*Habitat*Temp*							
original.best + interaction	Habitat*Temp + LandDiv + Temp(zi)	12	597.2	5.83	0.10	0.25	3.92
interaction	Habitat*Temp. + Temp(zi)	11	616.1	24.66	0.04	0.15	2.87
best	**LandDiv + Temp(zi)**	5	591.4	0.00	0.08	0.25	-
*Habitat*RH*							
original.best + interaction	Habitat*RH + LandDiv + Temp(zi)	12	594.6	3.22	0.11	0.26	2.16
interaction	Habitat*RH. + Temp(zi)	11	632.6	41.23	0.02	0.14	2.09
best	**LandDiv + Temp(zi)**	5	591.4	0.00	0.08	0.25	-
*Habitat*LandDiv*							
original.best + interaction = interaction	Habitat*LandDiv + Temp(zi)	11	594.7	3.33	0.12	0.29	4.70
best	**LandDiv + Temp(zi)**	5	591.4	0.00	0.08	0.25	-
*Habitat*MAT*							
original.best + interaction	Habitat*MAT + LandDiv + Temp(zi)	12	591.0	0.00	0.10	0.24	4.67
interaction	Habitat*MAT + Temp(zi)	11	622.1	31.06	0.04	0.14	5.22
best	**LandDiv + Temp(zi)**	5	591.4	0.36	0.08	0.25	-

Df: Degrees of freedom, AICc: Akaike's information criterion corrected for small sample size, ΔAICc: Difference in AICc relative to minimum value, Pseudo R^2: marginal (only fixed effects) and conditional (fixed + random effects) Nakagawa R^2 values, VIF_{max}: Highest variance inflation factor, SpecNum: plant species richness, Temp or RH: local mean temperature [°C] or mean relative humidity [%] during artificial caterpillar exposure, LandDiv: landscape diversity (Shannon index), MAT: Multi-annual mean temperature, zi: included as zero-inflation term

Chapter 4

Pest control and yield of winter oilseed rape depend on spatiotemporal crop-cover dynamics and flowering onset: implications for global warming

Ute Fricke, Sarah Redlich, Jie Zhang, Caryl S. Benjamin, Jana Englmeier, Cristina Ganuza, Maria Haensel, Rebekka Riebl, Sandra Rojas-Botero, Cynthia Tobisch, Johannes Uhler, Lars Uphus, Ingolf Steffan-Dewenter

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Abstract

Global warming can increase pest pressure, since temperature drives life cycles of crops, pests and their natural enemies with potential consequences on their phenological synchrony. Besides, land-cover composition and its spatiotemporal dynamics determine, e.g. (supplemental) foraging resources of crop pests and their enemies. Here, we investigated temperature effects on multiple aspects of winter oilseed rape (OSR) production and elucidate land-cover composition – encompassing crop-cover dynamics – and flowering onset as adaptation strategies.

Twenty-nine winter OSR fields were investigated along climate (multi-annual mean temperature, MAT) and land-use gradients across Bavaria, Germany. We determined crop growth stages (biweekly), abundances of pollen beetles and stem weevils, bud loss, stem damage, pollen beetle parasitism rate and crop yield. Land-use parameters (proportion of non-crop area, proportion of OSR, change in proportions of OSR between years) were calculated at nine spatial scales (0.2–5 km).

Towards higher MAT, OSR fields flowered earlier, and pollen beetle abundances and bud loss increased, while pollen beetle parasitism rate, stem weevil abundance and stem damage did not substantially change.

Pollen beetle abundances decreased towards larger OSR proportions (1-km scale), and from stronger to lower reduction of OSR proportions between years (5-km scale), with effects being more pronounced towards higher MAT; abundances were similar across proportions of non-crop area. In contrast, stem weevil abundances were independent from land-cover composition.

Crop yields decreased towards high pollen beetle abundances and bud loss, and increased towards fields with early flowering onset, but were similar across the MAT gradient.

Synthesis and applications: Similar OSR proportions in consecutive years – particularly at large spatial scales – can support low pollen beetle abundances through avoiding crowding on reduced oilseed rape proportions in a specific year. Early flowering of OSR may promote phenological escape from pollen beetle infestation in the most vulnerable bud stage. Thus, managing spatiotemporal crop-cover dynamics and flowering onset (e.g. through cultivar choice) can support adaptation of winter OSR production to warming climates, and potentially also that of further crops.

Introduction

Global climate change poses a major challenge for crop production (Pullens et al. 2019; Lehmann et al. 2020; Molotoks et al. 2021). For instance, productivity of crops will likely be subjected to direct effects from higher temperatures – e.g. accelerated crop development (Weymann et al. 2015), which may leave too little time for crop plants to reach the optimal size for seed production (Anten and Vermeulen 2016) –, but also indirect effects due to altered biotic interactions (natural pest control: Vucic-Pestic et al. 2011; herbivory: Lehmann et al. 2020). In addition, pest pressure on crops depends on landscape composition, e.g. the proportion of suitable habitat used for (supplemental) foraging by pests and their natural enemies (Zaller et al. 2008a; Rusch et al. 2011; Skellern and Cook 2018). Therefore, global warming – and land use change – can result in lower yields as reported for the world's dominant crops (Zhao et al. 2017). Yet too little is known about the combined impacts of temperature and land use on crop production, despite an urgent need for adaptation strategies of crop production to a warming climate.

Winter oilseed rape (OSR) is the most important oilseed crop in northern and central Europe, with the pollen beetle *Brassicogethes aeneus* and the stem weevils *Ceutorhynchus napi* and *C. pallidactylus* being among its major pests (Williams 2010). Pest pressure on OSR production is increasing due to the vast spread of pesticide-resistant pests (Heimbach and Müller 2013), while the effects of temperature on pest abundances are still largely unknown. Temperature may exacerbate pest pressure, since damage from many insect pest species is likely to increase with increasing temperatures (Lehmann et al. 2020). Temperature increase may partially release pollen beetles from natural control, since occurrence of pollen beetles and its parasitoid *Tersilochus heterocerus* are temperature-dependent, albeit temperature preferences differ (Johnen et al. 2010). Pollen beetles cause most damage at the bud stage in OSR fields (Seimandi-Corda et al. 2021), which makes timing of pollen beetle infestation and onset of flowering essential. Flower onset ahead of pollen beetle infestation harbours the potential to escape pollen beetle damage at the most susceptible early bud stage (Williams 2010). Higher temperatures may facilitate this potential, depending on the relative effects of temperature on the occurrence of pollen beetles (Junk et al. 2015) and the duration of OSR growth stages (Weymann et al. 2015). In addition, earlier flowering may also impact further biotic interactions, e.g. plant-pollinator interactions, and may impede reaching optimal size for seed production (Anten and Vermeulen 2016). Whether higher temperatures benefit or hamper high OSR yields, depends on their specific effect on the crop, pest and natural-enemy species, and on the biotic interactions among them (e.g. crop–pest, pest–natural-enemy interactions). To study this system in its complexity and to derive climate-adapted management strategies, extensive field studies are needed to complement in-depth studies on temperature effects on the single organisms (pests and natural enemies: Johnen et al. 2010; OSR: Weymann et al. 2015).

Land-cover composition impacts OSR pests (Skellern and Cook 2018). Pollen beetles and stem weevils – being specialized on cruciferous plants for oviposition (Williams 2010) – benefit from OSR cultivation. Hokkanen (2000) found increasing reproductive success and pest pressure of pollen beetles with time (years) of OSR cultivation. However, negative (Zaller et al. 2008a) and neutral (Rusch et al. 2013) effects of OSR area (proportion) on pollen beetle abundances have been reported, and also negative effects on stem weevil abundances (Zaller et al. 2008a). Spatiotemporal dynamics in OSR proportions, such as the change in OSR proportions between years, may also impact pest abundances, but evidence is scarce and mainly based on a single study focusing on pollen beetle abundances at 1-km scale (Schneider et al. 2015). For the overwintering of pollen beetles, non-crop areas such as grassland and forest are important (Rusch et al. 2012). Thus, in landscapes with larger proportions of non-crop area, pollen beetles may emerge in larger numbers in spring, increasing the local pollen beetle pool. However, natural enemies of the pollen beetle also benefit from non-crop areas, but rather at smaller spatial scales (Rusch et al. 2011), and can diminish the emerging offspring generation of pollen beetles in spring (Dainese et al. 2017). Stem weevil abundances seem to be indifferent towards non-crop areas (Zaller et al. 2008a). Land-cover composition offers management opportunities for improved OSR protection (Schneider et al. 2015; Skellern and Cook 2018), but these still have to be verified in terms of their suitability for multiple pests and under different climatic conditions.

To advance adaptation of winter OSR production to global warming, we investigate effects of temperature (multi-annual mean temperature), land-cover composition (at a range of spatial scales, 0.2–5 km) and their combined impacts on multiple aspects of winter OSR production, using an extensive multi-scale space-for-time approach (Redlich et al. 2021), and deduce management strategies. In particular, we address the following questions:

1. How does temperature affect flowering onset, pest abundances, crop damage and parasitism rates?
2. How does land-cover composition (proportion of non-crop area, proportion of OSR, change in proportion of OSR between years) affect pest abundances?
3. Are there interactive effects of temperature and land-cover composition on pest abundances?
4. Is the yield of winter OSR affected by temperature, flowering onset and pests (abundance, damage)?

Materials and methods

Study area and site selection

We selected 29 conventionally managed winter OSR fields (with different cultivars; treated with pesticides) within the LandKlif project covering climate and land-use gradients in Bavaria using a space-for-time approach (Fig. 1, Redlich et al. 2021).

Oilseed rape growth stage observation and sampling scheme

In spring 2019, OSR growth stages (of at least 50% of the plants) were observed biweekly at field level as described by Meier et al. (2001). Growth stages from emerging inflorescence (growth stage = 50) to crop senescence (growth stage = 97) were modelled over time with linear mixed models including site as random term (**Fig. S1**). Model slope and intercept were used to calculate the Julian date of flowering onset (growth stage = 60) per field using the linear equation.

OSR was sampled around full flowering (growth stage 64–65; end-April to mid-May) and at crop ripeness (growth stage 87–89; end-June to mid-August). OSR plants were sampled along two parallel transects starting 1 m from one field edge (not bordering a forest) with ≥ 20 m to field edges on either side and ≥ 5 m distance between transects (**Fig. 1**). In two cases only ≥ 16 m to one field edge were realized. When plant growth at the edge was poor, we started sampling a few meters into the field. Flowering OSR plants were cut at ground level every 3 m until 28 m into the field (10 samples per transect; total of 20 samples per field). Cut flowering plants were bagged and stored at -20 °C until further processing. OSR samples at crop ripeness were taken following the same sampling scheme as described above but sampling only every 6 m (total of 10 samples per field). Mature plants were stored in paper bags at a warm (23 °C), dry and well-ventilated place until further processing.

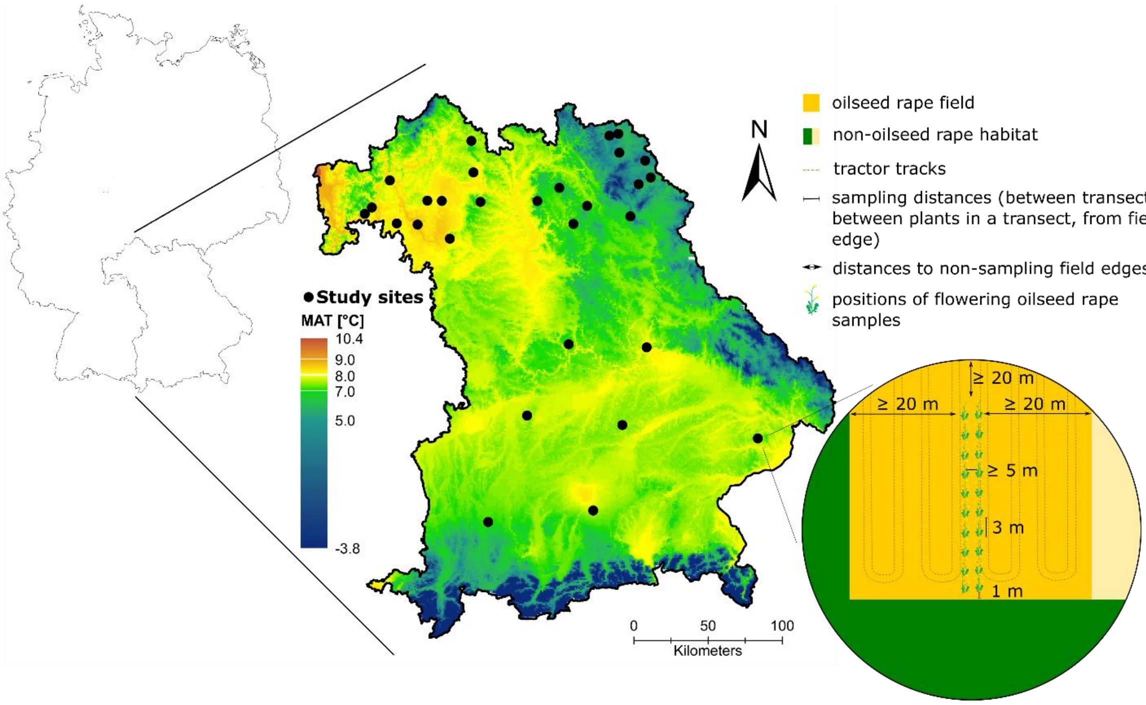

Figure 1 Locations and sampling scheme of the 29 oilseed rape fields studied in Bavaria, Germany. The climate map provides multi-annual mean temperatures (MAT, 1981–2010).

Pest abundance, crop damage and parasitism

Frozen flowering OSR plants were defrosted. Adult pollen beetles in the bag and on the plant were counted. All flowers and buds (> 3 mm, Hervé *et al.*, 2015) were opened using tweezers to count large pollen beetle larvae – which are preferred by *T. heterocerus* for oviposition (Williams 2010) – and black parasitoid eggs inside larvae larger than 2 mm (Berger et al. 2015) for the calculation of parasitism rates. All organs on the main raceme of flowering OSR were counted in five categories: pods, flowers, flower buds, bud loss (dead buds and budless stalks), and broken stalks. Broken stalks (= mainly broken buds, flowers, pods) were caused through transporting and handling of frozen samples and could be identified through visibly moist tips at the breakage, whereas bud loss indicates reduction of potential yield, e.g. due to pollen beetle infestation, stem weevil infestation, and nutrient or pollination deficiency (Zaller et al. 2008b; Jauker et al. 2012). The proportion of bud loss relative to all organs on the main raceme (incl. broken stalks) was calculated. Stems equal to or thicker than 5 mm were measured (length in cm) and cut open. Stem weevil larvae in opened stem pith were counted (= stem weevil abundance). Stem damage by stem weevil larvae was measured as length of orange-coloured pith. Proportion of damaged stem relative to total stem length was calculated.

Oilseed rape yields

To achieve plant yield, we counted all pods and the number of seeds of twenty pods per plant for every ripe and air-dried OSR plant. Thereafter, slight compression and shaking of the plants released the majority of seeds. Seeds were manually cleaned from plant parts. Four hundred seeds per plant were counted with a seed counter, dried in a drying oven at 60 °C until constant dry weight (ca. 24 h), and weighed. Plant seed yield was calculated as the product of the average single seed weight, the average number of seeds per pod, and the number of pods per plant.

Temperature and land-use predictors

We retrieved multi-annual mean temperature (MAT) based on gridded monthly averaged mean daily air temperatures (1-km resolution) from 1981–2010 per site (Deutscher Wetterdienst 2020). MAT was positively correlated with the mean temperature of the month May in the study year (Pearson's r = 0.88, **Fig. S2**, see also **Appendix S1**), indicating that long-term mean temperatures were to some degree related to short-term mean temperatures.

Land-use predictors were calculated at nine spatial scales from 0.2–5 km (in 200-m steps until 1 km, then 1-km steps) centred to the field edge in between transects. Proportions of non-crop area (non-crop%: summed proportion of forest, grassland and semi-natural habitat) were derived from detailed land-cover maps (combined ATKIS 2019, CLC 2018 and IACS 2019; see also **Appendix S2**). Based on IACS data (2018, 2019), we calculated the proportion of OSR (OSR%) in the study year and the change in OSR% relative to the preceding year (ΔOSR%) by $(OSR_{\text{study year}} - OSR_{\text{preceding year}})/OSR_{\text{preceding year}}$; positive values indicate increase, while negative values indicate a decrease. When no OSR was cultivated in proximity to the site in the preceding year, ΔOSR% could not be calculated. One OSR field was ploughed up except for a 100 m x 30 m strip. Since this happened after flowering samples had been taken, the initial OSR field size was considered.

Data analysis

Flowering onset

For 27 (out of 29) fields, we assessed at least four times the OSR growth stage between emerging inflorescence and crop senescence and thus could estimate dates of flowering onset. Flowering onset (field level) was modelled against MAT using linear models (continuous, normally-distributed data) in base-R version 4.0.3 (R Core Team 2020). The model containing MAT was compared with a null model by relative goodness of fit based on Akaike's information criterion corrected for small sample size (AICc) calculated using the R-package 'MuMIn' (Barton 2020). Models with lower AICc value were considered better, models differing by ΔAICc < 2 were treated as equal, and the more parsimonious model was selected. Model residuals were visually assessed using the R-package 'DHARMa' (Hartig 2020).

Pests, crop damage and parasitism

Data on pest abundances (adult pollen beetles, stem weevil larvae), crop damage (proportion bud loss and stem damage) and pollen beetle parasitism derived at OSR flowering were analysed on a per plant basis. Exclusion criteria of plant samples were defined – when needed – and only subsets were analysed. Prior to bud loss analysis, plants with > 5% broken organs on the main raceme were excluded. Stem damage analysis excluded plants without stem weevil larvae. Before analysing parasitism rates, plants were excluded when containing less than three large (> 2 mm) pollen beetle larvae. Complete sites were excluded when more than 17 plants met exclusion criteria (only sites with at least 3 plants per site were included in analysis).

Count data on pest abundances (pollen beetles, stem weevils) were modelled using negative binomial mixed effect models. Stem weevil abundances were zero-inflated (45% zeros), therefore a zero-inflation term was added. The pollen beetle parasitism rate and the proportion of bud loss were modelled using binomial generalized linear mixed effect models (proportions derived from count data), whereas the proportion of stem weevil damage relative to stem height was analysed with beta mixed effect models (proportions derived from continuous data). To facilitate the calculation of beta mixed effect models, ones were replaced by a slightly larger value than the largest non-one value (0.99; stem damage data contained no zeros and 2.6% ones = 8 ones). Due to an excess of zeros in the parasitism data, a zero-inflation term was introduced. Mixed effect models include site as random term (see also **Appendix S3**) and were fitted using the R-package 'glmmTMB' (Brooks et al. 2017). To account for the study design, we evaluated distance effects (from field edge to centre) – since initial pollen beetle infestation starts at the edges (Williams and Ferguson 2010) – but effects along a 28-m transect were small (**Table S1, Fig. S3**) and thus were not further considered.

Prior to analysis, predictor variables were z-transformed to prevent convergence problems (Harrison et al. 2018). To facilitate intuitively interpretable data- and model-presentation, graphs show unstandardized predictor variables, which were computed using the R-package 'ggeffects' (Lüdecke 2018).

When analysing the data (see also **Appendix S3**), we first addressed MAT effects on all five independent variables (2x pest abundance, 2x crop damage, 1x parasitism). Secondly, we analysed pest abundances in more detail including also landscape aspects (non-crop%, OSR% and ΔOSR%) at multiple spatial scales (0.6–5 km, 7 scales, additional predictor sets without ΔOSR%: 0.2–5 km, 9 scales, Pearson's correlation coefficients: **Table S2**) in a multimodel averaging approach using the R-package 'MuMIn' (Barton 2020). In a third step, we created models on pest abundances including interactive effects of MAT and landscape aspects at the specific spatial scales on which both contributed substantially as main effects.

Plant yield

Yield data were averaged per site to facilitate use of pest abundances and crop damage as predictor variables, since different OSR plants were analysed at flowering and crop ripeness due to destructive sampling. Averaged plant yield data were modelled using gamma generalized linear models (positive continuous data) in base-R (R Core Team 2020). Plant yield models were built on four sets of predictor variables to circumvent collinearity between predictor variables (**Table S3**) and overfitting. These sets of predictor variables encompassed 1) pest abundances (adult pollen beetles, stem weevil larvae), 2) crop damage (bud loss, stem damage), 3) MAT and 4) onset of flowering. Beside AICc, Kullback-Leibler-divergence-based R^2 were calculated to compare the best models of each predictor set (Cameron and Windmeijer 1997). Analysis of averaged plant yield encompassed all 29 fields, or 27 fields when flowering onset was included, since on two sites growth stage data was insufficient to calculate flowering onset.

Results

Temperature effects on oilseed rape phenology, pests, crop damage and parasitism

OSR fields flowered earlier towards higher MAT, although flowering onset varied considerably between sites with similar MAT (**Fig. 2A, Table S4**).

All OSR fields were infested with both pollen beetles and stem weevils except for one field, which was infested only with pollen beetles. We counted 3.8 ± 1.2 (mean ± se) adult pollen beetles and 4.6 ± 1.2 stem weevil larvae per plant. We observed an average of 40.0 ± 3.5% (mean ± se) and 17.0 ± 3.6% of bud loss and stem damage, respectively. Pollen beetle parasitism was low, with 16.7 ± 4.6% (mean ± se) of larvae containing black parasitoid eggs, which equals 2.0 ± 0.5 parasitized larvae per plant at the presence of 13.2 ± 2.5 large larvae per plant. Four OSR fields (out of 18 fields included in parasitism analysis) exceeded 30% of pollen beetle parasitism. The number of adult pollen beetles increased with increasing MAT, and so did the proportion of bud loss (**Fig. 2B, C**), whereas pollen beetle parasitism rate, abundances of stem weevil larvae and stem damage did not show a statistically significant pattern across the MAT gradient (**Fig. 2D-F, Table S4**).

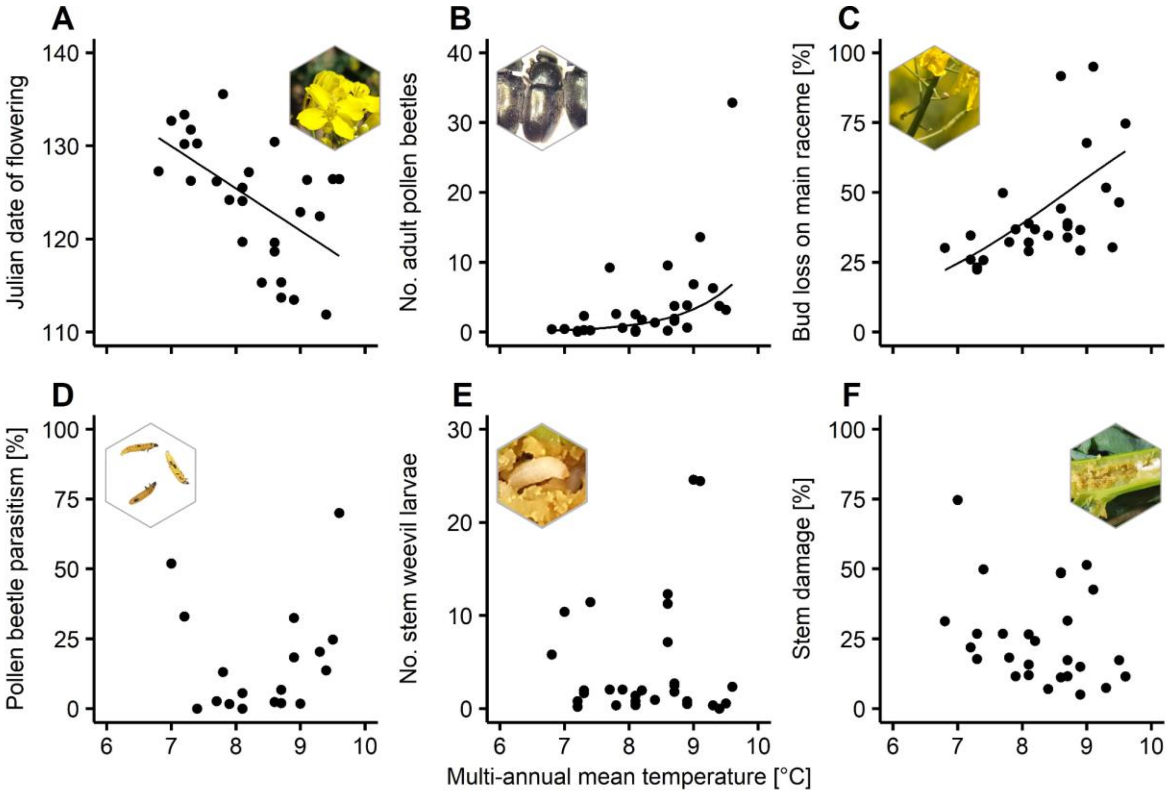

Figure 2 Relationships of multi-annual mean temperature (MAT) and A) flowering onset of oilseed rape fields (27 fields), B) adult pollen beetle abundances (29 fields), C) bud loss (25 fields), D) pollen beetle parasitism rate (18 fields), E) stem weevil larvae abundances (29 fields), and F) stem damage (27 fields). Dots indicate mean values per field. Solid, black lines present predictions of generalized linear mixed effect models – linear model in case of flowering onset –, when the best model includes MAT.

Temperature and land-cover composition effects on pest abundances

Land-cover composition – except for non-crop% – affected abundances of pollen beetles (**Fig. 3A, B, Table S5**), but not stem weevil larvae (**Fig. S4, Table S5**). Pollen beetle abundances decreased towards larger OSR% in intermediate surroundings (1 km, **Fig. 3C**) and from negative towards neutral or positive ΔOSR% in distant surroundings (5 km, **Fig. 3D**). Larger OSR% and more positive ΔOSR% supported a less steep increase of pollen beetle abundances towards higher MAT (**Fig. 3E, F**) – interaction terms were not supported (**Table S6**).

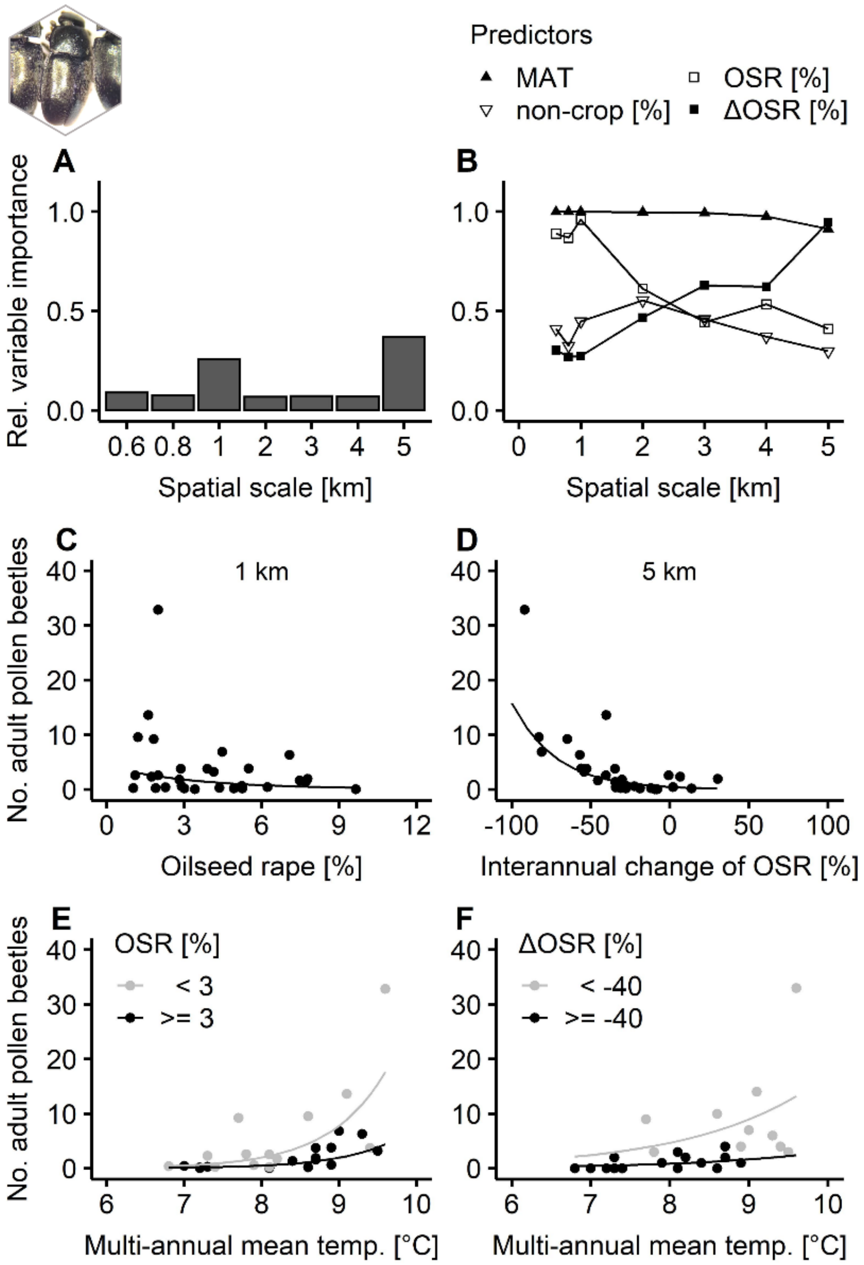

Figure 3 Effects of land-cover composition and multi-annual mean temperature (MAT) on adult pollen beetle abundances; Relative importance of A) each spatial scale (0.6–5 km) and B) each predictor (28 fields; not possible to calculate change in OSR% between years, ΔOSR%, for one field); Values range between zero (low) and one (high); Most relevant landscape predictors: C) the proportion of oilseed rape area (OSR%) in the study year at 1-km scale, D) ΔOSR% at 5-km scale (negative values: reduction, positive values: increase). Additive effects of MAT and the most relevant land-cover parameters (E, F: lighter colour–lower values, darker colours–higher values of land-cover parameters). In panels C–F) indicate dots mean values per site (29 fields) and solid lines predictions from generalized linear mixed effect models.

Temperature, flowering onset, pest abundances, and crop damage as predictors of oilseed rape yield

OSR plants yielded 22.9 ± 1.9 g seeds (mean ± se; range: 7.9–44.1 g). Despite large variation, plant yield did not change across the MAT gradient (**Fig. 4A, Table S7**). Higher mean abundance of adult pollen beetles (**Fig. 4B**) and higher average proportions of bud loss (**Fig. 4C**) led to lower mean plant yield per field, whereas mean stem weevil abundances and mean stem damage did not affect yields (**Fig. S5**). In contrast to negative effects of pollen beetle abundances, earlier flowering positively affected plant seed yield (**Fig. 4D**).

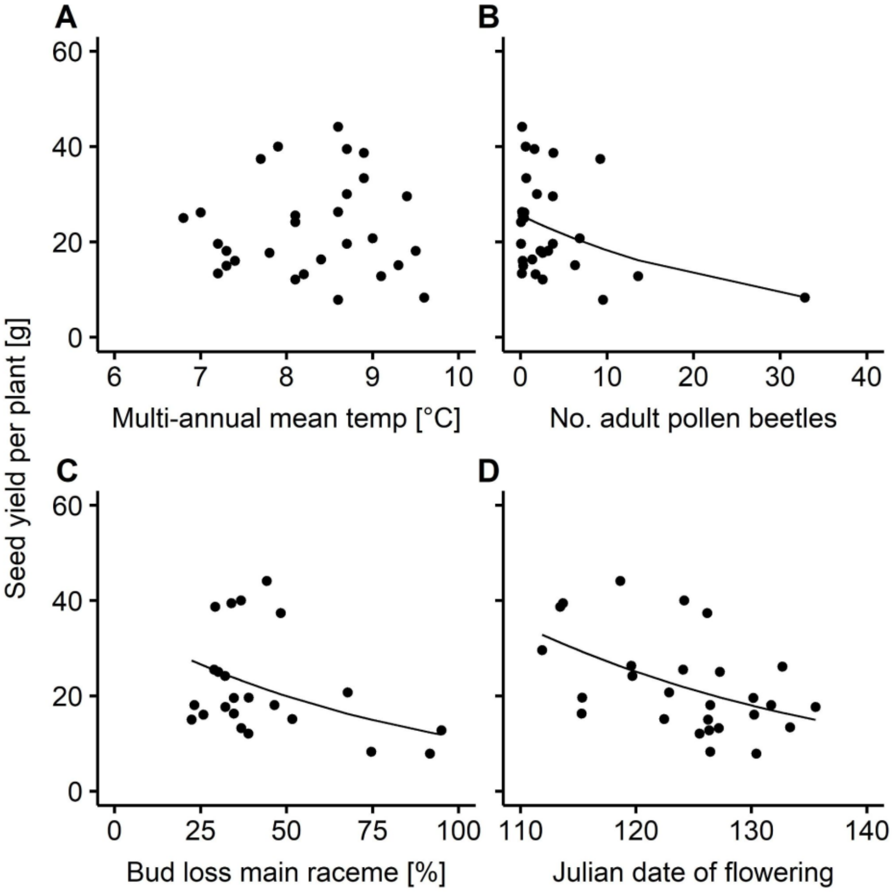

Figure 4 Relationships of averaged plant yield per site and A) multi-annual mean temperature, B) the mean number of adult pollen beetles per plant, C) the mean proportion of bud loss per plant, and D) flowering onset. Dots indicate mean values per site (number of sites: A–29, B–29, C–23, D–27), and solid lines best model predictions from generalized linear models including single predictor variables on averaged values per site.

Discussion

In this study, we investigated effects of temperature, land-cover composition (at various scales) and their combined impacts on multiple aspects of winter OSR production and deduced climate-adapted management strategies.

How does temperature affect flowering onset, pest abundances, crop damage and parasitism rates?

Higher MAT favoured earlier flowering of OSR fields. However, we observed quite some variation in flowering onset among sites with similar MAT, which may result from site-specific differences in microclimatic conditions during specific growth phases (Weymann et al. 2015) – which is not captured by MAT –, but also from further factors, such as cultivar-specific differences in the genetic makeup (Srikanth and Schmid 2011). In winter OSR, Weyman *et al.* (2015) identified temperature as the major driver of development time. Our results on earlier flowering onset with higher MAT (positively correlated with short-term temperature), support temperature as an important driver of development time – particularly onset of flowering – in winter OSR.

While both, pollen beetles and stem weevils, are predicted to occur earlier in warmer climates (Eickermann et al. 2014; Junk et al. 2015), not much is known about temperature effects on their abundances and associated crop damage. We observed higher abundances of pollen beetles and more bud loss towards higher MAT, whereas stem weevil abundances and stem damage were similar across the MAT gradient. This may indicate physiological differences between pollen beetles and stem weevils in response to temperature. Pollen beetles strongly increase feeding and oviposition rate towards higher temperatures under experimental conditions (Ferguson et al. 2014), while such experimental data are lacking on stem weevils; we speculate that the latter may show a weaker response.

Pollen beetle parasitism did not respond to MAT, despite positive MAT effects on pollen beetle abundances. This could suggest that natural pest control was not disrupted in regions with higher MAT. However, parasitism of pollen beetles was generally low and predominantly below the effective pest control threshold of about 30% parasitized individuals (Hawkins and Cornell 1994). The observed parasitism rates were comparable to other studies on conventional winter OSR fields in Bavaria (Schneider et al. 2015), but were lower than those from unsprayed winter OSR fields (Ulber et al. 2010b). Pesticide application is known to strongly reduce parasitoid abundances (Ulber et al. 2010a) and parasitism (Krimmer et al. 2021). For an effective integrated pest management strategy – encompassing parasitism –, crop management changes should be considered (Skellern and Cook 2017).

How does land-cover composition affect pest abundances?

In our study, non-crop% did not substantially affect abundances of stem weevil larvae and adult pollen beetles. Regarding stem weevil abundances, this confirms findings from Zaller *et al.* (2008a). Relevance of non-crop% for stem weevils may be limited, since they overwinter inside OSR fields, depending on species (Williams 2010). With respect to pollen beetle abundances, however, our observations contrast the increase towards larger non-crop% reported by Zaller *et al.* (2008a), which may result from varying proportions of high quality overwintering sites on non-crop%. For instance, litter thickness positively and vegetation height negatively impacts numbers of emerging pollen beetles in spring, but both forests and grasslands can be main sources of pollen beetle emergence, e.g. in different regions (Rusch et al. 2012). Thus, non-crop% as a predictor of pollen beetle abundances seems to be too unspecific. A more promising predictor could be the proportion of suitable overwintering habitat for pollen beetles, albeit difficult to determine. Since non-crop habitat can possibly also benefit natural-enemy species (Rusch et al. 2011), more precise evaluation of suitable (supplemental) habitats for multiple natural-enemy species may also support pest control against pollen beetles, and potentially also against stem weevils.

Strong reduction of OSR% between years led to strongly increased abundances of pollen beetles, which may result from crowding of the regional pollen beetle pool on the lessened OSR area (concentration effects). Our finding provides further evidence that spatiotemporal dynamics in OSR% affect pollen beetle abundances per plant (Schneider et al. 2015). However, in contrast to Schneider *et al.* (2015), we observed this effect on pollen beetles at 5-km scale, but not at 1-km scale (the only scale studied by Schneider *et al.*). Reduction of OSR% between years, at large spatial scales, may lead to long-distance dispersal of large numbers of pollen beetles and may overrule effects at smaller scales on fewer pollen beetles. However, when OSR% stay similar at large spatial scales between years, between-year changes in OSR% at smaller scales may drive pollen beetle dynamics.

Larger OSR% (at 1-km scale) reduced pollen beetle abundances per plant, potentially due to dilution of the invading pollen beetles. This confirms negative effects of OSR% on pollen beetle abundance (Zaller et al. 2008a), but contrasts neutral effects reported by Rusch et al. (2013). Larger OSR% at intermediate spatial scale may dilute pollen beetle densities – compared to crowding on OSR fields in landscapes with smaller OSR% –, but only when numbers of pollen beetles increased relative to the preceding year, e.g. through additional immigration from the far distance when OSR% decreased between years at large spatial scales. Therefore, effects of OSR% on pollen beetle abundances should be interpreted in their spatiotemporal context.

We observed effects of OSR% (1-km scale) and its spatiotemporal dynamics (5-km scale) on abundances of pollen beetles, but not of stem weevils. This may result from differences in pest species traits, e.g. dispersal behaviour (Segoli and Rosenheim 2012, addressing spatial crop cover). Stem weevils prefer short flights (Frank et al. 2010), whereas pollen beetles disperse over distances up to 13.5 km (Williams and Cook 2010). Therefore, a reduction in OSR% between years may lead to the redistribution of pollen beetles across large spatial scales and crowding on the lessened OSR area, whereas only a small proportion of stem weevils – particularly the ones close-by – may be able to reach OSR fields in such landscapes, preventing concentration effects on stem weevils.

Are there interactive effects of temperature and land-cover composition on pest abundances?

Towards higher MAT, pollen beetle abundances increased exponentially, but less strongly when OSR% was higher (1-km scale, e.g. > 3%), and when OSR% between years was only somewhat reduced (e.g. -40% <) or increased (5-km scale); these mitigation effects were additive. Since the strongest reduction in OSR% between years at 5-km scale occurred on sites with highest MAT – likely due to drought around sowing in August–September, which was a bigger problem in warmer regions (Personal communication with farmers: UF) –, separating these two effects on pollen beetle abundances is only possible to a certain extent. However, in areas with less than 40% reduction in OSR% between years (at 5-km scale), pollen beetle abundances were low, but also – slightly – increased towards higher MAT, which suggests that temperature does increase pollen beetle abundances, but that effects of spatiotemporal dynamics in OSR% are much stronger.

Is the yield of winter oilseed rape affected by temperature, flowering onset and pests (abundance, damage)?

Stem weevil abundances and stem damage did not substantially affect plant yield and did not respond to MAT, whereas pollen beetle abundances and bud loss decreased plant yield and increased towards higher MAT. Thus, stem weevils are – and potentially may remain, despite increasing temperatures – of minor importance as a pest to winter OSR compared to pollen beetles. Interestingly, plant yield was not affected through higher MAT – despite higher pollen beetle abundances and increased bud loss. Earlier flowering may have outrun predicted earlier infestation by pollen beetles towards higher MAT (Junk et al. 2015), which may have mitigated yield losses. However, early flowering OSR fields even achieved highest average plant yields per field, which may underline that onset of flowering depends, beside temperature, also on drivers such as the cultivar-specific genetic makeup (Srikanth and Schmid 2011). Cultivar choice – the earlier flowering, the higher the temperature – could potentially facilitate an increase of plant yields towards higher MAT.

Synthesis and management implications

Our results suggest that maintaining or increasing OSR% between years at large spatial scales (e.g. 5-km scale) supports low pollen beetle densities, presumably through dilution effects and natural pest regulation. Spatiotemporally constant OSR% may also benefit continuous resource-provisioning of pollinators and specialist parasitoids. However, adverse climatic conditions – such as drought around sowing – can drive spatiotemporal dynamics of OSR% and lead to crowding of pollen beetles on reduced OSR proportions. If communicated rapidly among farmers in a region, these years of adverse conditions could be harnessed to facilitate low-effort implementation of years without OSR as suggested by Schneider et al. (2015) and Zheng et al. (2020) to disrupt populations of OSR pests. Besides, early flowering – e.g. through cultivar choice – may be utilised to promote high crop yield also towards high MAT. Thus far, suboptimal plant size (Anten and Vermeulen 2016) and late frost events (Pullens et al. 2019) did not diminish yields of early-flowering winter OSR, and therefore benefits of early flowering prevailed (e.g. phenological escape from severe crop damage). In conclusion, our results underpin the potential of targeted landscape management and timing of flowering onset (e.g. through cultivar choice) for the mitigation of adverse effects of global warming on winter OSR production.

The concept of harnessing spatiotemporal crop-cover dynamics to support low pest densities may also be applicable to other crops and pest species, but transferability could depend on species traits, such as the dispersal range of pests and their natural enemies.

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Supplement

Appendix S1 Deriving short-term mean temperature during the study year

Thermologgers (ibutton, type DS1923) were mounted on a wooden pole 1.1 m above ground, facing north and roughly 0.15 m below a wooden roof as protection against direct solar radiation (one thermologger per site). Hourly temperature values were averaged for the month May to compare short-term temperature with long-term temperature (multi-annual mean temperature from 1981–2010).

Appendix S2 Deriving land-use predictors

The detailed land-cover map was created based on six main land-use types within Bavaria (semi-natural habitat, forest, grassland, arable, urban, water) and three different land-cover maps (ATKIS[1] 2019, IACS[2] 2019, CLC[3] 2018) at 6-km spatial scale around the centre point of the study sites. Boundary of different land-use types was defined by ATKIS and additional details were added using IACS and CLC data. Overlaps in data sources and land-use layers were handled through prioritization of specific land-use types and data sources: Semi-natural (CLC subclass ‘transitional woodland’ > IACS > ATKIS) > Forest (ATKIS) > Grassland (IACS > ATKIS) > Arable (IACS > ATKIS) > Urban (ATKIS) > Water (ATKIS).

Non-crop area was defined as the sum of area assigned to semi-natural, forest and grassland land-use type. Oilseed rape area in the study year (2019) and the preceding year (2018) was derived from IACS land-cover maps. Land-cover characteristics (proportions) were calculated in circles centred on the field edge in between sampling transects at multiple spatial scales (radii up to 5-km).

ATKIS[1]: Official topographical cartographic information system (dt. Amtliches topographisch kartographisches Informationssystem); provided by the Bavarian Office for Surveying and Geographic Information

IACS[2]: Integrated administration and control system; provided by the European Environment Agency of the European Union under the framework of the Copernicus programme

CLC[3]: Corine Land Cover; Coordination of information on the environment (corine); provided by the Bavarian State Ministry of Agriculture and Forestry

Appendix S3 Details on data analysis of pest abundances, crop damage and parasitism

Models containing as random term ‘site’ or ‘transect nested in site’ were compared by restricted maximum likelihood, but the more complex random effect structure did not improve the model fit (based on ΔAICc < 2 and parsimony) and led to modelling issues of incomplete data sets (when exclusion criteria were applied). Presented models contain only ‘site’ as a random term.

When analysing the data, we first addressed temperature effects on all five independent variables (2x pest abundance, 2x crop damage, 1x parasitism) comparing univariate models with null models based on ΔAICc < 2 and parsimony. Data on 29 fields were analysed, yet only 25, 27 and 18 fields (due to exclusion criteria) were used to analyse MAT effects on bud loss, stem damage and parasitism rates, respectively.

Secondly, we analysed pest abundances in more detail including – beside MAT – land-use aspects at multiple spatial scales. Land-use aspects comprise the predictors proportion of non-crop area, OSR% and ΔOSR% (0.6–5 km, 7 spatial scales). We did not analyse parasitism rates due to lack of data (see above). We also assessed a predictor set without ΔOSR% (0.2–5 km, 9 spatial scales) to facilitate analysis of land-use predictors at small scales without data losses (frequently not possible to calculate ΔOSR% at 0.2 and 0.4-km scale; for one site also not possible at scales < 1 km). To evaluate the importance of the predictor variables at various spatial scales, we employed multimodel averaging using the R-package ‘MuMIn’ (Barton, 2020). Models with all possible predictor combinations at each spatial scale were created separately for pollen beetle and stem weevil abundances, and including or excluding ΔOSR%. From there, the sum of Akaike weights (Σwi, range: 0–low to 1–high) was calculated of each spatial scale and of each predictor at every spatial scale indicating the relative importance of a spatial scale (compared to other studied spatial scales) and of a predictor variable (compared to other studied predictors) at a certain spatial scale, respectively (Burnham and Anderson 2002). To test for multicollinearity, we calculated variance inflation factors (VIF) using the R-package ‘performance’ (Lüdecke et al., 2020). Furthermore, Pearson’s correlation coefficients were calculated using the R-package ‘performanceAnalytics’ (Peterson and Carl, 2020), and are presented alongside predictor ranges in **Table S2**.

In a third step, we created models on pest abundances including interactive effects of MAT and land-use aspects at the specific spatial scales on which both main effects (MAT and specific land-use aspect) contributed substantially. This was the case for pollen beetle abundance at 1-km (MAT, OSR%) and 5-km (MAT, ΔOSR%) scale. These pollen beetle abundance models – including interactive effects of MAT and land-use aspects – were fitted to data from 29 sites. Model selection was conducted using ΔAICc < 2 and parsimony.

References

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Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information–theoretic approach, 2nd edn. Springer

Lüdecke, D. et al. (2020) ‘performance: Assessment of regression models performance’, CRAN. doi: 10.5281/zenodo.3952174.

Peterson, B. G. and Carl, P. (2020) ‘PerformanceAnalytics: Econometric tools for performance and risk analysis.’ Available at: https://cran.r-project.org/package=PerformanceAnalytics.

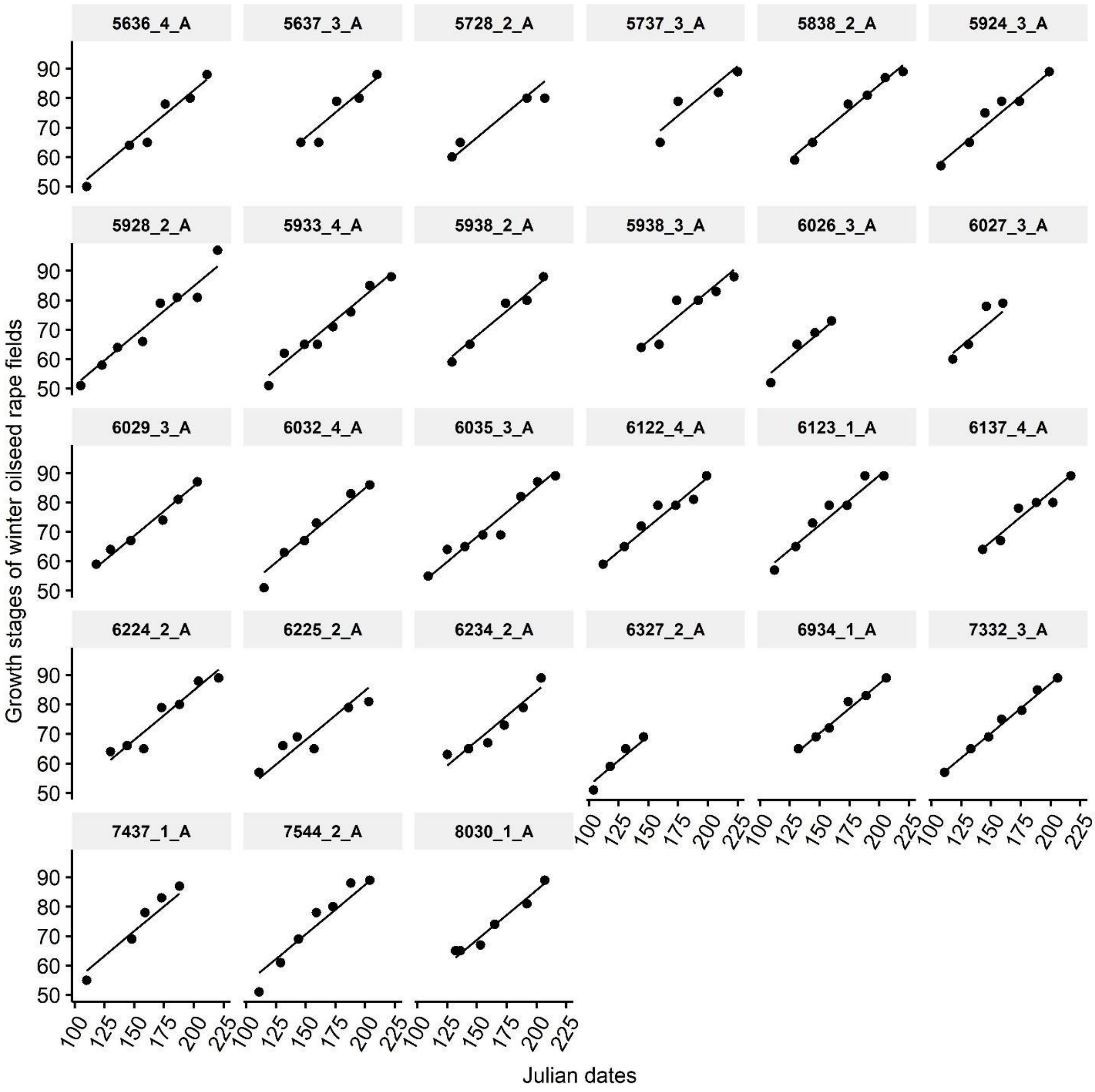

Figure S1 Winter oilseed rape development over the course of time presented as growth stages at field level (growth stage of at least 50% of plants, location identifier XXXX_X_A) for the estimation of flowering onset (growth stage = 60). Dots indicate field-based observations. Lines present predictions of linear mixed models including site as random term.

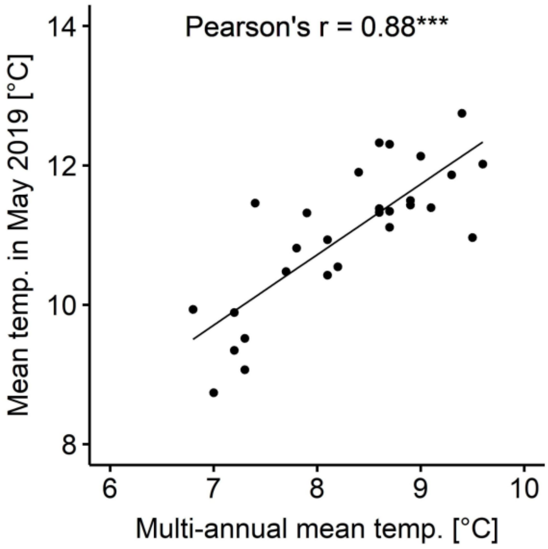

Figure S2 Correlation of multi-annual mean temperature (MAT) with short-term mean temperature measured in May of the study year on the sites, 1 m above ground. Significant correlation based on $P < 0.001$.

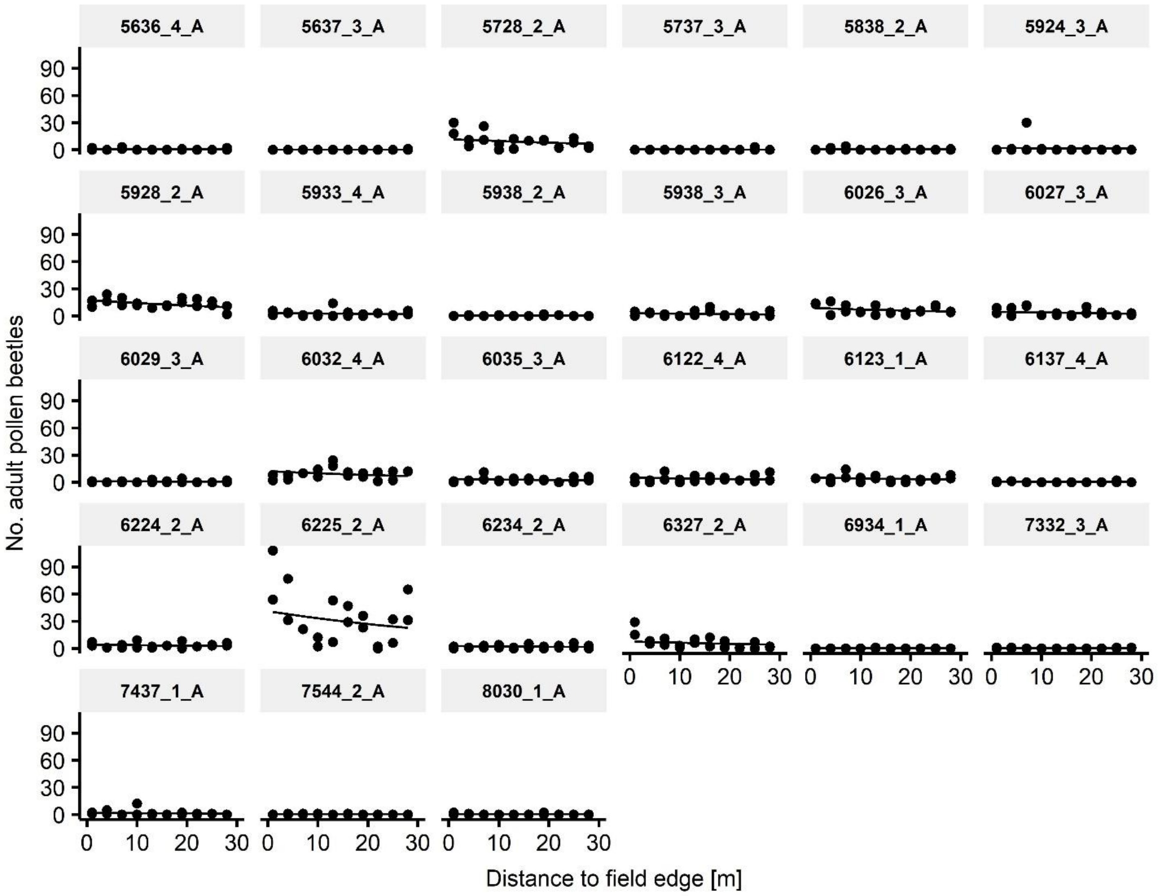

Figure S3 Distance effects from field edge to centre on adult pollen beetle abundances per field (location identifier XXXX_X_A). Dots indicate adult pollen beetle counts on individual oilseed rape plants at flowering. Prediction lines were derived from negative binomial mixed-effect models including site as random term.

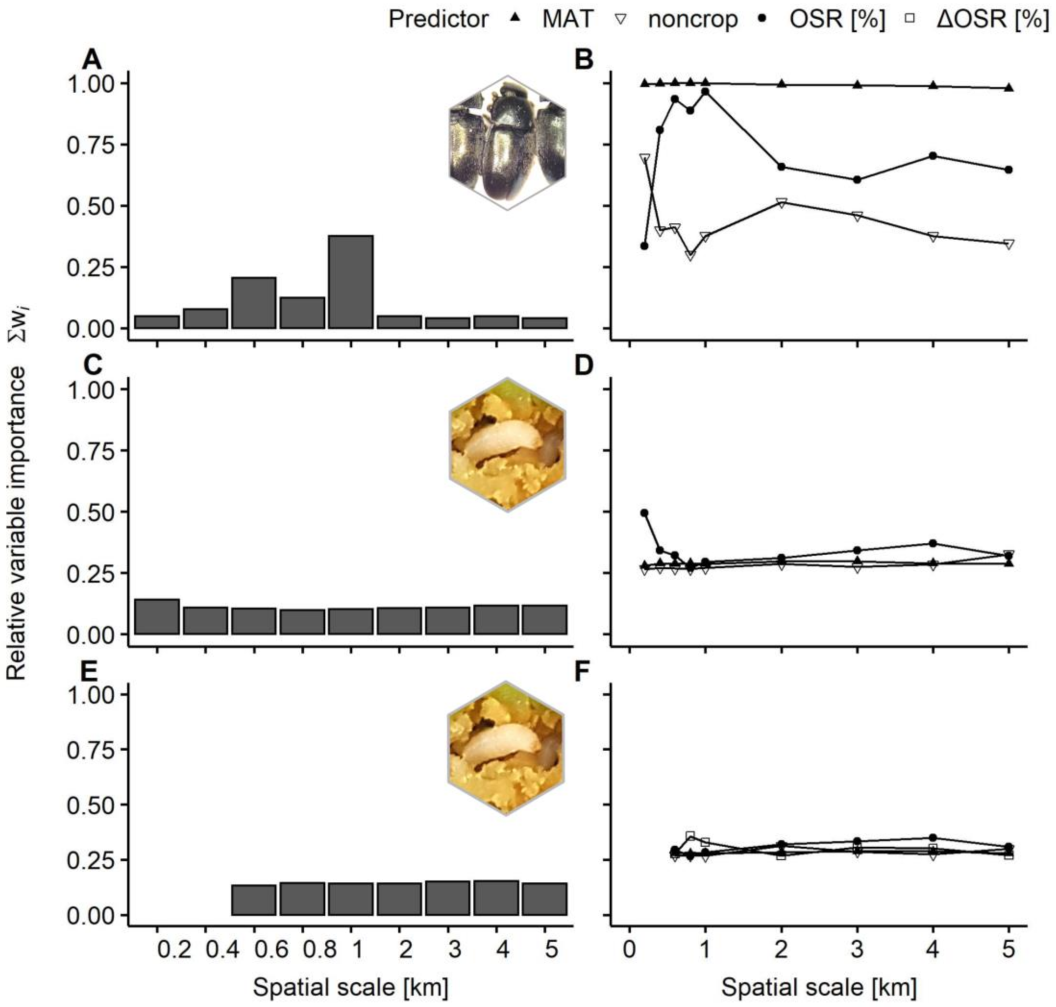

Figure S4 Effects of land-cover composition and multi-annual mean temperature (MAT) on abundances of A+B) adult pollen beetle and C-F) stem weevil larvae; Relative importance of each spatial scale (A+C: 0.2–5 km, E: 0.6–5 km) and of each predictor at each scale (B+D: 0.2–5 km, F: 0.6–5 km). Values range between zero (low) and one (high). Candidate predictors encompassed MAT, proportion of non-crop area (non-crop%), proportion of oilseed rape in the study year (OSR%), and additionally in E+F) change in OSR% between years (ΔOSR%). Data on 29 fields were analysed, except when the predictor ΔOSR% was included, then small spatial scales were excluded, and data on 28 fields were analysed (not possible to calculate ΔOSR% for one field). Multimodel averaging was conducted on negative binomial mixed effect models including site as a random intercept term, and in stem weevil abundances models also a zero-inflation term.

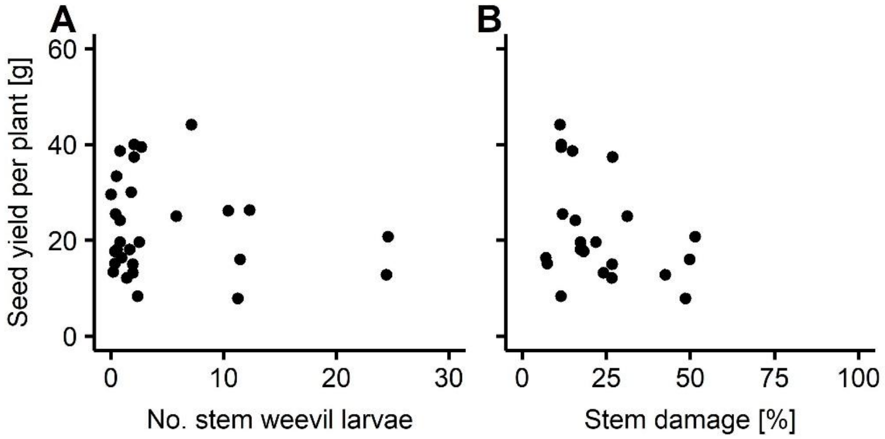

Figure S5 Averaged plant yield per field (black dots) relative to A) the mean number of stem weevil larvae per plant (29 sites) and B) the mean stem damage they cause (23 sites: crop damage data). Stem weevil abundance or stem damage did not substantially contribute to the explanation of seed yield (see Table S7).

Table S1 Distance effects (from field edge to centre) on adult pollen beetle abundance. Pollen beetle abundances were modelled using negative binomial mixed effect models including study site as random term. Bold font highlights the best model based on ΔAICc and parsimony. Standardized estimates provide information on strength and direction of distance effects.

Response variable	Predictor	Standard. estimate (mean±SE)	No. Plots	No. Plants	df	AICc	Pseudo R^2_m	Pseudo R^2_c
Adult pollen beetle abundances								
	Distance	-0.021 ± 0.006	27	537	4	2032.5	0.01	0.74
	(Null)	-	27	537	3	2041.5	-	0.73

df: Degrees of freedom, AIC_c: Akaike information criterion corrected for small sample size, R^2: marginal (fixed effects) and conditional (fixed + random effects) Nakagawa R^2 values, Distance: Distance from field edge towards centre in metre

Table S2 Predictor variable details und Pearson's correlation coefficients for standardized predictors included in multimodel averaging on adult pollen beetle and stem weevil larvae abundance models based on 29 study sites at small scales (0.2, 0.4 km) and 28 study sites at all other scales (interannual change in oilseed rape could not be calculated for one site). Significant correlations based on $\alpha = 0.05$ are indicated as following: $P < 0.05$*, $P < 0.01$**, $P < 0.001$***.

								Pearson's correlation coefficients		
Scale [km]	Predictor	Min.	1st Quantile	Median	Mean	3rd Qu.	Max	MAT	non-crop%	OSR %
0.2	MAT	6.8	7.7	8.4	8.3	8.9	9.6			
	non-crop%	0.0	6.6	18.2	21.3	31.9	71.3	-0.16		
	OSR%	5.6	15.6	20.1	22.8	31.0	49.7	0.42*	-0.10	
0.4	MAT	6.8	7.7	8.4	8.3	8.9	9.6			
	non-crop%	0.0	12.4	18.3	25.7	40.2	68.0	-0.32		
	OSR%	1.4	6.2	8.0	10.3	12.9	22.5	0.21	-0.18	
0.6	MAT	6.8	7.7	8.4	8.3	8.9	9.6			
	non-crop%	2.4	11.1	30.9	30.2	45.5	79.3	-0.39*		
	OSR%	2.1	4.4	5.5	6.7	9.3	15.5	0.21	-0.35	
	ΔOSR%	-83.7	-20.1	26.3	153.9	70.0	2954.5	0.14	-0.16	0.32
0.8	MAT	6.8	7.7	8.4	8.3	8.9	9.6			
	non-crop%	7.5	14.1	31.8	33.5	48.6	81.2	-0.39*		
	OSR%	1.3	2.9	4.3	5.1	7.7	11.6	0.23	-0.35	
	ΔOSR%	-86.5	-33.3	5.2	25.2	53.6	396.6	0.04	0.34	0.14
1.0	MAT	6.8	7.7	8.4	8.3	8.9	9.6			
	non-crop%	7.7	18.1	38.5	37.2	54.8	79.0	-0.40*		
	OSR%	1.0	2.0	3.4	3.9	5.5	9.7	0.20	-0.35	
	ΔOSR%	-87.1	-45.7	-0.3	-6.7	27.8	140.9	-0.08	0.20	0.24
2.0	MAT	6.8	7.7	8.4	8.3	8.9	9.6			
	non-crop%	2.8	23.0	45.2	43.4	63.6	84.8	-0.27		
	OSR%	0.4	1.2	1.9	2.5	3.1	11.1	0.03	-0.30	
	ΔOSR%	-85.8	-60.9	-44.8	-39.0	-23.8	49.8	0.02	0.22	0.41*
3.0	MAT	6.8	7.7	8.4	8.3	8.9	9.6			
	non-crop%	3.5	26.3	46.2	46.0	64.1	87.9	-0.33		
	OSR%	0.2	1.0	1.4	2.1	3.0	9.0	-0.04	-0.26	
	ΔOSR%	-87.9	-52.7	-47.2	-38.1	-19.9	38.5	-0.17	0.20	0.57**
4.0	MAT	6.8	7.7	8.4	8.3	8.9	9.6			
	non-crop%	9.8	33.0	47.5	47.3	64.6	82.5	-0.43*		
	OSR%	0.2	0.8	1.3	1.9	2.7	7.2	-0.06	-0.22	
	ΔOSR%	-92.5	-51.1	-26.3	-33.9	-15.6	29.3	-0.41*	0.37	0.36
5.0	MAT	6.8	7.7	8.4	8.3	8.9	9.6			
	non-crop%	17.0	31.6	48.6	48.0	61.7	80.2	-0.47*		
	OSR%	0.2	0.9	1.4	1.8	2.7	5.6	-0.15	-0.21	
	ΔOSR%	-91.8	-52.7	-30.9	-31.9	-9.3	30.4	-0.47*	0.37	0.28

Min.: Minimum, Max.: Maximum, MAT: multi-annual mean temperature, non-crop%: non-crop proportion (grassland%+forest%+ semi-natural%), OSR%: proportion of oilseed rape in the study year 2019, ΔOSR%: change in OSR% between years

Table S3 Pearson's correlation coefficients for standardized (field-averaged) predictors included in plant yield models based on 29 sites, or 27 sites when assessing correlation with flowering onset. Significant correlations based on α = 0.05 are indicated as following: *P* < 0.05*, *P* < 0.01**, *P* < 0.001***.

		Pearson correlation coefficients				
Spatial scale [km]	Predictor	MAT	PB abundance	SW abundance	Bud loss	Stem damage
	MAT					
	PB abundance	0.49**				
	SW abundance	0.11	0.21			
	Bud loss	0.44*	0.69***	0.61***		
	Stem damage	-0.23	0.04	0.80***	0.39*	
	Flowering onset	-0.57**	0.06	0.11	0.15	0.33

MAT: multi-annual mean temperature, PB: pollen beetle, SW: stem weevil, Bud loss: bud loss on main raceme at flowering

Table S4 Model output of univariate models testing for temperature effects on flowering onset, pest abundances, crop damage and parasitism rates. Flowering onset data are at field level, while all other data are at plant level. Standardized estimates (mean ± se) are provided indicating strength and direction (positive, neutral, negative) of MAT effects on response variables. Prior to analysing bud loss, stem damage and pollen beetle parasitism rate, data were excluded on heavily damaged plants (> 5% broken floral organs), plants without stem weevil larvae and plants with less than three large pollen beetle larvae, respectively, and also fields with data on less than three plants.

Response variable	Model family	Predictor	Stand. estimates (mean± se)	No. Plots	No. Plants	df	AICc	Pseudo R^2_m	Pseudo R^2_c
Flowering onset	gaussian	**MAT**	-3.64±1.01	27	-	3	173.5	(0.30)	-
		-	-	27	-	2	181.4	-	-
Adult pollen beetle abundance	nbinom	**MAT**	1.24±0.30	29	577	4	2154.8	0.28	0.72
		(Null)	-	29	577	3	2166.1	-	0.72
Stem weevil larvae abundance	zinbinom	**(Null)**	-	29	577	4	2406.3	-	0.42
		MAT	-0.17±0.34	29	577	5	2408.0	<0.01	0.43
Bud loss	binom	**MAT**	0.55±0.19	25	320	3	3111.0	0.07	0.27
		(Null)	-	25	320	2	3116.6	-	0.27
Stem damage	beta	**(Null)**	-	27	304	3	-243.0	-	0.70
		MAT	-0.29±0.16	27	304	4	-244.0	0.10	0.70
Pollen beetle parasitism rate	zibinom	**(Null)**	-	18	174	3	587.3	-	0.37
		MAT	0.20±0.35	18	174	4	585.5	0.01	0.38

Df: Degrees of freedom, AICc: Akaike information criterion correcting for small sample size, Pseudo R^2: Nakagawa R^2 values providing marginal (only fixed effect) and conditional (fixed + random effect) R^2 values – flowering onset adjusted R^2, gaussian: linear model, nbinom: negative binomial mixed model, zinbinom: zero-inflated nbinom, binom: logistic mixed effect model, zibinom: zero-inflated binom, beta: beta mixed model

Table S5 Model output of pest abundance models (negative binomial mixed effect models; incl. zero-inflation term in case of stem weevil abundance) which present all possible combinations of multi-annual mean temperature and land-use parameters at the best spatial scales identified by multimodel averaging. Bold font highlights the best model per spatial scale by ΔAICc and parsimony. Models encompass data on 557 plants at 28 fields (change in oilseed rape proportions couldn't be calculated for one field).

Response variable – spatial scale Predictors	df	AICc	ΔAICc	Pseudo R^2_m	Pseudo R^2_c	VIF_{max}
Pollen beetle abundances – 1km						
MAT+OSR%	5	2101.1	0.0	0.42	0.72	1.05
MAT+non-crop%+OSR%	6	2101.5	0.4	0.43	0.72	1.31
MAT+ΔOSR%+OSR%	6	2103.2	2.0	0.42	0.72	1.14
MAT+non-crop%+ΔOSR%+OSR%	7	2103.4	2.3	0.43	0.72	1.41
MAT	4	2107.0	5.8	0.30	0.72	-
MAT+ΔOSR%	5	2108.6	7.5	0.31	0.72	1.01
MAT+non-crop%	5	2108.9	7.8	0.30	0.72	1.21
MAT+non-crop%+ΔOSR%	6	2110.6	9.5	0.31	0.72	1.25
non-crop%+OSR%	5	2115.9	14.8	0.17	0.72	1.13
non-crop%+ΔOSR%+OSR%	6	2117.9	16.8	0.17	0.72	1.27
non-crop%	4	2118.6	17.5	0.06	0.72	-
(Null model)	3	2119.0	17.9	-	0.73	-
OSR%	4	2119.1	18.0	0.05	0.73	-
non-crop%+ΔOSR%	5	2120.4	19.3	0.07	0.72	1.04
ΔOSR%	4	2120.5	19.3	0.01	0.73	-
ΔOSR%+OSR%	5	2121.0	19.9	0.06	0.73	1.07
Pollen beetle abundances – 5km						
MAT+ΔOSR%	5	2100.4	0.0	0.42	0.72	1.29
MAT+ΔOSR%+OSR%	6	2101.3	0.9	0.43	0.72	1.37
MAT+non-crop%+ΔOSR%	6	2102.4	2.0	0.42	0.72	1.50
MAT+non-crop%+ΔOSR%+OSR%	7	2103.1	2.7	0.43	0.72	1.55
ΔOSR%	4	2105.5	5.1	0.32	0.72	-
non-crop%+ΔOSR%+OSR%	6	2106.3	5.9	0.37	0.72	1.38
ΔOSR%+OSR%	5	2106.5	6.1	0.34	0.73	1.08
MAT+OSR%	5	2106.5	6.1	0.34	0.73	1.02
non-crop%+ΔOSR%	5	2106.5	6.1	0.34	0.72	1.17
MAT	4	2107.0	6.6	0.30	0.72	-
MAT+non-crop%+OSR%	6	2107.0	6.6	0.36	0.73	1.47
MAT+non-crop%	5	2108.7	8.3	0.31	0.72	1.30
non-crop%+OSR%	5	2112.5	12.1	0.24	0.73	1.05
non-crop%	4	2116.9	16.5	0.10	0.73	-
OSR%	4	2117.8	17.4	0.09	0.73	-
(Null model)	3	2119.0	18.6	-	0.73	-
Stem weevil larvae abundance – 1km						
(Null model)	4	2365.2	0.0	-	0.66	-
ΔOSR%	5	2366.6	1.4	0.02	0.66	-
OSR%	5	2366.9	1.8	<0.01	0.66	-
MAT	5	2367.1	1.9	<0.01	0.66	-
non-crop%	5	2367.2	2.0	<0.01	0.66	-
MAT+ΔOSR%	6	2368.4	3.2	0.02	0.66	1.01
ΔOSR%+OSR%	6	2368.5	3.3	0.02	0.66	1.06
non-crop%+ΔOSR%	6	2368.5	3.4	0.02	0.66	1.04
MAT+OSR%	6	2368.9	3.7	<0.01	0.66	1.04
non-crop%+OSR%	6	2369.0	3.8	<0.01	0.66	1.14
MAT+non-crop%	6	2369.1	3.9	<0.01	0.66	1.18
MAT+ΔOSR%+OSR%	7	2370.4	5.3	0.02	0.66	1.12
MAT+non-crop%+ΔOSR%	7	2370.5	5.3	0.02	0.66	1.23
non-crop%+ΔOSR%+OSR%	7	2370.5	5.4	0.02	0.66	1.28
MAT+non-crop%+OSR%	7	2370.9	5.8	0.01	0.66	1.30
MAT+non-crop%+ΔOSR%+OSR%	8	2372.5	7.3	0.02	0.66	1.41

Df: Degrees of freedom, AICc: Akaike's information criterion corrected for small sample size, ΔAICc: Difference in AICc relative to minimum value, Pseudo R^2: marginal (only fixed effects) and conditional (fixed + random effects) Nakagawa R^2 values, VIF_{max}: Highest variance inflation factor, MAT: multi-annual mean temperature, non-crop%: summed proportion of forest, grassland and semi-/natural habitat, OSR%: oilseed rape proportion in the study year, ΔOSR%: change in oilseed rape proportions between years

Table S6 Model output of adult pollen beetle abundance models considering interaction effects of significant main effects of temperature and land use at best spatial scales identified using multimodel averaging (1 km: 29 study sites, 5 km: 28 study sites). Asterisk between predictor variables indicates that both main effects and their interaction term were included. Bold font highlights best negative binomial mixed models per scale based on ∆AICc and parsimony.

Spatial scale [km]	Predictors	df	AICc	∆AICc	Pseudo R^2_m	Pseudo R^2_c
1.0						
	MAT+OSR%	5	2148.6	0.0	0.40	0.72
	MAT*OSR%	6	2150.6	2.0	0.40	0.72
	MAT	4	2154.8	6.2	0.28	0.72
	OSR%	4	2166.1	17.5	0.05	0.72
	-	3	2166.1	17.5	-	0.72
5.0						
	MAT+∆OSR%	5	2100.4	0.0	0.42	0.72
	MAT*∆OSR%	6	2102.3	1.9	0.42	0.72
	∆OSR%	4	2105.5	5.1	0.32	0.72
	MAT	4	2107.0	6.6	0.30	0.72
	-	3	2119.0	18.6	-	0.73

df: Degrees of freedom, AIC$_c$: Akaike information criterion corrected for small sample size, Pseudo R^2: marginal (fixed effects) and conditional (fixed + random effects) Nakagawa R^2 values, MAT: 30-year mean temperature, non-crop%: non-crop proportion (summed proportions of forest, grassland and (semi-)natural habitat), OSR%: oilseed rape proportion in study year, ∆OSR%: change in oilseed rape proportions between years

Table S7 Plant yield data were modelled using generalized linear models with gamma distribution on different predictor sets and all possible predictor combinations. Bold font highlights best models per predictor set.

Predictor set	No. Plots	Model parametrization	AICc	adj. Kullback-Leibler R^2	VIF_{max}
Pest abundances	29				
		Adult pollen beetles	212.7	0.16	-
		Stem weevil larvae	218.1	-0.01	-
		both	215.1	0.13	1.04
		(Null)	216.4	0	-
Crop damage	23				
		Bud abscission	170.8	0.14	-
		Stem damage	171.7	0.11	-
		both	172.5	0.15	1.23
		(Null)	172.9	0	-
Temperature	29				
		(Null)	216.41	-	-
		MAT	218.88	-0.04	-
Flowering onset	27				
		Flowering onset	196.0	0.20	-
		(Null)	200.8		-

AIC_c: Akaike information criterion corrected for small sample size, VIF_{max} :Maximum variance inflation factor

Chapter 5

General discussion

Harnessing human action for nature

Climate and land-use change threaten biodiversity (Thomas et al. 2004; Díaz et al. 2019), but little is known on the combined effects of climate and land use on biodiversity and the consequences for ecosystem functions (Mantyka-Pringle et al. 2012; Santos et al. 2021). This is where the LandKlif project (2018-2023) comes in, aiming to disentangle combined effects of climate and land use on biodiversity, ecosystem functions and services in a timely manner, using a multi-scale space-for-time approach. My thesis is part of LandKlif covering the ecosystem functions herbivory (Chapter 2), predation (Chapter 3) and the related ecosystem service pest control (Chapter 4).

The research I led within LandKlif revealed that the habitat type adjacent to open herbaceous vegetation as well as diverse vegetation affected leaf-chewing herbivory differentially among plant functional groups (Chapter 2), while diverse landscapes favoured higher predation rates (Chapter 3). Leaf-chewing herbivory on legumes was lower in forests (e.g. glade, clearing) than in grasslands and decreased with increasing plant richness at family level, but not at species level (Chapter 2). These effects of adjacent habitat type and plant richness on herbivory do not indicate a risk to ecosystem functioning in forests or diverse vegetation, but nutrient flow from legumes to higher trophic levels may be redirected from herbivory to decomposition (Cebrian and Lartigue 2004), and the partial release of legumes from leaf-chewing herbivores may be harnessed for plant species protection. In comparison, arthropod predation rates were similar across habitat types and natural gradients of plant richness, but were frequently higher in more diverse landscapes, which provides a first direction of environmental conditions favouring high top-down control of herbivores, and possibly also of pests (Chapter 3). Thus, land use at multiple spatial scales may be harnessed to promote or regulate invertebrate leaf-chewing herbivory among plant functional groups and arthropod predation rates at ground-level.

Herbivory and predation in arable systems translate into crop damage or pest abundances, and natural pest control, respectively. This, I studied in more detail in oilseed rape with a focus on two major insect pests, pollen beetles dominated by *Brassicogethes aeneus*, and – to a lesser extent also – stem weevils *Ceutorhynchus napi* and *C. pallidactylus*, and on the major parasitoid of pollen beetle larvae *Tersilochus heterocerus* (Chapter 4). Stem weevil abundance and damage were not substantially affected by any temperature and land-use parameter tested, and parasitism of pollen beetle larvae was generally low (< 30%) with only few exceptions (Chapter 4). Nonetheless, pollen beetle abundances differed largely between sites, and particular high numbers were observed when the oilseed rape area in the surrounding was strongly reduced compared to the preceding year. Large reduction in oilseed rape occurred especially in warmer regions, which experienced drought around autumn sowing, contributing to higher numbers of pollen beetles per plant in warmer regions. In parallel, oilseed rape advanced flowering onset with increasing temperature, which was associated with higher seed yields. Thus, early flowering of oilseed rape may have favoured escape from pollen beetle infestation in the most vulnerable bud stage. Phenology and landscape management offer solutions to control pesticide-resistant pests and hold potential to make pollen beetle management more environment-friendly. Yet, to harness this potential a rethinking in pest management and collaboration among farmers is needed (see below, "Reconciling agriculture with nature").

My contribution to LandKlif feeds into the observations that land use and temperature affect arthropod diversity and ecosystem functions, albeit differently, while interactive effects of land use and climate are scarce and occur rather at taxonomic than community level, e.g. at the level of order or family (Chapter 2; LandKlif, Ganuza et al. 2022). Land-use effects were largely independent of local and multi-annual mean temperature, while temperature was frequently of minor importance compared to land use – i.e. herbivory (Chapter 2), predation (Chapter 3), biomass and richness of flying insects (LandKlif, Uhler et al. 2021) – which finds support in literature stating that from a global perspective land-use effects currently still outweigh climate effects (Díaz et al. 2019). Therefore, habitat and landscape management offer options to promote biodiversity and ecosystem services, and to regulate ecosystem functions such as herbivory and predation, largely independent of temperature. However, climate change implies multiple changes beyond mean temperature rise and this at a fast pace (Halsch et al. 2021; IPCC 2022). Thus, provided management options will need revaluation as climate change progresses, which is discussed in more detail below. However, actions to halt biodiversity loss and to modulate herbivory and predation in an ecologically sustainable way are needed now, and LandKlif, and my research within, contribute to this.

Promoting favourable conditions for plants, arthropods and trophic interactions

Conditions promoting species richness may also benefit higher levels of ecosystem function provisioning, as each species is to some extent functionally unique (Gamfeldt and Roger 2017). Therefore, we assumed that the level of ecosystem function provisioning may differ on open herbaceous vegetation depending on the adjacent habitat type (e.g. representing differences in arthropod community composition and habitat amount), landscape composition (e.g. landscape diversity, proportion of grassland area) and plant richness. Yet, adjacent habitat type and plant richness affected herbivory differently among plant functional groups (Chapter 2), while predation rates only responded to landscape diversity (Chapter 3), and amount of oilseed rape area elicited strong effects on pollen beetle abundances, particularly when amount strongly decreased compared to the preceding year (Chapter 4).

Adjacent habitat type

Herbivory on legumes was lower on open herbaceous vegetation adjacent to forest (e.g. forest glade) than in grasslands, but herbivory on forbs and grasses did not substantially change. Thus, forest glades may provide refuge to legumes from leaf-chewing herbivory specialized on them. This may have several reasons, (i) forests may constitute a barrier to dispersal to some species (Schmitt et al. 2000) and (ii) forest glades may encompass less habitat amount and thus the presence of specialist herbivores to legumes may be less likely (Fahrig 2013). It is unlikely that the observed pattern is driven by generalist herbivores as only herbivory on legumes changed among habitat types and as predation rates were not affected by habitat type, though measured predation rates may capture only attack activities from certain arthropod predators due to sentinel prey traits (e.g. trait-matching, see Brousseau et al. 2018), and thus adds only weak evidence. However, the remaining, slight damage experienced by legumes in forests, may result from generalist herbivores, such as grasshoppers which predominately feed on grasses but to a smaller extent also on legumes and forbs (Unsicker et al. 2005). There might also be forb species experiencing partial release from leaf-chewing herbivores in forests, which was not captured by the chosen functional group approach as the group forbs contained several plant families. Legume species might also differ in the level of release from leaf-chewing herbivory in forests, albeit herbivores are frequently specialized within plant families (Haddad et al. 2001). Variation in the level of herbivory on legumes in forests may also result from site-specific properties, e.g. the completeness of enclosure within forest, the distance to the next patch of open herbaceous vegetation or other habitat related factors, which needs further consideration. Nonetheless, lower herbivory on legumes in forests underlines the potential of forests as refuge from leaf-chewing herbivory (see also Dostálek et al. 2018).

Habitat amount

Ecological and evolutionary theory predicts that larger habitat amount favours more diverse communities (MacArthur and Wilson 1963; Fahrig 2013), which may result in higher process rates (Griffin et al. 2013; Gamfeldt and Roger 2017). However, herbivory on open herbaceous vegetation was not affected by habitat amount estimated by managed grassland proportion (Chapter 2). This may result from the coarse estimate of habitat amount, which may not capture actual amount well enough, or from an incomplete biodiversity-herbivory relationship. The latter means a change in herbivore community is not necessarily followed by a change in herbivory, e.g. when few common generalists provide similar levels of herbivory as more diverse herbivore communities (Rossetti et al. 2017). Besides, herbivore species contributing to leaf-chewing herbivory on legumes, forbs and grasses likely differ in their dispersal ability and in their host plant preferences, so that also a predictor of habitat amount precisely indicating the amount of available open herbaceous vegetation, may differently well capture actual resource availability to a specific herbivore. For example, when looking at a single herbivore species, the pollen beetle, specialized on brassicaceous plants for oviposition and a major pest of oilseed rape, a different picture emerges. Pollen beetle abundances per plant were lower when oilseed rape proportions were higher in the intermediate surrounding (Chapter 4). Even more strongly pollen beetle abundances responded to changes in oilseed rape proportions between years. A strong reduction of oilseed rape production area between years led to a strong increase in pollen beetle numbers per plant. This impressively shows crowding or concentration effects of a specialist herbivore species on its host plant. However, similar oilseed rape proportions between two years translated into similarly low pollen beetle abundances among the observed plots. The situation is much more complicated, however, when averaging across many herbivore and plant species. Analogous to the pollen beetle–oilseed rape system, the effect of habitat amount on herbivory may be small under continuous conditions, but may become particularly apparent when habitat amount changes. Thus, maintaining habitat amount is likely to prevent herbivore or pest outbreaks due to concentration effects. This may also bring along the positive side effect that prey availability to predators may be more similar across years, which favours natural balancing between herbivore and predator abundances.

Landscape diversity

Diverse landscapes favoured higher arthropod predation rates (Chapter 3), but did not affect invertebrate herbivory among plant functional groups (Chapter 2). This does not necessarily mean that predation does not impact herbivory (Schmitz et al. 2000; Halaj and Wise 2001), as predation rates are limited by the used method and thus may not capture predation rates of the complete predator community (Chapter 3). Besides, leaf-chewing herbivores feeding on legumes, forbs and grasses may be diverse in their traits (e.g. body size, cuticular toughness), so that predation rates may predict predation by predators with matching traits better than of other (Brousseau et al. 2018). Therefore, the proportion of realized interactions of predators and herbivores, contributing to measured predation rates and herbivory, may vary so that the captured fraction of herbivory and predation rates provided by the arthropod community may respond independently from each other to environmental factors.

Diverse landscapes can provide complementary or supplementary resources to organisms moving between habitat patches with beneficial effects on their population size (Dunning et al. 1992). Movement between habitat types is known for several carabid species (Magura 2002; Rand et al. 2006; Allema et al. 2019), which is the group of predators driving predation rates on artificial caterpillars on ground-level, but also being commonly the most abundant group of ground-active arthropods (Ferrante et al. 2014). Predation rates on open herbaceous vegetation benefitted from diverse landscapes in the intermediate surrounding (2-km radius), independently of the dominant habitat type in the vicinity (Chapter 3). This may suggest, however, that rather than benefits from complemented resource use from adjacent habitat types, higher landscape diversity possibly translates into reduced distances between suitable habitats and thus increased connectivity of habitats exploited by predators contributing to measured predation rates. This explanation is in line with a high variability in predation rates among plots in diverse landscapes, as the one or more suitable habitat types may be present in different proportions, combinations or configurations (Dunning et al. 1992; Rand et al. 2006; Fahrig 2017). Despite factors introducing variability, landscape diversity promoted predation rates. This may serve as a starting point for future research investigating the underlying mechanisms and deriving more specific recommendations for landscape management to promote top-down regulation of herbivores, and potentially also of pests.

Plant richness at species and family level

Plant species richness did neither affect herbivory nor predation, albeit plant species richness may affect community composition of herbivores and predators (Schuldt et al. 2019), but plant richness at family-level differentially influenced herbivory among plant functional groups (Chapter 2+3).

Opposing effects of plant species richness on herbivory reported in literature range from positive, neutral to negative effects (Unsicker et al. 2006; Jactel and Brockerhoff 2007; Ebeling et al. 2014; Loranger et al. 2014). The direction of the plant species richness effect may depend on the ratio of specialist to generalist herbivores being present on a site (Shinohara and Yoshida 2021). Considering that specialist herbivores are frequently specialized within a plant family (Haddad et al. 2001), and built up higher densities in pure stands than in diverse vegetation (Root 1973), plant richness at higher taxonomic level, such as the family level, may decrease herbivory by specialist herbivores more strongly than plant richness at species level (Jactel and Brockerhoff 2007). However, plant richness at family level compared to species level may also more strongly affect generalist herbivores, which benefit from higher plant biomass in more diverse vegetation. This may be the case when more taxonomically diverse vegetation comprises more complementary plants with greater difference in plant characteristics, and thus possibly increases plant biomass more strongly than plant species richness. Yet, herbivory on legumes decreased with increasing plant richness at family level (but not at species level), whereas herbivory increased on forbs and remained largely unchanged on grasses (Chapter 2). Thus, herbivory by common generalist herbivores such as grasshoppers feeding predominately on grasses, but also on forbs and legumes (Unsicker et al. 2005), may be less affected in taxonomically diverse vegetation (i.e. plant richness at family level) than specialist herbivores feeding on legumes.

Plant species richness can affect arthropod predation rates through increased structural diversity, which may facilitate more niche spaces possibly lowering intraguild predation, but also through a higher probability of complementarity among predators when predator richness increases with plant species richness (Hertzog et al. 2017). However, we observed neither effects of plant richness at species nor family level on arthropod predation rates at ground level. Considering that arthropod predators commonly prefer prey related to their body size and to further ‘matching’ traits (Brousseau et al. 2018), the used type of artificial caterpillars may have captured only attack from rather large-bodied arthropod predators, and mainly from carabids, the most common predators on artificial caterpillars at ground-level (Ferrante et al. 2014). Therefore, only when composition or behaviour of predator species matching sentinel prey traits are affected by plant richness, predation rates may also respond. Furthermore, plant species richness effects on predator richness can be weak (Schuldt et al. 2019) and responses in predation rates accompanied by large variation (Hertzog et al. 2017). Thus, other factors influencing predator communities in a large spatial scale study may introduce ‘noise’ rendering potentially small effects of plant richness on predation rates invisible. Looking at effects of plant richness on higher trophic levels from a perspective of energy fluxes, plant richness – commonly related to higher vegetation biomass – increases energy flux to both herbivores and predators (Barnes et al. 2020). Therefore, plant richness may promote energy flux to arthropod predators at community level, but not predation rates capturing attack by part of the predator community.

Taxonomic resolution and spatial scales

Observations at different taxonomic resolutions revealed that arthropod species richness or ecosystem functions may remain similar or increase in response to certain differences in land use or temperature at low resolution (e.g. community level), while specific insect orders or plant families respond contrastingly (Chapter 2; Ganuza et al. 2022). For instance, more forest cover at multiple spatial scales promotes species richness of insect pollinators, albeit pollinator orders respond differently (Ganuza et al. 2022). Similarly, forests, particularly glades or clearings, may also affect performance of some plant functional groups, i.e. legumes, when forests provide refuge from damage to invertebrate leaf-chewing herbivores (Chapter 2). This may be of relevance to species protection and species-specific interactions, albeit species richness and processes at the community level may remain similar along environmental gradients for a longer time, when contrasting effects at lower taxonomic level (e.g. order, family, species) cancel each other out or introduce variation along gradients.

Rapid ecosystem function assessment, e.g. of herbivory and predation, can provide valuable additional insights into ecosystems beyond biodiversity assessment (Meyer et al. 2015), as demonstrated within LandKlif (e.g. Chapter 2+3). However, rapid assessment without knowledge on the applied filters, e.g. only part of the predator community attacking the used sentinel prey with its inherent traits, provides an incomplete picture of ecosystem functions. Therefore, a deeper mechanistic understanding is needed, regarding which approach captures the function provisioning of which species, orders or parts of a community. Capturing the ecosystem function provisioning by a share of the community can be sufficient, e.g. when this part matches the traits of a target pest species, but particularly in more diverse and complex semi-natural systems, the obtained results should be interpreted carefully. This may also be important when it comes to choosing spatial scales for implementing management options, as these may differ depending on the species present in a community, which may only be incompletely captured by rapid assessment. Improving ecosystem function assessment by a more mechanistic understanding of the underlying filters will facilitate to derive management options favouring ecosystem function provisioning more generally or to tailor it to specific pest species.

Trophic interactions in a warming world

Elevated temperatures can affect plants, herbivores, predators and interactions among them in multiple ways, including altered development times, nutrient needs and phenological mismatch between interaction partners (Bale et al. 2002; Rasmann and Pellissier 2015; Rosenblatt and Schmitz 2016), ultimately causing local extinction of species and shifts in the geographic distribution of species (Bale et al. 2002; Thomas et al. 2004; Rasmann and Pellissier 2015). Therefore, we assumed that the community composition of plants, herbivores and predators as well as herbivory and predation may differ along large spatial temperature gradients. Yet, herbivory and predation rates did hardly respond to temperature (Chapter 2+3), albeit higher multi-annual mean temperatures promoted arthropod biomass and richness, e.g. of flying insects (Uhler et al. 2021). Thus, different arthropod communities may provide on average similar levels of herbivory and predation along a temperature gradient. This supports the idea that common generalist species may be relevant for maintaining functions (Rossetti et al. 2017), but large variation of herbivory and predation rates among plots in similar climates also emphasises the importance of key species and species composition (Griffin et al. 2013; Alhadidi et al. 2018). With respect to one particular plant-herbivore system, winter oilseed rape and the pollen beetle, temperature affected phenology as well as drought-related reduction in habitat amount (here: oilseed rape) with consequences on pest abundances and seed yield (Chapter 4). Thus, some agricultural ecosystems may be more vulnerable to climate change than more diverse semi-natural ecosystems, albeit management options to decrease vulnerability are more plentiful, and probably also more quickly realized, in agricultural than semi-natural ecosystems.

Herbivory and predation under climate change

Minor importance of multi-annual mean temperature for herbivory among plant functional groups and predation rates along the covered gradient (~6–10°C), suggests that climate warming may not strongly alter these processes in the near future. However, climate change implies more than warming and effects may differ along the spatial and the projected temporal trajectory. Along spatial climate gradients, communities had more time to adapt than they will likely have to adapt to global warming in the future, as warming happens at a much faster rate (IPCC 2018). Currently, space-for-time approaches and studies along the temporal trajectory may provide similar results regarding climate change effects on biodiversity (Blois et al. 2013). However, climate variability is increasing (Jentsch et al. 2007). Thus, the full impact of climate change on biodiversity and ecosystem functions is neither captured by the temporal trajectory until present nor by a space-for-time approach. Climate change is a multifaceted phenomenon including changes in patterns of temperature and precipitation with regard to their minimum, maximum, mean and variance, which can expose species in their current geographic distribution to conditions, which are closer to optimal, suboptimal, extreme or lethal (Halsch et al. 2021). At present, highest consensus regarding climate change exists on global warming, thus an increase in mean global temperature (Cook et al. 2016). Therefore, a space-for-time approach provides important clues, e.g. little temperature effects on herbivory and predation rates at present, while long-term monitoring will be needed to allow careful reconsiderations in the future.

Diverse communities are assumed to cope better with climate change, due to an ‘insurance’ effect (Oliver et al. 2015). This is a higher probability of a diverse community to comprise species, which perform well under altered environmental conditions. Consequently, factors influencing herbivore communities, such as plant richness and land use, may modulate temperature effects on ecosystem functions. However, we did not observe substantial interactive effects of temperature and land use on herbivory among plant functional groups and on arthropod predation rates (Chapter 2+3). As arthropod communities may have had more time to adapt to the current conditions, than they will have with global warming (IPCC 2018), interactive effects of temperature with plant richness and land use may become more apparent in the future, when insurance effects reach their limits in extremely impoverished arthropod communities.

Pest management under climate change

Phenology of both plants and herbivores is temperature dependent (Rasmann and Pellissier 2015), which may not lead to a complete mismatch in warmer climates, but may help to avoid or reduce infestation in the most vulnerable development stage. This is the case in oilseed rape. Oilseed rape flowered earlier in warmer regions, which was associated with higher seed yields (Chapter 4). This was particularly the case for oilseed rape fields that flowered even earlier than expected based on regression of flowering onset and multi-annual mean temperature, which possibly occurred due to cultivar-specific differences in flowering time or responses in flowering time to temperature. Thus, early flowering oilseed rape may escape damage from pollen beetles in the most vulnerable bud stage (Williams 2010). Therefore, phenological mismatch, potentially disturbing plant-insect interactions in natural systems, may be harnessed in crop systems to increase crop fitness.

Extreme events may have larger impact than an increase in mean temperature (Jentsch et al. 2007). For instance, warmer regions were facing drought around sowing of winter oilseed rape, which led to strong reductions in oilseed rape production area, and ultimately in severe increases of pest abundances per plant (Chapter 4). Drought reduced the oilseed rape production area, as it made farmers rethink their crop rotation scheme or forced them to plough up poorly performing oilseed rape fields in spring (personal communication with farmers). This example also illustrates the importance of considerations at the landscape scale. With increasing drought risk due to climate change (IPCC 2018), collective efforts may assist both to avoid strong fluctuation in the production area of a specific crop between 'normal' years and to facilitate zero-oilseed rape years in years of adverse weather conditions. Thus, climate change as multifaceted phenomenon may not only have direct ecological consequences (Jentsch et al. 2007), but also indirectly through changes in cropping area, ultimately bringing the risk of crop migration and a further decline in natural lands (Sloat et al. 2020).

Reconciling agriculture with nature

A key challenge to humanity is to increase agricultural production without causing environmental harm. Therefore, a transformation towards sustainable agriculture is important. Sustainability means that any action does not harm the environment. Coming from chemical pesticides as dominant and often single pest control strategy that is known for its environmental damage (Pretty et al. 2001; Aktar et al. 2009; Krauss et al. 2011; Rehman et al. 2014), an important step will be to reduce chemical pesticide use to minimize environmental damage, while maintaining high crop yields, and paving the way for alternative strategies to reach a no-environmental-damage scenario.

High crop yields depend on effective pest management, which is at its optimum, when crop damage falls below the level, which is compensated by plant growth. From this, three complementary pathways to pest management arise: reduced pest abundances per plant through (i) increased pest mortality and (ii) pest dilution effects (e.g. resource availability, push-pull system), and (iii) optimized crop plants coping better with pest incidences. Each of these pathways holds many measures to control pests (**Fig. 1**).

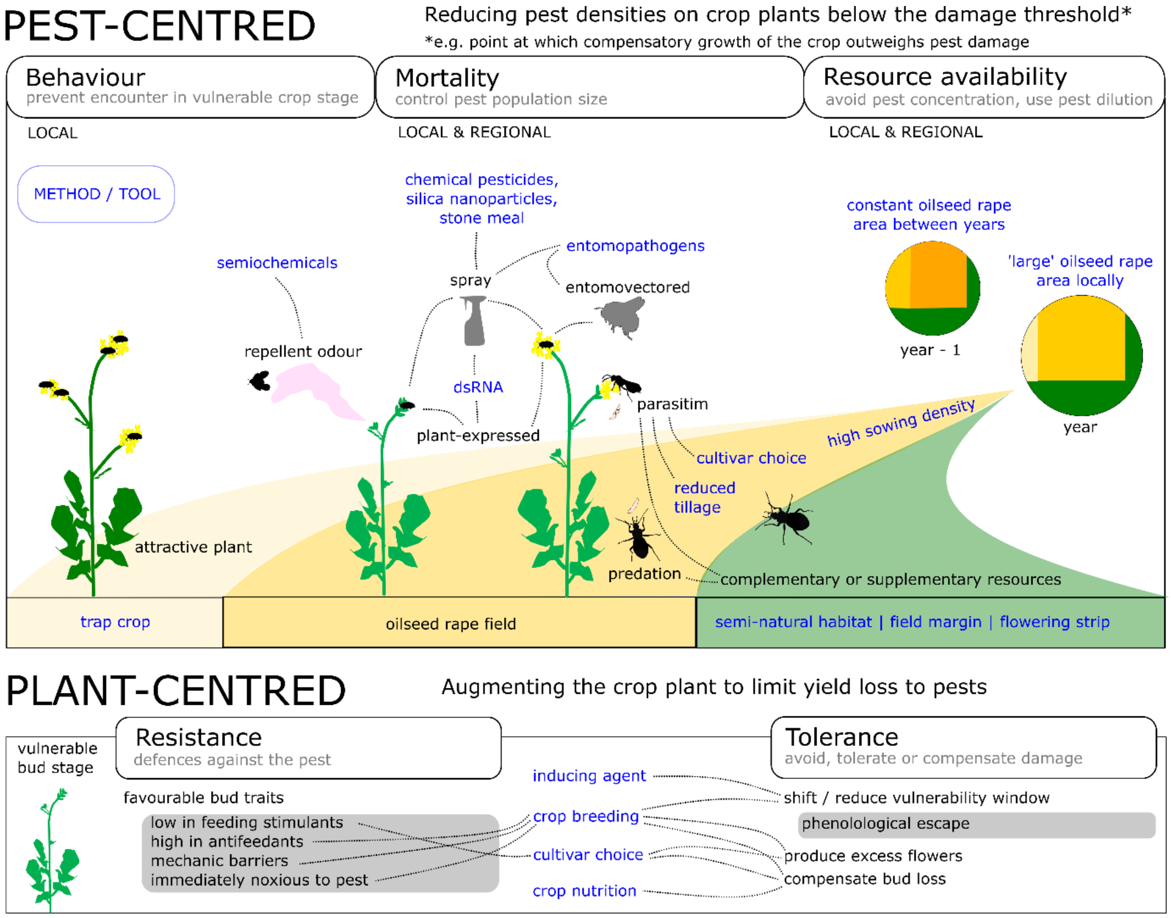

Figure 1 Diverse pest management strategies from the perspective of the pest and the plant, illustrated on the example of the pollen beetle in winter oilseed rape. Dotted lines link methods/tools (blue font) with mechanisms (black font); dsRNA: double-stranded RNA for pest species-specific gene silencing.

Pest mortality

With respect to an important pest and crop, namely the pollen beetle causing damage to oilseed rape (Williams 2010; Chapter 4; Gagic et al. 2016), many pest management measures have been investigated (**Fig. 1**). Yet, the most common pest control strategy against the pollen beetle still is the application of chemical pesticide, despite reduced efficacy due to pesticide resistance (Slater et al. 2011; Heimbach and Müller 2013), and the environmental damage it causes (Ulber et al. 2010a; Rehman et al. 2014; Krimmer et al. 2021). Chemical pesticide use as pest control strategy focuses on the treatment of pest-infested crop plants, and thus depends on quick mortality of the pest. When pest reduction occurs outside the vulnerability window of the crop, e.g. reduction of pollen beetles on oilseed rape plants at a growth stage other than the bud stage (Williams 2010), economic benefits are likely limited within the season.

Mortality agents with high specificity

Alternative mortality agents to chemical pesticides are entomopathogens, e.g. the microsporidian *Nosema meligethi* specialized to the genus of the pollen beetle (Hokkanen and Lipa 1995; Hokkanen and Menzler-Hokkanen 2017), or double-stranded RNA (dsRNA), which species-specifically switches off an essential biological process in the pest means RNA interference (Reviewed in Zotti et al. 2018; RNAi; Willow et al. 2020, 2021a). However, these more target-specific, and thus more environment-friendly, mortality agents act more slowly (days to weeks) than conventional chemical pesticides with high mortality within 24 hours (Slater et al. 2011). To harness those environment-friendly measures, it will require to rethink pest management, as any pest reduction contributes to lower pest numbers in the following year, and thus to crop damage prevention (**Fig. 2**). The benefit of implementing such a preventive pest management strategy may be small for the individual farmer, but high when farmers act collectively. Thus, to move towards sustainable agriculture, a shift in thinking from pest treatment to crop damage prevention is needed as well as collective farming approaches.

Dose reduction of mortality agents

During the transition process towards sustainable agriculture, but also to reduce costs of mortality agents with high specificity, strategies for dose reduction will be required. This is approached by spray formulations with carriers such as nanoparticles for more controlled release (Yusoff et al. 2016; reviewed in Li et al. 2021), precision farming for spatially explicit application (reviewed in Finger et al. 2019) and entomovector technology that uses insects, for instance bumble bees, as carriers of a mortality agent (Hokkanen and Menzler-Hokkanen 2017). Thereby, entomovectored applications are restricted to crops in flowering stage, which comes too late for protection of oilseed rape against pollen beetle infestation in its most vulnerable bud stage (Williams 2010), yet contributes to a preventive pest management strategy.

Insecticides based on physical properties

Regarding nanoparticles as carriers, safety issues cannot be ruled out at present (Yadav et al. 2022), while at the same time certain nanoparticles are under research for their insecticidal properties (Rastogi et al. 2019; Thabet et al. 2021). These insecticidal properties of silica nanoparticles ground in suffocation through the clogging of the spiracles (openings of the respiratory system) or desiccation through damage to the cuticle (Rastogi et al. 2019). These properties are also used when applying dusts as insecticides (Ebeling 1971; Ulrichs et al. 2006), e.g. stone meal against pollen beetles in organic farming (Dorn et al. 2014). Albeit, the added adjuvant seems to be decisive for the effectiveness of stone meal under field conditions (see Dorn et al. 2014). Thus, due to their physical properties dusts and silica nanoparticles may serve as insecticides against pests that are resistant to chemical pesticides. Yet, these alternative measures to treat pest-infested crops should not block the development of preventive pest management strategies, which will be needed to move from pest management that minimizes environmental damage to a no-environmental damage scenario.

Natural enemies

To reconcile agriculture with nature, natural enemies are likely to play an important role (Bommarco et al. 2013), since the promotion of natural enemies benefits both biodiversity and pest control (Griffin et al. 2013). In case of the pollen beetle, however, natural enemies mainly contribute to crop damage prevention in the following year as ground-active predators and parasitoids attack the egg or larval stage of the pollen beetle (Ulber et al. 2010b; Williams et al. 2010), while pollen beetle larvae cause little damage to oilseed rape (Williams 2010). To promote natural control of the pollen beetle, collective approaches could facilitate the optimization of landscapes for the maximal benefits of natural enemies. Parasitism rates of pollen beetle larvae, e.g. by *Tersilochus heterocerus* and *Phradis* spp., increase with the area of semi-natural habitat in the vicinity and proximity to oilseed rape fields of the previous year (Rusch et al. 2011). Ground-active beetles preying on larvae of the pollen beetle benefit from perennial landscape elements at field boundaries or within fields and small field size with high proportion of field edge (reviewed in Williams et al. 2010). Yet also crop management changes benefit natural enemies of the pollen beetle such as reduced tillage and reduced input of agrochemicals (Nilsson 2010; Ulber et al. 2010a; Williams et al. 2010). Predation and parasitism of pollen beetle larvae act complementary on pollen beetle abundances, particularly when semi-natural habitat is low, whereas predation dominates the control of pollen beetles in regions with high proportion of semi-natural habitats, e.g. 50% (Dainese et al. 2017). However, optimal landscapes for natural pest control appear to be context-specific, which does not yet allow for general recommendations for landscape management, although a better mechanistic understanding could facililtate this in the future (Alexandridis et al. 2021). Optimization of natural control in annual crops within rotations will also be challenging, because even generalist predators prefer certain prey types (Brousseau et al. 2018), which makes it necessary to consider both the spatial and temporal dimension.

Resource availability (crop and landscape management)

Host plant availability to the pest at multiple scales from crop plant density to crop production area affects pest densities in a crop. High plant densities tend to decrease pollen beetle damage (Valantin-Morison et al. 2007), though not consistently (Rusch et al. 2013; Skellern and Cook 2017). This inconsistency may result from differences in the cultivar-specific capacity to compensate bud damage (Pinet et al. 2015), and differences in the phenotypic response of plants to high plant density such as reduced branching (Leach et al. 1999) that may differently affect the compensatory capacity of a cultivar. Yet, cultivar-specific studies on plant density effects and pollen beetle damage are lacking. Beside plant density, the crop field size affects the number of locally available host plants. This can lead to dilution effects on pollen beetles (Valantin-Morison et al. 2007), but also this effect is inconsistent (Rusch et al. 2013; Schneider et al. 2015; Skellern and Cook 2018). This may result from counteracting effects of crop field size on pollen beetle density, as the effect is modulated by certain pest traits. Thus, low reproduction rate within the season and low dispersal range favour dilution effects (Segoli and Rosenheim 2012). Pollen beetles produce one generation per season, but are relatively good dispersers with dispersal ranges exceeding 13 km (Williams and Cook 2010). Thus, the dispersal range of the pollen beetle may modulate the dilution effect of crop field size, which could be influenced by changes in oilseed rape area between years. For example, a strong reduction in oilseed rape area from one to the other year may favour long-distance dispersal, and thus concentration of pollen beetles from the large surrounding on the available oilseed rape area, which may affect pest densities much more strongly than crop field size (see Chapter 4). Therefore, coordinating oilseed rape area across years likely prevents ‘outbreaks’ of pollen beetles, whereas the costs and benefits associated with higher plant density and larger crop field size need to be carefully weighed.

Measures affecting pest densities are unlikely to directly affect pest mortality, unless resource limitation is reached (e.g. zero-oilseed rape year). Nonetheless, they are a valuable complement in a preventive pest management strategy, and particularly the coordination of the crop production area (e.g. similar across years) may come at low costs when farmers are organised in collectives.

Pest behaviour

Low pest densities on the crop can also be achieved through interference with pest behaviour. For example, sachets with lavender oil placed in the oilseed rape field prior to infestation repel pollen beetles (‘push’, Mauchline et al. 2013), which may be lured in a more attractive trap crop such as *Brassica rapa* or *B. nigra* (‘pull’) established as perimeter around the oilseed rape field (Cook et al. 2006; Veromann et al. 2012; Skellern and Cook 2018). Yet, studies combining both a repellent and a trap crop in a push-pull system for oilseed rape are lacking, beside practical techniques for slow release of repellents in oilseed rape fields (Mauchline et al. 2018). Furthermore, the success of trap crops such as *B. rapa* is variable (Kühne et al. 2013). The success may depend on the realised difference in flowering time between *B. rapa* and oilseed rape (Cook et al. 2007), but also on traits of the main crop. Early flowering can lead to phenological escape from pollen beetle infestation at the most vulnerable crop stage (Chapter 4; Williams 2010). Thus, prior to implementation of a push-pull-strategy against the pollen beetle, considerations should be given to the risk of high infestation in bud stage and whether it justifies the costs and efforts.

Crop resistance and tolerance

At present oilseed rape cultivars differ in their ability to cope with pollen beetles, which includes some cultivars that are partially resistant or tolerant to pollen beetles (Hervé et al. 2014b; Pinet et al. 2015). For example, oilseed rape cultivars with high regrowth potential tolerate more bud damage (Pinet et al. 2015), early flowering cultivars partially escape bud damage from pollen beetles (Chapter 4; Williams 2010) and cultivars with low sucrose concentration in the outer part of the bud (perianth) are less damaged by pollen beetles (Hervé et al. 2014a). However, fully resistant cultivars against pollen beetles do not exist so far (Hervé and Cortesero 2016; Hervé 2018).

Crop breeding

Promising approaches in crop breeding include the exploitation of natural variation in resistance among oilseed rape genotypes, introgression of resistance from other brassicaceous species (e.g. *Sinapis alba*) and introduction of resistance transgenes (Hervé and Cortesero 2016; reviewed in Hervé 2018). Thus, in the future, oilseed rape cultivars could be mechanically defended against pollen beetles, for example, when buds carry dense trichomes alike oilseed rape seedlings with dense trichomes transformed with genes from *Arabidopsis thaliana* (Gruber et al. 2006). At present, advances using the RNAi technique are particularly promising (Zotti et al. 2018; Willow et al. 2020; De Schutter et al. 2022). RNAi was demonstrated to increase pollen beetle mortality, when pollen beetles fed on dsRNA treated flower buds or anthers (Willow et al. 2020, 2021a). After feeding on dsRNA-treated anthers for 3 days, mortality of adult pollen beetles exceeds 80% within 14 days (Willow et al. 2021b). Pollen beetle larvae die quicker than pollen beetle adults upon dietary exposure to dsRNA (Willow et al. 2021a), yet mortality of adults increases when they continuously take up dsRNA (Willow et al. 2021b). Genetically modified plants can continuously express pest species-specific RNAi with low risk to humans and farm animals, while bioinformatics streamline a thorough risk assessment (Zotti et al. 2018; Arpaia et al. 2020; De Schutter et al. 2022). At present, oilseed rape plants expressing dsRNA targeted to the pollen beetle are not yet available, and their cultivation would require changes in EU legislation (De Schutter et al. 2022). Besides, using the RNAi method against pollen beetles also needs a rethinking in pollen beetle management as the slow mortality of the pest upon dsRNA exposure does not suit as treatment of pest-infested plants, but contributes to crop damage prevention in the following years.

Pest management aiming at crop damage prevention may offer new opportunities for crop breeding. While crop resistance or compensatory growth may pay off primarily for the individual farmer in the season, increased pest mortality (even if slow), reduced oviposition rate and slower larval development accompanied by prolonged exposure to parasitoids may reduce the regional pest pool and feed into a preventive pest management strategy. Regarding the oviposition behaviour of the pollen beetle, differences in preference are known between cultivars (Hervé et al. 2014b) and brassicaceous species (Hopkins and Ekbom 1999), which may be one starting point for crop breeding for a preventive pest management strategy.

Crop nutrition

Crop nutrition shapes several bud and flower traits of oilseed rape, which can affect pollen beetle abundance per plant, and can also increase the regrowth capacity of oilseed rape to compensate damage (reviewed in Skellern and Cook 2017). Yet, responses to fertilizer regimes are variable.

Thus, compensatory growth does not always respond to fertilizer amount (Pinet et al. 2015) and pollen beetle abundance can be lower at certain fertilizer amounts, but these still vary from trial to trial (Skellern and Cook 2017). Thus, albeit a good nitrogen status was demonstrated to reduce crop damage to pollen beetles (Valantin-Morison et al. 2007; Rusch et al. 2013), more research is needed to give practical advice on optimal fertilization with respect to crop damage prevention and compensation.

Inducing agents

Inducing agents may help to modulate crop phenotype towards partial resistance and tolerance against a pest (Dicke and Hilker 2003). Plasticity in flowering time offers an opportunity for phenological escape of oilseed rape from infestation of the pollen beetle in the bud stage (Williams 2010; Srikanth and Schmid 2011). The treatment of oilseed rape in early bud stage with the phytohormone methyl jasmonate was demonstrated to promote early flowering (Pak et al. 2009). Besides, the oilseed rape relative *Sinapis arvensis* flowered early when infested with the mustard leaf beetle *Phaedon cochleariae* at the vegetative stage (Hoffmeister et al. 2016). In the latter case, the mechanism is yet unknown, but may help to identify an inducing agent that modulates the flowering time when applied in vegetative stage. Besides, the successful induction of early flowering could depend on the combination of cultivar, inducing agent and timing of application. For example, the treatment of spring oilseed rape with jasmonate at the vegetative stage did not promote earlier flowering (unpublished data), which suggests that jasmonates do not generally promote early flowering in oilseed rape. Beside flowering time, there is no specific inducible resistance or tolerance trait of oilseed rape known against the pollen beetle, though the sugar metabolism could be a starting point. Sucrose content in buds increases the food intake of pollen beetles associated with increased crop damage and pollen beetle fecundity (Hervé et al. 2014b), while sugar content in plant tissues can change in response to herbivory (Ferrieri et al. 2013; Machado et al. 2017). However, the levels of fructose and glucose seem to change, more than those of sucrose. Furthermore, it is important to keep in mind that inducing defences in favour of one pest may come at the cost of lowered defences regarding another pest (Halitschke et al. 2008; Kroes et al. 2015). Yet, as early flowering can increase oilseed rape yield (Chapter 4), possibly due to phenological escape (Williams 2010), inducing agents may allow direct intervention when pollen beetle infestation is forecasted to appear at the field within the vulnerability window of the crop (see Johnen et al. 2010).

Plant defence priming

In distinction to inducing stimuli, which directly act upon a plant, priming stimuli make a plant respond more quickly, strongly and prolonged to the coming attacker (Martinez-Medina et al. 2016). Priming agents encompass volatile organic compounds and microorganisms among others, which elicit molecular changes, e.g. in the chromatin structure. This prepares a plant for a coming attacker at low costs (Martinez-Medina et al. 2016). However, thus far, it seems unlikely that 'priming' prepares oilseed rape against the pollen beetle, as pollen beetles have little contact with the plant defence system of oilseed rape, due to preferably foraging on pollen from open flowers (Cook et al. 2007).

Sustainable pollen beetle management: From theory into practice

There are many measures for the management of pollen beetles (**Fig. 1**), but only few are available as marketable product or practitioner's guideline to farmers in the EU (**Fig. 2**). This calls for research, which identifies underlying crop and pest traits, and site-specific conditions that are relevant for the success of a measure. Some of the measures that are commonly used in research, such as landscape parameters indicated as radii around study sites, will need 'translation' for comprehensive spatial planning at regional level. Furthermore, it is not only about combining several measures but about integrating them so that they act synergistically (Stenberg 2017). On top, sustainable pest management will require rethinking from the treatment of pest-infested crops to the prevention of crop damage in the following years. This transition process will require trust and exchange among farmers and scientists. An important contribution to this could be made by farmer clusters. They tighten relationships and increase trust among members, which lays the foundation for knowledge transfer (Joffre et al. 2020). Besides, collective farming practices are known to benefit increased risk awareness and adoption of sustainable practices (Joffre et al. 2019). In the last decade, farmer clusters emerged in the UK (https://www.farmerclusters.com/) and Japan (Zollet and Maharjan 2021), and the number of research projects pioneering participatory approaches with multiple actors in the landscape is increasing, e.g. 'FRAMEwork' (www.framework-biodiversity.eu), 'FInAL' (www.final-projekt.de), 'KOOPERATIV' (www.uni-goettingen.de/kooperativ/projekt). So far, however, there is no project that specifically targets crop damage prevention through reducing pest populations and densities in the medium to long term.

Despite the fact that sustainable pest management strategies against the pollen beetle are not yet fully matured (**Fig. 2**), some aspects can be easily implemented: (i) select partial resistant or tolerant cultivars (e.g. early flowering), (ii) strengthen awareness of concentration effects on pollen beetles when the cultivation area of oilseed rape is strongly reduced relative to the previous year, which could promote a more constant cultivation area across years or facilitate the implemention of years without oilseed rape cultivation, and (iii) reduce pesticide use against the pollen beetle to a minimum, especially outside the most vulnerable bud stage. These aspects may help to immediately reduce the use of pesticides and thus environmental damage, while at the same time increasing crop yields in the presence of pesticide-resistant pollen beetles. The transition towards sustainable insect pest management that promotes high crop yield without causing environmental damage is urgently needed, as this is an important aspect to halt biodiversity loss (Wagner et al. 2021).

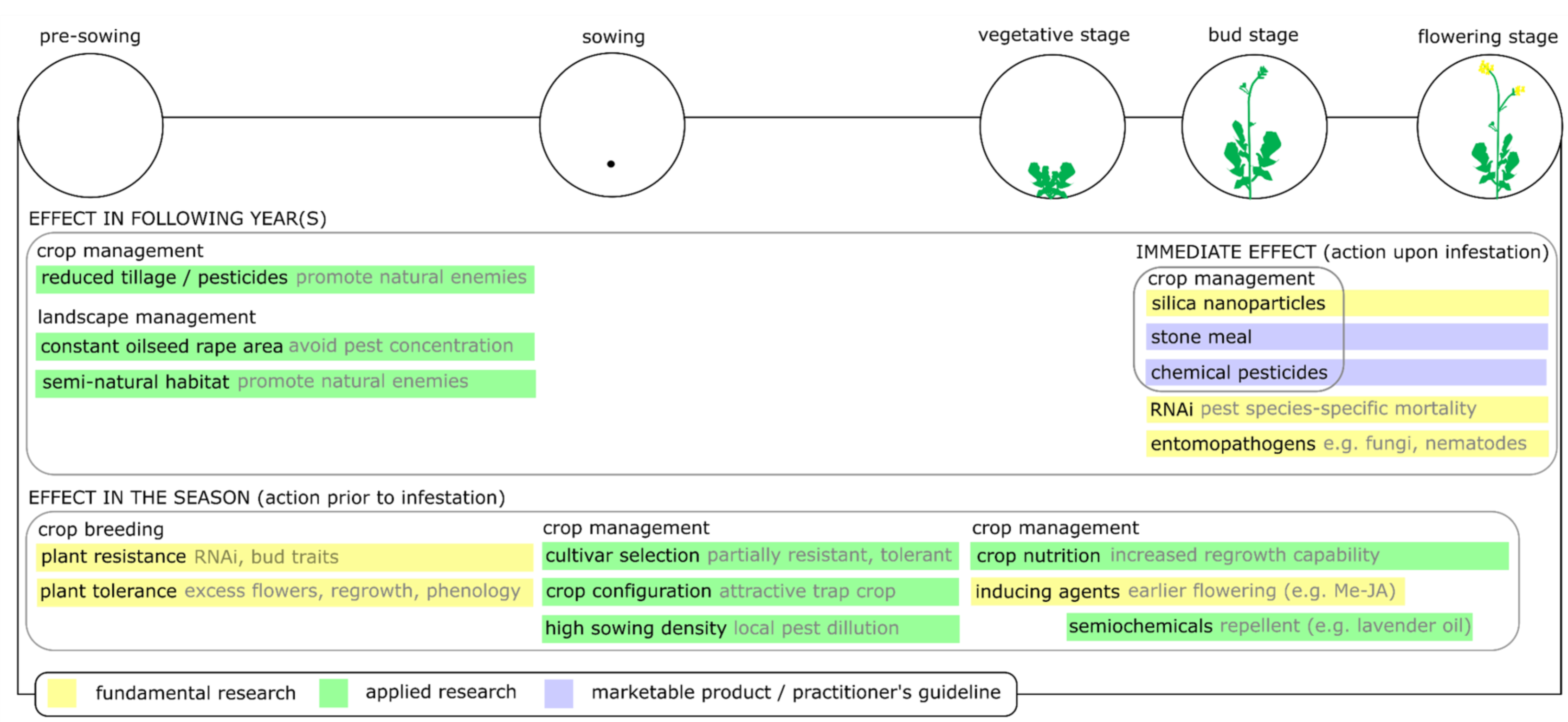

Figure 2 Pest management strategies and their potential for temporal integration along the life history of the crop illustrated on the example of the pollen beetle, a major pest of winter oilseed rape. Strategies are grouped by time between action and effect. Immediate effects on pest mortality also affect pest population size of the following year(s). Some strategies aim for immediate effectiveness, but have not reached it yet (dashed rectangle). Methods / tools are presented and grey font highlights accompanying examples. Colours indicate the current state of a strategy from fundamental research to marketable product or practitioner's guideline.

Conclusion

Anthropogenic land-use and climate change pose a major threat to biodiversity and thus to ecosystems, while human well-being and existence depend on their integrity (IPBES 2019). At present, temperature seems to affect arthropod community composition more strongly than ecosystem functions (Chapter 2+3; Uhler et al. 2021), and to elicit various effects at higher taxonomic resolution (e.g. order or family level), which cancel out to few or noisy effects at low resolution (e.g. community level; Chapter 2; Ganuza et al. 2022). Thus, ecosystem functions such as herbivory and predation barely responded to temperature at present (Chapter 2+3). Nonetheless, it is likely that a tipping point will come, when compensation through functional redundancy in arthropod communities is depleted (see Oliver et al. 2015). It is still unclear when this will happen, but this is probably the latest point at which interactive effects of temperature and land use will influence ecosystem functions in addition to biodiversity (see Mantyka-Pringle et al. 2012; Ganuza et al. 2022). However, what is certain, is that beside the need to discontinue actions driving land-use and climate change, mitigation strategies to global warming will be needed and the sooner solutions are found, the better the outlook for human well-being (IPCC 2022). Thereby, biodiversity is our insurance asset (Oliver et al. 2015). In order to halt the current decline in biodiversity, management strategies for the environment-friendly regulation of herbivores and their damage to plants are essential (see Wagner et al. 2021). In my thesis, I identified habitat, landscape and phenological aspects, which may contribute to such a strategy (Chapter 2–4). However, further efforts will be needed to make the beneficial effects of, for example, diverse vegetation (Chapter 2), diverse landscapes (Chapter 3) and continuity in arable landscapes (Chapter 4) usable for practical implementation (see above, “Reconciling agriculture with nature”). LandKlif and my thesis within the project thus provide important starting points for at least partially temperature-resilient management strategies that promote biodiversity and regulate ecosystem functions in an environmentally sound manner, thus contributing to securing human well-being for future generations.

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Author contributions

Chapter 2 has been submitted to Oecologia as: Fricke U, Redlich S, Zhang J, Tobisch C, Rojas-Botero S, Benjamin C, Englmeier J, Ganuza C, Riebl R, Uhler J, Uphus L, Ewald J, Kollmann J, Steffan-Dewenter I (under review). Plant richness, land use and temperature differently shape invertebrate leaf-chewing herbivory on plant functional groups.

Contributions

UF, SR and ISD conceived the idea of this manuscript. UF, JZ, CT, SRB, JEwald, JK and ISD designed the methodology. UF, SR, JZ, CT, SRB, CB, JEnglmeier, CG, RR, JU and LU collected data. UF analysed the data. UF wrote the first manuscript draft in consultation with SR and ISD. All authors commented critically on the manuscript and approved its final version.

Contribution of the candidate

Publication details	Description of the own contribution
Writing of the article Which parts of the article have been written to which extent by the candidate?	The writing of the article was led by Ute Fricke including the writing of the first draft and the implementation of comments from co-authors, and reviewers of the Journal of Ecology and Oecologia
Performed research Which experimental procedures have been conducted by the candidate?	Collection of leaves in multiple LandKlif regions (joint field work of several early career scientists and student assistants in different regions of Bavaria, Germany), assessment of leaf damage, guidance of student assistances in leaf-damage assessment
Conceptual design of the research To which extent did the candidate contribute to the conceptional design of the research project?	Within the framework of the LandKlif project, protocols for leaf collection and leaf-damage assessment have been developed by Ute Fricke.
Data analysis To which extent did the candidate contribute to the data analysis?	Data were analysised by Ute Fricke.
Overall contribution of the candidate (in%)	80–90

Confirmation by Co-authors

Name Co-author	**Signature**	**Date**
Sarah Redlich		29.04.2022
Jie Zhang		09.05.2022
Cynthia Tobisch		29.04.2022
Sandra Rojas-Botero		29.04.2022
Caryl S. Benjamin		29.04.2022
Jana Englmeier		29.04.2022
Cristina Ganuza		29.04.2022
Rebekka Riebl		29.04.2022
Johannes Uhler		29.04.2022
Lars Uphus		29.04.2022
Jörg Ewald		29.04.2022
Johannes Kollmann		29.04.2022
Ingolf Steffan-Dewenter		05.05.2022

Chapter 3 has been published in PLOS ONE as: Fricke U, Steffan-Dewenter I, Zhang J, Tobisch C, Rojas-Botero S, Benjamin C, Englmeier J, Ganuza C, Haensel M, Riebl R, Uhler J, Uphus L, Ewald J, Kollmann J, Redlich S (2022). Landscape diversity and local temperature, but not climate, affect arthropod predation among habitat types.

Contributions

UF, SR and ISD conceived the ideas; UF, JZ, CT, SRB, JEw, JK and ISD designed the methodology. UF, SR, JZ, CT, SRB, CB, JEn, CG, MH, RR, JU and LU collected data. UF analysed the data. UF led the writing of the manuscript. All authors commented critically on the drafts and approved the final version of this manuscript.

Contribution of the candidate

Publication details	Description of the own contribution
Writing of the article Which parts of the article have been written to which extent by the candidate?	The writing of the article was led by Ute Fricke including the writing of the first draft and the implementation of comments from co-authors and reviewers of PLOS ONE.
Performed research Which experimental procedures have been conducted by the candidate?	Conduct of the artificial caterpillar experiment includinig field assessment of attack marks in one LandKlif region (joint field work of several early career scientists and student assistants in different regions of Bavaria, Germany), and assessment of attack marks on collected artificial caterpillars from all regions in the lab.
Conceptual design of the research To which extent did the candidate contribute to the conceptional design of the research project?	Within the framework of the LandKlif project, protocols for artificial caterpillar production, experimental conduct, and assessment of attack marks were developed or provided by Ute Fricke.
Data analysis To which extent did the candidate contribute to the data analysis?	Data were analysed by Ute Fricke.
Overall contribution of the candidate (in%)	80–90

Confirmation by Co-authors

Name Co-author	**Signature**	**Date**
Ingolf Steffan-Dewenter		05.05.2022
Jie Zhang		09.05.2022
Cynthia Tobisch		29.04.2022
Sandra Rojas-Botero		29.04.2022
Caryl S. Benjamin		29.04.2022
Jana Englmeier		29.04.2022
Cristina Ganuza		29.04.2022
Maria Hänsel		29.04.2022
Rebekka Riebl		29.04.2022
Johannes Uhler		29.04.2022
Lars Uphus		29.04.2022
Jörg Ewald		29.04.2022
Johannes Kollmann		29.04.2022
Sarah Redlich		29.04.2022

Chapter 4 has been submitted to the Journal of Applied Ecology as: Fricke U, Redlich S, Zhang J, Tobisch C, Rojas-Botero S, Benjamin CS, Englmeier J, Ganuza C, Haensel M, Riebl R, Uhler J, Uphus L, Steffan-Dewenter I (under review). Pest control and yield of winter oilseed rape depend on spatiotemporal crop-cover dynamics and flowering onset: implications for global warming.

Contributions

UF, SR and ISD conceived the ideas; UF, JZ and ISD designed the experiments; UF, SR, JZ, CT, SRB, CB, JE, CG, RR, JU and LU collected data; UF analysed the data; UF led the writing of the manuscript. All authors commented critically on the drafts and approved the final version.

Contribution of the candidate

Publication details	Description of the own contribution
Writing of the article Which parts of the article have been written to which extent by the candidate?	The writing of the article was led by Ute Fricke including the writing of the first draft and the implementation of comments from co-authors.
Performed research Which experimental procedures have been conducted by the candidate?	Bi-weekly observation of oilseed rape growth stages, collection of oilseed rape samples at flowering and crop maturity in one LandKlif region (joint field work of several early career scientists and student assistants in different regions of Bavaria, Germany), assessment of pest abundances, crop damage and crop yield in the lab, guidance of student assistances in lab assessment of oilseed rape samples
Conceptual design of the research To which extent did the candidate contribute to the conceptional design of the research project?	Within the framework of the LandKlif project, protocols for growth stage assessment oilseed rape sampling in the field and processing of oilseed rape samples in the lab were developed or provided by Ute Fricke.
Data analysis To which extent did the candidate contribute to the data analysis?	Data were analysis by Ute Fricke.
Overall contribution of the candidate (in%)	80–90

Confirmation by Co-authors

Name Co-author	Signature	Date
Sarah Redlich		29.04.2022
Jie Zhang		09.05.2022
Cynthia Tobisch		29.04.2022
Sandra Rojas-Botero		29.04.2022
Caryl S. Benjamin		29.04.2022
Jana Englmeier		29.04.2022
Cristina Ganuza		29.04.2022
Maria Hänsel		29.04.2022
Rebekka Riebl		29.04.2022
Johannes Uhler		29.04.2022
Lars Uphus		29.04.2022
Ingolf Steffan-Dewenter		05.05.2022

Publication list

Publications and manuscripts as part of this doctoral thesis

Fricke U, Redlich S, Zhang J, Tobisch C, Rojas-Botero S, Benjamin C, Englmeier J, Ganuza C, Riebl R, Uhler J, Uphus L, Ewald J, Kollmann J, Steffan-Dewenter I (under review). Plant richness, land use and temperature differently shape invertebrate leaf-chewing herbivory on plant functional groups. Oecologia. [preprint of an earlier version available at: Research Square. doi: 10.21203/rs.3.rs-1016363/v1]

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Publications, to which I contributed within my doctorate programme

Benjamin CS, Uphus L, Lüpke M, Rojas-Botero S, Dhillon MS, Englmeier J, **Fricke U**, Ganuza C, Haensel M, Redlich S, Riebl R, Tobisch C, Uhler J, Zhang J, Menzel A, Peters W (2022) Modelling the relative abundance of roe deer (*Capreolus capreolus* L.) along a climate and land-use gradient. Animals 12:. https://doi.org/10.3390/ani12030222

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Publications related to work prior to my doctorate

Fricke U, Lucas-Barbosa D, Douma JC (2019) No evidence of flowering synchronization upon floral volatiles for a short lived annual plant species: Revisiting an appealing hypothesis. BMC Ecol 19:1–9. https://doi.org/10.1186/s12898-019-0245-9

Wang Y, Rensink AH, **Fricke U**, Riddle MC, Trent C, van de Zande L, Verhulst EC (2022) Doublesex regulates male-specific differentiation during distinct developmental time windows in a parasitoid wasp. Insect Biochem Mol Biol 142:. https://doi.org/10.1016/j.ibmb.2022.103724

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Affidavit / Eidesstattliche Erklärung

I hereby declare that my thesis entitled: „Herbivory, predation and pest control in the context of climate and land use" is the result of my own work. I did not receive any help or support from commercial consultants. All sources and / or materials applied are listed and specified in the thesis. Furthermore I verify that the thesis has not been submitted as part of another examination process neither in identical nor in similar form. Besides I declare that if I do not hold the copyright for figures and paragraphs, I obtained it from the rights holder and that paragraphs and figures have been marked according to law or for figures taken from the internet the hyperlink has been added accordingly.

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Place, Date Signature

Hiermit erkläre ich an Eides statt, die Dissertation: „Herbivorie, Prädation und Schädlingskontrolle im Kontext von Klima und Landnutzung", eigenständig, d. h. insbesondere selbständig und ohne Hilfe eines kommerziellen Promotionsberaters, angefertigt und keine anderen, als die von mir angegebenen Quellen und Hilfsmittel verwendet zu haben. Ich erkläre außerdem, dass die Dissertation weder in gleicher noch in ähnlicher Form bereits in einem anderen Prüfungsverfahren vorgelegen hat. Weiterhin erkläre ich, dass bei allen Abbildungen und Texten bei denen die Verwertungsrechte (Copyright) nicht bei mir liegen, diese von den Rechtsinhabern eingeholt wurden und die Textstellen bzw. Abbildungen entsprechend den rechtlichen Vorgaben gekennzeichnet sind sowie bei Abbbildungen, die dem Internet entnommen wurden, der entsprechende Hypertextlink angegeben wurde.

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