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The role of biodiversity in maintaining multifunctionality in grasslands

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Summary

In 2015, the United Nations Set 17 global goals to transform our world to be more sustainable and equitable by achieving, amongst others, worldwide food security, responsible consumption and production, and protecting Life on Land. Trade-offs and conflicts between goals are evident, such as between Zero Hunger (Goal 2) and Life on Land (Goal 15), where expanding agriculture to address hunger may lead to deforestation and land degradation, impacting biodiversity. Human activities like urban expansion, deforestation, and climate change are identified as direct drivers of land degradation, affecting food and water security for 1.3 billion people exposed to such conditions. The management and maintenance of ecosystem services (the benefits nature provides for humans, such as food production and climate regulation) and their underlying processes, known as ecosystem functions, are now receiving increasing attention in politics and research. Grasslands, which offer various ecosystem services, cover approximately 40% of the land in Germany, forming a vital ecosystem that requires preservation in the face of future climate and other challenges. As the world deals with connected problems, as highlighted by the Sustainable Development Goals, the attention to sustaining and restoring ecosystem services becomes a key component in achieving a more sustainable and resilient global future in nationwide politics.

Several steps are needed to develop sustainable land use: First, understanding which ecosystem functions limit each other and, consequently, limit their simultaneous provision, called multifunctionality, is required. This was reported inconsistently in previous studies and needs further exploration. Second, investigating these interdependencies could help to develop targeted strategies for more sustainable land use. Third, a practical strategy must be designed to establish sustainable land use practices. Our knowledge of positive biodiversity effects on multifunctionality stems from extensive biodiversity experiments, but our understanding is restricted under intensive management. In summary, I want to answer how biodiversity and its components, such as species- and functional group richness, affect individual ecosystem functions, the relationships among them, and multifunctionality. I provide a more detailed understanding of the positive effect of biodiversity on ecosystem functioning. To answer these questions, I used a combination of statistical synthesis of large data sets and collection of data of extensively (the Jena Experiment) and intensively (LegacyNet Experiment) managed grassland biodiversity experiments.

My research investigated a broad spectrum of ecosystem functions. Species- and functional group richness emerged as positive drivers of individual ecosystem functions (EFs). My research revealed that functional traits play an essential role in the effects of biodiversity, as various functional groups drive different ecosystem functions. These positive effects of species- and functional group richness indicated complementary resource use and competition. Species richness not only caused an increase in individual ecosystem functions but also caused synergies among ecosystem functions. Additionally, these relationships among ecosystem functions were shown to be highly variable over time. I showed the positive impact of incorporating plant diversity in intensively managed grassland leys, demonstrating enhanced multifunctionality.

My research contributed to the discussion and future alignment of research by showing that ecosystem functions need to be measured over a long time to identify the relationships among them and define which trade-offs are impossible to remove using management practices. This suggests that long-time studies are necessary to determine the constraints and identify the possible multifunctionality that management practices can reach. Second, we showed that further analysis of the compartments of biodiversity by separating them in plant and soil history did not show significant results. Still, it stated that complex interactions within plant communities drive the effects of biodiversity. These results challenge the static trade-off assumption between biodiversity and agricultural production.

By stating the interconnectedness between ecosystem functions, my study provided insights for developing solutions for sustainable land use, contributing to the 17 Sustainable Development Goals. Concerning Responsible Consumption and Production (Goal 12), my research demonstrated how ecosystem-friendly alternatives, such as using multispecies mixtures, can reduce agriculture degradation and potentially enhance production stability through increased biodiversity. My primary contribution lies within addressing Biodiversity Loss (Goal 15), where my study implicitly underscores the threat to ecosystem function provision, revealing that different plant species drive various ecosystem functions included in the multifunctionality index, emphasising the urgent need for sustainable terrestrial ecosystem use. In conclusion, my research offers insights into sustainable land use, addressing critical aspects of the 2030 Agenda for Sustainable Development. My research emphasises practical solutions and highlights the interconnectedness of ecosystem functions, providing a foundation for a more informed and holistic approach to sustainable land use and conservation. By unravelling the complexities of grasslands and their ecosystem services, my research underscores the importance of achieving a sustainable and resilient global future as we navigate future challenges.

Zusammenfassung

Im Jahr 2015 haben die Vereinten Nationen 17 globale Ziele festgelegt, um unsere Welt nachhaltiger und gerechter zu gestalten, indem sie unter anderem weltweite Ernährungssicherheit, verantwortungsvollen Konsum und Produktion sowie den Schutz des Lebens an Land erreichen. Konflikte zwischen Zielen sind offensichtlich, beispielsweise zwischen „Kein Hunger“ (Ziel 2) und „Leben an Land“ (Ziel 15), wo die Ausweitung der Landwirtschaft um Hunger zu bekämpfen zu Entwaldung und Landdegradation führen kann, was Auswirkungen auf die Artenvielfalt hat. Menschliche Aktivitäten wie Stadterweiterung, Entwaldung und Klimawandel gelten als direkte Ursachen der Landdegradation und beeinträchtigen die Ernährungs- und Wassersicherheit von 1,3 Milliarden Menschen, die solchen Bedingungen ausgesetzt sind. Das Management und die Aufrechterhaltung von Ökosystemdienstleistungen (die Vorteile, welche die Natur für den Menschen bereitstellt, wie etwa Nahrungsmittelproduktion und Klimaregulierung) und die ihnen zugrunde liegenden Prozesse, sogenannte Ökosystemfunktionen, erhalten zunehmend Aufmerksamkeit in Politik und Forschung. Grünlandflächen, die verschiedene Ökosystemdienstleistungen erbringen, bedecken etwa 40 % der Fläche Deutschlands und bilden ein lebenswichtiges Ökosystem, das angesichts zukünftiger klimatischer und anderer Herausforderungen erhalten bleiben muss. Während sich die Welt mit den Problemen beschäftigt, wie in den Zielen für nachhaltige Entwicklung hervorgehoben, wird die Aufmerksamkeit für die Erhaltung und Wiederherstellung von Ökosystemdienstleistungen zu einer Schlüsselkomponente für die Erreichung einer nachhaltigeren und widerstandsfähigeren globalen Zukunft in der landesweiten Politik.

Um eine nachhaltige Landnutzung zu entwickeln, sind mehrere Schritte erforderlich: Zunächst muss verstanden werden, welche Ökosystemfunktionen sich gegenseitig einschränken und folglich ihre gleichzeitige Bereitstellung, die sogenannte Multifunktionalität, einschränken. Dies wurde in früheren Studien widersprüchlich berichtet und bedarf weiterer Untersuchungen. Zweitens könnte die Untersuchung dieser Wechselwirkungen dazu beitragen, gezielte Strategien für eine nachhaltigere Landnutzung zu entwickeln. Drittens müssen praktische Strategien zur Etablierung nachhaltiger Landnutzungspraktiken entwickelt werden. Unser Wissen über die positiven Auswirkungen der Biodiversität auf die Multifunktionalität stammt aus umfangreichen Biodiversitätsexperimenten, unser Verständnis ist jedoch bei intensivem Management eingeschränkt. Zusammenfassend möchte ich beantworten, wie sich die Biodiversität und ihre Komponenten, wie der Artenreichtum und die Anzahl funktioneller Gruppen auf einzelne Ökosystemfunktionen, die Beziehungen zwischen ihnen und die Multifunktionalität auswirken. Ich zeige detaillierte Einsichten der positiven Wirkung von Biodiversität auf das Funktionieren von Ökosystemen. Um diese Fragen zu beantworten, habe ich eine

Kombination aus statistischer Synthese großer Datensätze und der Sammlung von Daten aus extensiv (das Jena-Experiment) und intensiv (LegacyNet-Experiment) verwalteten Grünland-Biodiversitätsexperimenten verwendet.

Meine Forschung untersuchte ein breites Spektrum an Ökosystemfunktionen. Der Arten- und Funktionsgruppenreichtum erwies sich als positive Treiber für individuelle Ökosystemfunktionen. Meine Forschung ergab, dass funktionale Merkmale eine wesentliche Rolle bei den Auswirkungen der Biodiversität spielen, da verschiedene funktionelle Gruppen unterschiedliche Ökosystemfunktionen steuern. Diese positiven Effekte des Artenreichtums und der Anzahl funktioneller Gruppen deuteten auf komplementäre Ressourcennutzung und Konkurrenz hin. Der Artenreichtum führte nicht nur zu einer Steigerung einzelner Ökosystemfunktionen, sondern führte auch zu Synergien zwischen Ökosystemfunktionen. Darüber hinaus wurde gezeigt, dass diese Beziehungen zwischen Ökosystemfunktionen im Laufe der Zeit sehr unterschiedlich sind. Ich habe die positiven Auswirkungen der Einbeziehung der Pflanzenvielfalt in intensiv bewirtschaftete Grünlandflächen aufgezeigt und eine verbesserte Multifunktionalität nachgewiesen.

Meine Forschung trug zur Diskussion und zukünftigen Ausrichtung der Forschung bei, indem sie zeigte, dass Ökosystemfunktionen über einen langen Zeitraum gemessen werden müssen, um die Beziehungen zwischen ihnen zu identifizieren und um zu definieren, welche Kompromisse durch Managementpraktiken nicht beseitigt werden können. Dies legt nahe, dass Langzeitstudien erforderlich sind, um die Einschränkungen zu definieren und um die mögliche Multifunktionalität zu ermitteln, welche durch Managementpraktiken erreicht werden kann. Zweitens erbrachte meine Untersuchung, dass eine weitere Analyse der Kompartimente von Biodiversität durch Trennung nach Pflanzen- und Bodengeschichte keine signifikanten Ergebnisse. Dennoch wurde gezeigt, dass komplexe Wechselwirkungen innerhalb von Pflanzengemeinschaften die Auswirkungen der Biodiversität vorantreiben. Diese Ergebnisse stellen die Annahme eines statischen Konflikts zwischen Biodiversität und landwirtschaftlicher Produktion in Frage.

Durch die Feststellung der Vernetzung zwischen Ökosystemfunktionen lieferte meine Studie Erkenntnisse für die Entwicklung von Lösungen für eine nachhaltige Landnutzung und trug so zu den 17 Zielen für nachhaltige Entwicklung bei. In Bezug auf verantwortungsvollen Konsum und verantwortungsvolle Produktion (Ziel 12) hat meine Forschung gezeigt, wie ökosystemfreundliche Alternativen, wie die Verwendung von Mehr-Arten-Mischungen, die Verschlechterung der Landwirtschaft verringern und möglicherweise die Produktionsstabilität durch erhöhte Artenvielfalt verbessern können. Unser Hauptbeitrag liegt in der Bekämpfung des Verlusts der biologischen Vielfalt (Ziel 15), wobei unsere Studie implizit die Bedrohung der Bereitstellung von Ökosystemfunktionen unterstreicht und aufzeigt, dass verschiedene Pflanzenarten verschiedene Ökosystemfunktionen steuern, die im Multifunktionalitätsindex enthalten sind, was die dringende Notwendigkeit einer nachhaltigen Nutzung terrestrischer Ökosysteme unterstreicht. Zusammenfassend bietet unsere Forschung Einblicke in die nachhaltige Landnutzung und befasst sich mit kritischen Aspekten der Agenda 2030 für nachhaltige Entwicklung. Meine Forschung legt den Schwerpunkt auf praktische Lösungen und unterstreicht die Vernetzung von Ökosystemfunktionen, wodurch eine Grundlage für einen fundierteren und ganzheitlicheren Ansatz für nachhaltige Landnutzung und -erhaltung geschaffen wird. Indem ich die Komplexität von Grasland und ihren Ökosystemleistungen entschlüssel, unterstreicht meine Forschung, wie wichtig es ist, bei der Bewältigung zukünftiger Herausforderungen eine nachhaltige und widerstandsfähige globale Zukunft zu erreichen.

Foreword

When envisioning a meadow, the average person conjures an image of a mixture of many plant species, vibrant, tall, short, and swaying in the wind. The buzzing of bees can be heard, butterflies flutter around, and the chirping of cicadas becomes the defining sound of warm summer evenings. In the children's movie "Heidi," the main character playing in a flower meadow symbolises a carefree, sheltered childhood. In Monet's painting "Dans la Prairie," a woman lies in a flower meadow, completely absorbed in a book (Fig. 1). The sea of flowers almost fills the entire painting, radiating tranquillity, ease, and security. Meadows are, in film as well as in art, a means of expressing carefreeness and security.

However, when looking for flower meadows like those in Monet's painting today, one often encounters mowed green strips. Gardens are maintained to resemble the English lawn, an ornamental lawn with only a few grass species. Agriculturally used grasslands are usually cultivated so intensively that biodiversity cannot establish itself. The associated decline in insects has already become common knowledge in society but is reaching new lows rapidly. Even in politics, it has been recognised that action must be taken against species extinction and the associated loss of species-rich habitats.

The value of biodiversity can be discussed in many ways: as a cultural asset that one wants to preserve for future generations, as services that provide practical value for us humans, or even economically by explaining the costs of loss and how ecosystems should be designed for profit maximisation. The following work examines grasslands and their ecological processes to explore and optimise conflicts of interest. In other words, it investigates how important biodiversity in grasslands is for various processes and how it can be used in agriculture to operate more sustainably.

Figure 1: “Dans la prairie” is an oil-on-canvas painting created by the French artist Claude Monet in 1876. The artwork captures Monet’s wife, Camille, lying in a flower-filled meadow in Argenteuil, north of Paris. This figure stems from (Wikipedia 2021).

1. Introduction

1.1 Transformation of the world: Addressing global challenges with the Sustainable Development Goals

Every 5 minutes, the world population of humans increases by 694 individuals, while the number of consumers grows even more rapidly, with an additional 1563 people able to purchase goods and services (The World Counts 2024). While these figures may be subject to debate due to variations in estimation methods, alternative calculations still underscore the pressing demand for resources. The scarcity of these resources contributes to distress. It exacerbates inequalities between countries and regions, potentially leading to reduced political and economic stability, raising crisis risk, and reducing access to necessities and opportunities for economic growth and development. Meanwhile, humans' need for resources is one main driver of biodiversity loss. Every 5 minutes, one species goes extinct. Biodiversity loss will weaken the resilience and capacity of ecosystems to adjust to environmental changes and maintain the stability of Earth´s system (Correia and Lopes 2023). While researchers have long warned of the ongoing threat of biodiversity loss and its far-reaching consequences for humanity (Perrings, Folke et al. 1992, Díaz, Fargione et al. 2006, Cardinale, Duffy et al. 2012), political responses have emerged slowly.

However, in 2015, the United Nations Member States set 17 global goals to work together on a more sustainable and equitable future calling for action (Resolution 2015). The 2030 Agenda for Sustainable Development aims to improve our world, and its goals are formed around the 5 P´s: People, Prosperity, Planet, Peace, and Partnership (Fig. 1, Tab. 1). They are formed to reduce social inequalities while minimising the negative impact of human activities on the environment (United Nations 2023).

Figure 2: Overview of the Sustainable Development Goals (SDGs). The SDGs are 17 interconnected goals adopted by the United Nations in 2015. They aim to address global challenges such as poverty, inequality, climate change, and sustainable development by 2030. The figure was adapted from (Whitfield and Fanjul 2021).

Table 1: Description of the 17 Sustainable Development Goals categorised into the five P´s, the overreaching topics summarising the goals (Resolution 2015).

The 5 P´s	The 17 Goals	Description
People	1 No Poverty	End poverty in all its forms everywhere
	2 Zero Hunger	End hunger, achieve food security and improved nutrition, and promote sustainable agriculture.
	3 Good health and well-being	Ensure healthy lives and promote well-being for all at all ages.
	4 Quality Education	Ensure inclusive and equitable quality education and promote lifelong learning opportunities for all.
	5 Gender Equality	Achieve gender equality and empower all women and girls.
	6 Clean Water and Sanitation	Ensure availability and sustainable management of water and sanitation for all.
Prosperity	7 Affordable and clean energy	Ensure access to affordable, reliable, sustainable, and modern energy for all.
	8 Decent work and economic growth	Promote sustained, inclusive, sustainable economic growth, full and productive employment, and decent work.
	9 Industry, innovation, and infrastructure	Build resilient infrastructure, promote inclusive and sustainable industrialisation, and foster innovation.
	10 Reduced Inequalities	Reduce inequality within and among countries.
Planet	11 Sustainable cities and communities	Make cities and human settlements inclusive, safe, resilient, and sustainable.
	12 Responsible Consumption and Production	Ensure sustainable consumption and production patterns.
	13 Climate action	Take urgent action to combat climate change and its impacts.
	14 Life below water	Conserve and sustainably use the oceans, seas, and marine resources for sustainable development.
	15 Life on Land	Protect, restore, and promote sustainable use of terrestrial ecosystems, sustainably manage forests, combat desertification, and halt and reverse land degradation and biodiversity loss.
Peace	16 Peace, Justice, and strong institutions	Promote peaceful and inclusive societies for sustainable development, provide access to justice for all, and build effective, accountable, and inclusive institutions at all levels.
Partnership	17 Partnerships for the goals	Strengthen the means of implementation and revitalise the Global Partnership for Sustainable Development.

These goals have become more urgent regarding current challenges, such as the climate crisis, biodiversity loss, the war in Ukraine, and the effects of the COVID-19 pandemic (Pattberg and Bäckstrand 2023). The COVID-19 pandemic caused the most considerable rise in between-country inequality in three decades, interrupting poverty reduction and worsening global health through large declines in childhood vaccinations. The war in Ukraine caused conflict and human rights violations, leading to migration and deaths while showing that food security is an issue even in developed countries. The climate crisis is worsening, with an increase in global temperature from already 1.1 °C above pre-industrial levels, while heat waves, droughts, flooding, and wildfires occur more frequently (United Nations 2023). In 2023, the progress assessment showed that action is still needed. While some goals, e.g., Goal 15 (Life on Land), make good progress, with 25% of the targets being “on track or [target] met” and 40% of the targets stagnate. Other goals like Goal 13 (Climate Action) need more action, where no targets are considered “on track or [target] met”, 60% of the targets show “fair progress, but need acceleration”, and ~20% of the targets show “stagnation or regression” (United Nations 2023).

While the Sustainable Development Goals (SDGs) are designed to be interconnected and mutually reinforcing, there can be trade-offs between specific goals (Pattberg and Bäckstrand 2023). For example, a conflict exists between goal 2 (Zero Hunger) and goal 15 (Life on Land): Expanding agricultural activities to address hunger might lead to deforestation or other land degradation, impacting biodiversity and ecosystems. Some of these conflicts strengthen with crises, as the number of people facing hunger and food insecurity has been rising with the pandemic, conflicts, climate change, and inequalities have been growing lately. Human activities like urban expansion, deforestation, grassland conversion, and climate change drive land degradation worldwide (Pattberg and Bäckstrand 2023). Between 2015 and 2019, at least 100 million hectares of healthy and productive land were degraded yearly, affecting food and water security globally and impacting the lives of 1.3 billion people, who are estimated to be directly exposed to land degradation. In summary, crises like war, pandemics, and human activities affect the state of play of the SDGs (United Nations 2023).

1.2 Ecosystem services and functions are important for the Sustainable Development Goals

In the context of the topic “planet” (Tab. 1) and all the SDGs related to the environment, the concept of ecosystem services (ES) becomes critically important. Maintaining and restoring healthy ecosystems can support sustainable agriculture, enhance biodiversity, mitigate climate change, and improve water and air quality. Thus, to address the various SDGs and their global challenges comprehensively, it becomes necessary to explore the role of ES. ES are the contributions of ecosystems to human well-being and can be grouped into four categories: provisioning, regulating, supporting, and cultural services (Millennium Ecosystem Assessment 2005). Provisioning Services describe the material or energy output from ecosystems, such as food and water, and other resources, such as wood and medicines. Regulating services act as regulators in an ecosystem; they provide processes to regulate air and soil quality, temperature, or flood and disease control. Supporting services summarises almost all other services forming the basis of ecosystems, such as habitat provision for plants or animals, maintaining nutrient cycles, soil formation, and primary production. The last category is cultural services, describing non-material benefits, such as intellectual development, recreation, and aesthetic values (Millennium Ecosystem Assessment 2005). All ecosystem services are hard to monitor. Therefore, ecosystem functions are investigated, which describe natural processes or characteristics of energy flow and energy exchange that occur in various animal and plant communities of the different ecosystems of the world (Naeem 1998, Garland, Banerjee et al. 2021). Energy exchange happens in the food chains, in the decomposition of organic matter, or biomass production, fueled by photosynthesis (Janssen, Lambreva et al. 2014). These dynamics of one component affect the dynamic of other components, driven by the genetic, phylogenetic traits and behaviours of organismal communities (Cavender-Bares, Kozak et al. 2009, Janssen, Lambreva et al. 2014, Mittelbach and McGill 2019).

Currently, landscapes are managed as areas providing individual ecosystem services. Land-sparing is the dominant choice from governments, policy, industry, and sustainability-focused groups, meaning that our production needs are met through intensively used areas. At the same time, species-rich habitats are conserved in other regions (Cutress 2022). The opposite is land-sharing, focusing on increasing multiple ecosystem services in each area, meaning production is spread, and biodiversity is encouraged throughout the landscape (Cutress 2022). This dichotomy between land-sparing and land-sharing raises the critical question of which approach is more effective for sustainable land management. By investigating the balance between agricultural productivity and biodiversity preservation within a single patch of land, we can better estimate the potential benefits of land-sharing. This evidence can help policymakers and land managers understand the advantages and trade-offs of these two approaches, aiming to identify strategies that improve ecosystem services in different landscapes.

The provision of multiple ecosystem services or -functions is called multifunctionality, describing the simultaneous execution of multiple ecosystem functions carried out by the diverse species within the ecosystem (Hector and Bagchi 2007). For the future, we as humans need to ensure that the provision of ecosystem services is secured to ensure the long-term sustainability of our natural resources, the well-being of all life forms, and the resilience of our ecosystems in the face of climate change and other environmental challenges. Therefore, ecosystem functions forming the basis need to be investigated, and ecosystems must be managed to provide many ecosystem functions simultaneously. The concept of "ultimate multifunctionality" takes this a step further by aiming to achieve the highest possible level of ecosystem functions across a landscape. This idea emphasises optimising the delivery of a broad range of EFs and, consequently, ecosystem services, all within the same ecosystem. Understanding and managing for ultimate multifunctionality can create productive, diverse, highly resilient, and sustainable landscapes. This holistic approach is crucial for addressing complex environmental issues and ensuring that ecosystems can continue supporting human needs and biodiversity in the long term.

However, despite the importance of multifunctionality, the last half-century has seen a significant decline in many ecosystem services (Millennium Ecosystem Assessment 2005, Hasan, Zhen et al. 2020). This decline can be attributed to various factors impacting ecosystem services and functions, including climate change. For example, drought and heat can affect the rate of photosynthesis in plants or the rate of decomposition of organic matter, which in turn can affect the availability and quality of food, water, and other provisioning services (Weed, Ayres et al. 2013). Additionally, climate change can cause a change in the severity of natural catastrophes, such as the frequency and intensity of precipitation patterns and floods (Trenberth 2011, Mahecha, Bastos et al. 2022). Changes in temperature and precipitation patterns can impact the growth and distribution of plant species (Morison and Morecroft 2006), affecting the availability of food and habitat for other species, leading to changes in organismal composition and biotope types (Rubanschi, Meyer et al. 2023). Land use intentionally utilises areas to manage natural resources to meet individual services. For example, half of all habitable land (globally) is used for agriculture (Ellis, Klein Goldewijk et al. 2010) to meet our requirements for food. However, over the last decades, management has become more intensive, leading to more crops per unit of arable land (Ritchie 2019). Intensive agriculture causes biodiversity loss, mainly causing habitat loss (Sánchez-Bayo and Wyckhuys 2019). But also other services, such as pollination service, natural pest regulation, forage production, soil quality, wild food, and cultural appreciation of landscape, declined when semi-natural grasslands were converted into intensively managed areas, abandoned, or afforested (Prangel, Kasari-Toussaint et al. 2023). Anthropogenic activities also cause pollution, which disrupts several ecosystem services. Pollution affects pollinators, where airborne particulate matter can stick to the insect body hairs, risking the health of the pollinators and, consequently, the pollination service (Plutino, Bianchetto et al. 2022). Pollution through synthetic pesticides and fertilisers was shown to cause biodiversity loss (Sánchez-Bayo and Wyckhuys 2019). Lastly, air pollution can reduce human health by affecting the respiratory system or worsening pre-existing heart and lung diseases, reducing life expectancy and premature death (Kampa and Castanas 2008). There is expected to be an increasing decline of ecosystem services due to human population growth and, consequently, a growing urban area development and higher consumption of natural resources (Millennium Ecosystem Assessment 2005, Hasan, Zhen et al. 2020). Managing the trade-off between human needs and the maintenance of our ecosystems to prove goods and services, in the long run, is the main challenge in the future (Foley, DeFries et al. 2005, Hooper, Chapin et al. 2005).

1.3 Grassland ecosystems are under threat and require preservation

About 90% of our cultivated landscapes are subject to artificial control, facing suppressed self-regulatory services of natural biological systems (Ringler 1995). One ecosystem that offers various ecosystem services and is often intensively managed and degraded is grasslands, which cover approximately 40% of the land in Germany, forming a vital ecosystem that requires preservation (Bardgett, Bullock et al. 2021). Grasslands become rare because they are used for agriculture, taking advantage of their rich soils. In Europe, almost 90% of semi-natural grassland got lost within the last century due to political and economic reasons (Cousins, Auffret et al. 2015, Waldén 2018). Grasslands are affected negatively by current land management practices, which improve crop yields but affect the environment negatively, leading to land degradation, decreasing water quality, and lower abundance of native pollinators (Gordon, Peterson et al. 2008, Foley, Ramankutty et al. 2011). Only 8% of grassland and savannah areas worldwide are protected, whereas 92% are in danger of destruction (Dudley, Eufemia et al. 2020). Since 1950, the world's ecosystems have changed more than ever in human history, mainly due to converting land into croplands or for confined livestock production, covering one-quarter of Earth's terrestrial surface (Fig. 3) (Millennium Ecosystem Assessment 2005).

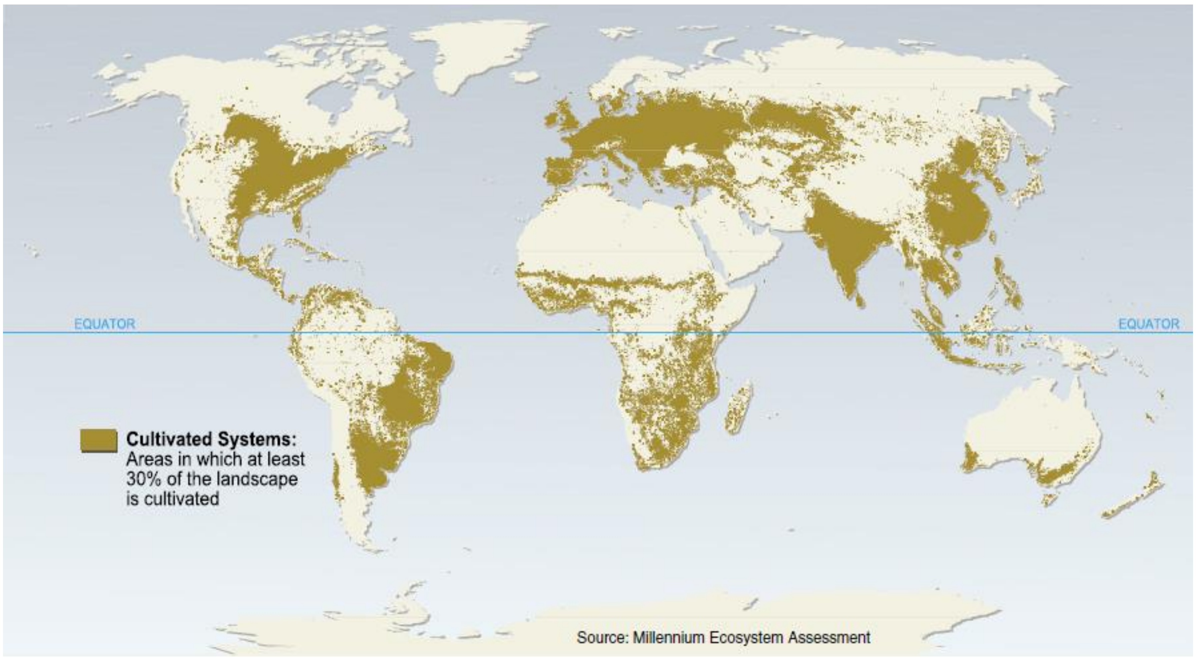

Figure 3: Distribution of cultivated land worldwide. These areas include landscapes where at least 30% transformed into croplands, shifting cultivation, confined livestock production, or freshwater aquaculture. This figure stems from the (Millennium Ecosystem Assessment 2005).

Grasslands provide high biodiversity and can support many unique species, especially in temperate regions (Petermann and Buzhdygan 2021). High plant diversity in grasslands was shown to lead to increased energy storage, flow, and community-energy-use efficiency across the entire trophic network (Buzhdygan, Meyer et al. 2020), meaning enhanced cycling of nutrients within the ecosystem, the productivity, and the presence of other plants and organisms. Due to ~30 years of research, it is well known that biodiversity is crucial for the functioning of ecosystems (Naeem, Thompson et al. 1994, Tilman and Downing 1994, Balvanera, Pfisterer et al. 2006, Cardinale, Srivastava et al. 2006, Cardinale, Matulich et al. 2011, Tilman, Isbell et al. 2014, van der Plas 2019). Biodiversity enhances ecosystems' overall stability (Tilman and Downing 1994, Tilman, Reich et al. 2006, Griffin, O'Gorman et al. 2009, Isbell, Craven et al. 2015, Oliveira, Moore et al. 2022, Wagg, Roscher et al. 2022, Bazzichetto, Sperandii et al. 2023) and resilience (Truchy, Angeler et al. 2015). Furthermore, a loss in biodiversity would reduce the predictability of the provision of ecosystem functions, as it increases the variability of ecosystem functioning (Loreau, Naeem et al. 2001, Eisenhauer, Schielzeth et al. 2019, Wu, Xu et al. 2023), making it harder to anticipate how ecosystems will respond to changes and stresses. While all organisms, including humans, depend on multiple ecosystem functions and services, ironically, anthropogenic activities drive many species close to extinction, causing severe impacts on various ecosystem functions (Cardinale, Duffy et al. 2012, Hooper, Adair et al. 2012, Tilman, Reich et al. 2012, Correia and Lopes 2023). Therefore, intensively managed grasslands are increasingly recognised for improving the productivity and sustainability of agricultural field sites when multi-species mixtures are established (Kirwan, Connolly et al. 2014).

1.4 The impact of grassland biodiversity on ecosystem functioning

Research into biodiversity effects on ecosystem function has been conducted through various experiments, each revealing distinct insights into the biodiversity-ecosystem function (BEF) relationship. Three types of experiments, varying in design (such as management intensity), have been pivotal in unravelling the underlying mechanisms (Correia and Lopes 2023): First, small-grain and highly controlled experiments, such as the long-running Jena Experiment initiated in 2002 (Roscher, Schumacher et al. 2004), manipulated plant community composition to provide detailed insights into the mechanisms behind biodiversity effects (Manning, Loos et al. 2019). These experiments, involving the random assembly of communities with varying species diversity, enable measuring various ecosystem functions. Small-grain and highly controlled experiments under realistic, intensive management, such as the LegacyNet experiment (Brophy, Finn et al. 2024), can help to identify practical implementations and suggest achievable solutions for sustainable land use by utilising high-productive plant species assembled in communities of varying species richness. Even under intensive management, multispecies mixtures could enhance ecosystem functioning in grassland leys (Tilman, Reich et al. 2012). The second type of experiment are experiments conducted under real-world, low management intensity systems, such as the Biodiversity Exploratories in Germany, allowing for the investigation of how biodiversity and land-use change interact in grasslands and forests, affecting ecosystem functions and services (Fischer, Bossdorf et al. 2010, Manning, Loos et al. 2019). The third type of study are large-scale studies and meta-analyses, which are crucial in understanding the broader implications, particularly informative for landscape-scale management and formulating national-scale policies. However, after three decades of research, a general trend in the positive relationship between biodiversity and ecosystem functioning was confirmed for terrestrial, freshwater, and marine ecosystems (Correia and Lopes 2023). Key findings from these diverse experiments consistently point towards biodiversity as a driver of productivity through compensation (Hector, Schmid et al. 1999, Hector, Loreau et al. 2002). Compensation refers to the ability of diverse ecosystems to maintain or enhance overall productivity by balancing the performance of different species, even when individual species might experience variations in productivity. Furthermore, biodiversity works as a promoter of ecosystem functioning, especially in stressful environments. The robustness and relevance of these results to real-world ecosystems (Jochum, Fischer et al. 2020) underscore the significance of biodiversity research in informing both local management practices, such as in croplands, and broader landscape-scale strategies.

1.5 Biodiversity components and ecological principles are the drivers of ecosystem functioning

The exploration of biodiversity components encompasses species abundance (species richness), functional traits of plants, the evolutionary history of plants, and interactions with other species (summarised by the identity of functional groups or functional group richness). Species richness is the most used metric to measure biodiversity and captures the diversity of individual species within a community, emphasising the role of each species in influencing ecological dynamics (Kiester 2013). For example, plant species richness caused increases in the diversity and abundance of many organisms, such as pollinators, herbivores, and nematodes (Scherber, Eisenhauer et al. 2010, Weisser, Roscher et al. 2017), but also increases in productivity, comparable to the effect of fertiliser and increasing mowing frequency (Weisser, Roscher et al. 2017). Not only species richness but species identity plays an essential role in the impact of biodiversity. Results from studies suggest that species identity can be more important than species richness in some ecosystem functions, e.g., nematode diversity (De Deyn, Raaijmakers et al. 2004), N_2O emissions (Abalos, De Deyn et al. 2014), or bacterial and fungal community composition in the root zone (Burns, Anacker et al. 2015). Furthermore, different species promote ecosystem functioning during different years, at different places, for different functions, and under different environmental change scenarios (Isbell, Calcagno et al. 2011). The performance or fitness of a plant species is determined by its physical, biochemical, behavioural, temporal, or phenological traits and affects the requirements and tolerances of the species' habitat

(Cadotte, Carscadden et al. 2011). For example, root traits are linked to the yield decline observed in monocultures over an extended period (Dietrich, Eisenhauer et al. 2023). Studies even found that the functional trait composition explained biodiversity effects (e.g., on community biomass) much more than species richness (Roscher, Schumacher et al. 2012). Using these traits, species can be categorised into functional groups, such as grasses, herbs, and legumes. These functional groups contain information on the variety of ecological roles and interactions among plant groups but not about functional variation among species within functional groups (Díaz and Cabido 2001, Ebeling, Pompe et al. 2014). Functional and ecological similarities are influenced by the evolutionary history of species (Cadotte, Cardinale et al. 2008). Consequently, plant communities with diverse phylogenetic backgrounds can account for more variation in ecosystem functions, like plant community biomass. This enhanced explanatory power is attributed to the broader ecological niches created by distantly related species (Cadotte, Cardinale et al. 2008). Plant genes contribute to the complex mechanisms underlying the positive effects of biodiversity on ecosystem functions. For example, genetically diverse plant communities can promote community productivity by improving nutrient cycling (Semchenko, Saar et al. 2017). Genetic variation is also needed for future ecological dynamics, as phenotypic variation shapes the response of organisms to their environments (Stange, Barrett et al. 2021). In summary, the components of biodiversity, including species- and functional group richness, species identity, genetic variation, ancestry, and species traits, all contribute to biodiversity. They are critical to the functioning of our planet’s ecosystems.

Biodiversity significantly influences ecosystem functioning through its impact on interactions between plant species, guided by ecological principles such as competition (Connell and Slatyer 1977, Slade, Bagchi et al. 2019), facilitation (Connell and Slatyer 1977, Brooker, Maestre et al. 2008), and complementarity (Connell and Slatyer 1977, Barry, Mommer et al. 2019). Competition arises when two or more species compete for shared resources, such as nutrients, water, or sunlight (Connell and Slatyer 1977, Slade, Bagchi et al. 2019), while facilitation occurs when one species benefits another by providing resources or shelter (Connell and Slatyer 1977). Complementarity highlights the coexistence of different species with different resource requirements (Connell and Slatyer 1977, Temperton, Hobbs et al. 2004). A critical insight emerges from the strengthening relationship between biodiversity and ecosystem functioning over time (Cardinale, Duffy et al. 2012, Reich, Tilman et al. 2012, Meyer, Ebeling et al. 2016, Guerrero-Ramírez, Craven et al. 2017, Dietrich, Ebeling et al. 2024). To further understand this effect, expanding biodiversity-ecosystem-functioning research allows us to disentangle the effects of biodiversity in plant- and soil history (Vogel, Ebeling et al. 2019, Schmid, van Moorsel et al. 2021, Maciá-Vicente, Francioli et al. 2023). This involves unravelling whether diverse plant communities influence belowground processes, such as the assemblage of microorganisms

(Schmid, van Moorsel et al. 2021, Maciá-Vicente, Francioli et al. 2023), or aboveground processes, like photosynthesis and biomass production (Vogel, Ebeling et al. 2019), leading to positive biodiversity effects in the long-term. By comprehensively understanding these components and their role in shaping species interactions, we gain the knowledge needed to proactively contribute to the conservation and resilience of Earth´s diverse ecosystems.

1.6 Translating Biodiversity Research into Sustainable Land Management Strategies

While the positive effects of biodiversity on ecosystem functioning have already been shown multiple times, the practised implementation of these insights is limited. There are subsidies available for farmers engaged in extensive mowing management, incorporating legumes as cover crops, or planting flower stripes to provide bees and other animals with a food source, habitat, or other vital services such as pollination (Landwirtschaft 2023). These initiatives contribute to biodiversity conservation, support sustainable agricultural practices, and enhance the overall environmental well-being. Consequently, to develop more practicable actions, the focus is increasingly shifting towards the practical implementation of theoretical frameworks and understanding the complex effects of biodiversity and its components on ecosystem functions. Several key strategies emerge to bridge this gap and translate research findings into actionable measures. Firstly, there is a crucial need to develop robust monitoring and assessment protocols for consistently identifying and quantifying ecosystem services (ES) and ecosystem functions (EF) while addressing their inherent limitations. An improved comprehension of ecosystem functions that constrain each other (trade-offs) is necessary (Rodriguez, Beard Jr et al. 2006, Manning, van der Plas et al. 2018, Meyer, Ptacnik et al. 2018), requiring accurate measurements of ecosystem functions to define these trade-offs. One potential benefit is a better understanding of how ecosystems persist and adapt in rapidly evolving environments (Correia and Lopes 2023). Second, identifying these interdependencies is crucial for developing targeted strategies that lead to more effective and sustainable restoration outcomes or more sustainable land use. Third, practical strategies must emphasise sustainable land use practices to mitigate human impacts on ES and EF. While previous research has demonstrated the robustness and relevance of biodiversity experiment results under extensive management (Jochum, Fischer et al. 2020), a restricted understanding of the advantages of multispecies mixtures for multifunctionality under intensive grassland management remains. This knowledge gap may limit the applicability of biodiversity-ecosystem functioning research in agriculture, characterised by variations in species richness, the use of cultivated species, and differing management intensities (Manning, Loos et al. 2019, Felipe-Lucia, Soliveres et al. 2020, Jochum, Fischer et al. 2020). Tailored management approaches, considering local conditions and community needs, are essential and should be informed by a strong foundation of practical knowledge derived from intensive management studies. Further, developing and implementing policies and regulations play a crucial role in addressing the limitations and complexities of multifunctionality. Such policies should encourage sustainable practices, incentivise conservation efforts, and provide clear land-use planning guidelines. In summary, strategies for practical implementation involve refining monitoring and assessment methodologies, fostering collaboration, tailoring sustainable land use practices, informing policies based on research, and actively engaging communities. Integrating these strategies facilitates the transition from theoretical frameworks to practical solutions, ensuring the sustainable management of ecosystem services and functions.

1.7. Overall aims and structure of this thesis

To contribute to the key strategies for translating research findings into actionable measures, my dissertation pursues two primary objectives. First, I aim to explore the reported inconsistencies in ecosystem functions and their relationships, shedding light on the challenges faced by current monitoring and assessment protocols. Second, I explore the impact of biodiversity and its components - such as species richness, functional group richness, individual functional groups, and the influence of plant- and soil history – on diverse ecosystem functions and their interactions under intensive and extensive management. While biodiversity's effects on ecosystem functioning have been investigated for years, I want to address a detailed understanding of how biodiversity affects ecosystem functions in several dimensions. My research goes beyond assessing species and functional group richness to investigating different functional groups' effects and interactions. This investigation extends to multifunctionality within intensive land management to propose practical solutions for sustainable grassland management. By examining multifunctionality and how underlying synergies and trade-offs are affected by species richness, I provide a more detailed understanding of the positive effect of biodiversity on ecosystem functioning. How does the biodiversity of plant communities, including species and functional group richness, shape ecosystem functioning in grassland ecosystems? This involves exploring the impact of biodiversity on various individual ecosystem functions, understanding the drivers and consequences of relationships among ecosystem functions, and assessing the influence of biodiversity on multifunctionality, with a focus on both species and functional group richness. To address these inquiries, I conducted a combination of statistical synthesis of large data sets and collected data from intensively managed grassland leys across various grassland biodiversity experiments. The dissertation comprises three chapters dedicated to the effects of biodiversity on individual ecosystem functions (Chapter 1), the relationships among ecosystem functions, additionally focusing on the variation of ecosystem functions and their relationships (Chapter 2), and the exploration of multifunctionality under intensive management (Chapter 3).

Chapter 1: Grasses and plant diversity determine the foliar pathogen damage of grassland plant communities of different community histories

The interaction between plants and pathogens can influence ecosystem functioning and disrupt the stability of grassland ecosystems. This paper investigates how different biodiversity components, such as species- and functional group richness and functional group identity, affect community pathogen damage and the pathogen damage of each functional group. Additionally, the role of the age of grasslands is investigated, meaning the development of pathogen damage over the years in combination with plant- and soil history.

- (1) Does community pathogen damage decrease with species and /or functional group richness, and does the proportion of individual functional groups drive the community pathogen damage?
- (2) Does the age of the grassland (plant- and soil history) also play a role in determining the pathogen damage of plant communities (history effect)?
- (3) Are the plant pathogens of functional groups affected the same way as community pathogen damage by species and /or functional group richness, functional group identity, and age of the grassland (year, plant- and soil history)?

Chapter 2: Relationships between ecosystem functions vary among years and plots and are driven by plant species richness

Providing multiple EFs (multifunctionality) is a management aim, but trade-offs can occur between different ecosystem functions. While relationships among EFs were investigated previously, it was noticed that they are highly variable compared between studies. Here, the variability of pairwise relationships was investigated to estimate the reliability of findings on EF relationships. Additionally, understanding the relationships between ecosystem functions and their underlying drivers is essential for managing ecosystems for multifunctionality. The following questions were asked:

- (1) How variable are EF relationships over time?
- (2) What drives the relationship among EFs? How much do years, seasons, species richness, and the identity of the plots (representing the identity of the studied plant communities) contribute to these relationships by affecting pairs of EFs in similar or opposing ways?

Chapter 3: Functional group richness increases multifunctionality in intensively managed grasslands

Grassland leys are increasingly recognised for improving the productivity and sustainability of agricultural field sites when species mixtures are included in crop rotations. Large biodiversity experiments in semi-natural grasslands show positive effects of plant species richness on ecosystems and their functions, among other productivity. However, doubts have been raised regarding the generalisability of these findings due to concerns about the selected plant species and the extensive management practices applied in these experiments. To investigate how species richness, functional group richness, and individual plant species affect multiple EFs and multifunctionality under intensive agricultural management, the following questions were asked:

- (1) Does Multifunctionality increase with species and /or functional group richness?
- (2) Which functional groups and individual plant species drive multifunctionality?
- (3) Are individual EFs affected the same way as multifunctionality by species and /or functional group richness and individual plant species or functional group identity?

2. Methods

2.1 The Jena Experiment

2.1.1 Design of the Main Experiment

The Jena Experiment is a long-term ecological research project investigating the relationship between plant diversity and ecosystem functioning. The Jena Experiment was established in May 2002 at a former arable field near Jena (Germany) (Roscher, Schumacher et al. 2004, Weisser, Roscher et al. 2017). 82 plots were established on the field, each containing different plant communities with various compositional features. The plots were sown with a species richness of 1, 2, 4, 8, 16, and 60 grassland plant species, where each replicate was a unique species composition. The plant species for communities with 1-16 species were randomly chosen from a pool of 60 plant species typical for Arrhenatherum grasslands, leading to a different species composition in each replicate. In contrast, the plots with the highest species richness level included all plant species; therefore, all replicates had the same species composition (Table 2). Thus, various compositional features are included in the different plant communities on the plots (Jochum, Fischer et al. 2020). The experiment distinguished four functional groups, namely grasses, small herbs, tall herbs, and legumes, based on ecologically relevant attributes (Roscher, Schumacher et al. 2004). Species richness and functional group richness, the number of functional groups per plant community, were varied as independently as possible (Roscher, Schumacher et al. 2004). Each plot underwent mowing twice a year and weeding twice to three times a year without applying fertilisers (Roscher, Schumacher et al. 2004). The selected mowing schedule aligns with the typical management for extensively used hay meadows in the region (Weisser, Roscher et al. 2017). Two monocultures were abandoned due to the initial weak establishment of the target species in the early years, leading to 80 plots used for the analysis. The experiment was set up in blocks, representing differences in soil due to the nearby river (Saale) (Fig. 4) (Roscher, Schumacher et al. 2004). Two of my studies (Chapters 1 and 2) were conducted within the Jena Experiment.

Table 2: Plant species richness levels of the main experiment of the Jena experiment with the respective number of replicates. The (+2) represents two monocultures of *Bellis perennis* and *Cynosurus cristatus*, which were given up due to a cover <10%.

Diversity level	Number of replicates
1	14 (+2)
2	16
4	16
8	16
16	14
60	4
Total	80 (+2)

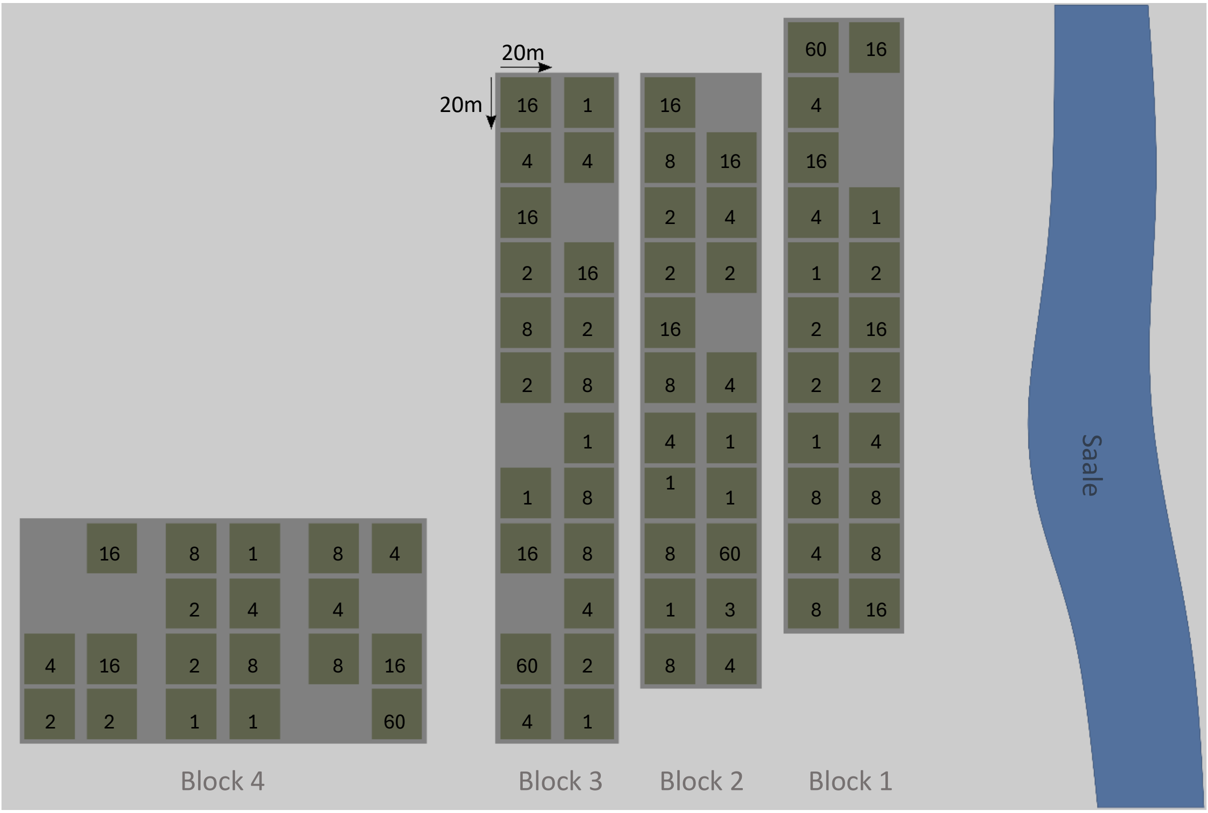

Figure 4: Experimental design of the Jena Experiment (Main) with blocks. Small green quadrats represent the individual plots, where the original form and size was 20m × 20m, but in 2010, the plot size was reduced to 6 × 5.5 m. Here, the original form of the plots is shown (Weisser, Roscher et al. 2017). Some plots are not shown, as they served as comparisons and differed in treatment, e.g., bare ground, succession with and without mowing (Weisser, Roscher et al. 2017). The individual plots contain the number of species each. The plots were arranged in blocks based on the gradient in soil parameters orthogonal to the Saale River (e.g., sand, silt, and clay content). The design used a randomised block structure, with each block having an equal number of plots per combination of species- and functional group richness. The design of the graphic is based on (Weisser, Roscher et al. 2017).

2.1.2 Design of the ΔBEF Experiment

The ΔBEF Experiment (DELTa-BEF; short for DEterminants of Long-Term Biodiversity Effects on Ecosystem Functioning Experiment) was initiated in 2016 as part of the Jena Experiment to investigate the mechanisms underlying the strengthening relationships between biodiversity and ecosystem functioning over time (Vogel et al. 2019). The experiment involved reestablishing the plant communities of the Main Experiment that had started in 2002 (Roscher et al. 2004) under various plant and soil histories on the subplots, measuring 1.5m * 3m: (1) no plant- and soil history (-PH -SH), (2) no plant history but with soil history (-PH +SH), and (3) both plant and soil history (+PH +SH) (Figure 5). Plant history status was manipulated by sowing either seeds utilised in establishing the Main Experiment (no history, -PH) or leaving the established plant communities from the Main Experiment (with history, +PH). Soil history was manipulated by replacing the top 30 cm with agricultural soil from a nearby field site next to the Main Experiment resembling the initial conditions of the Main Experiment (no history, -SH) or by maintaining soil from the original plots (with history, +SH). Hereafter, when referring to all subplots collectively, they are denoted as “history”. The aim was to compare these treatments with the original communities set up in 2002 to test whether old communities have stronger plant diversity effects on plant productivity than young ones and if this depends on soil- or plant-related processes (Vogel, Ebeling et al. 2019). The ΔBEF Experiment as part of the Jena Experiment was utilised for my study presented in Chapter 1.

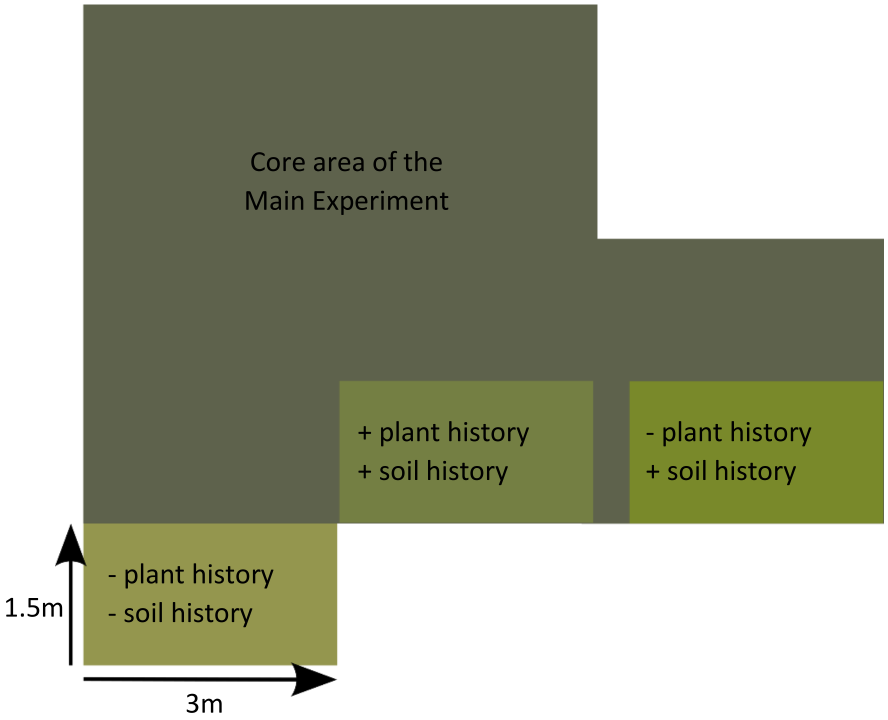

Figure 5: The three distinct experimental subplots of the ΔBEF Experiment within the Main experiment, representing a specific combination of plant- and soil history. Histories were implemented by either maintaining the existing plant communities and soil composition since 2002, introducing new plant communities with the original seeds, or altering the soil by replacing the top 30 cm with agricultural soil from a nearby field site. The subplots are visually differentiated based on the absence/presence (-/+) of plant history and soil history, providing an overview of the experimental design. The design of the graphic is based on (The Jena Experiment 2024).

2.2 The LegacyNet Experiment

2.2.1 Design of the field site in Freising

Within the framework of LegacyNet (Brophy, Finn et al. 2024), at the fieldsite in Freising (Germany), grassland leys were established in 2020. Compared to classic biodiversity experiments, forage plants, typical for agriculture in the region, were used to establish plots with different species richness levels (1, 2, 3, 4, and 6 species) and 1-3 functional group levels (herbs, grasses, and legumes). The grasses were *Lolium perenne* and *Phleum pratense*, the legumes were *Trifolium pratense* and *Trifolium repens*, and the herbs were *Cichorium intybus* and *Plantago lanceolata*. In the 50 different plots, a simplex design was realised with different species combinations on all species richness levels and all possible levels of functional groups (Table 3) (for further information, see Chapter 3). Because of the species selection, all communities, including more than two species, had at least a functional group richness of two. Therefore, species richness and functional group richness were strongly correlated (cor=0.77, p<0.001). Furthermore, the experiment was set up in blocks, representing a slight slope and distance to the neighbouring maise field and cycle path (Fig. 6). The LegacyNet Experiment (the fieldsite in Freising) was utilised for my study presented in Chapter 3.

Table 3: Plant species richness levels of the LegacyNet field site in Freising with the respective number of replicates.

Diversity level	Number of replicates
1	18
2	18
3	8
4	3
6	3
Total	50

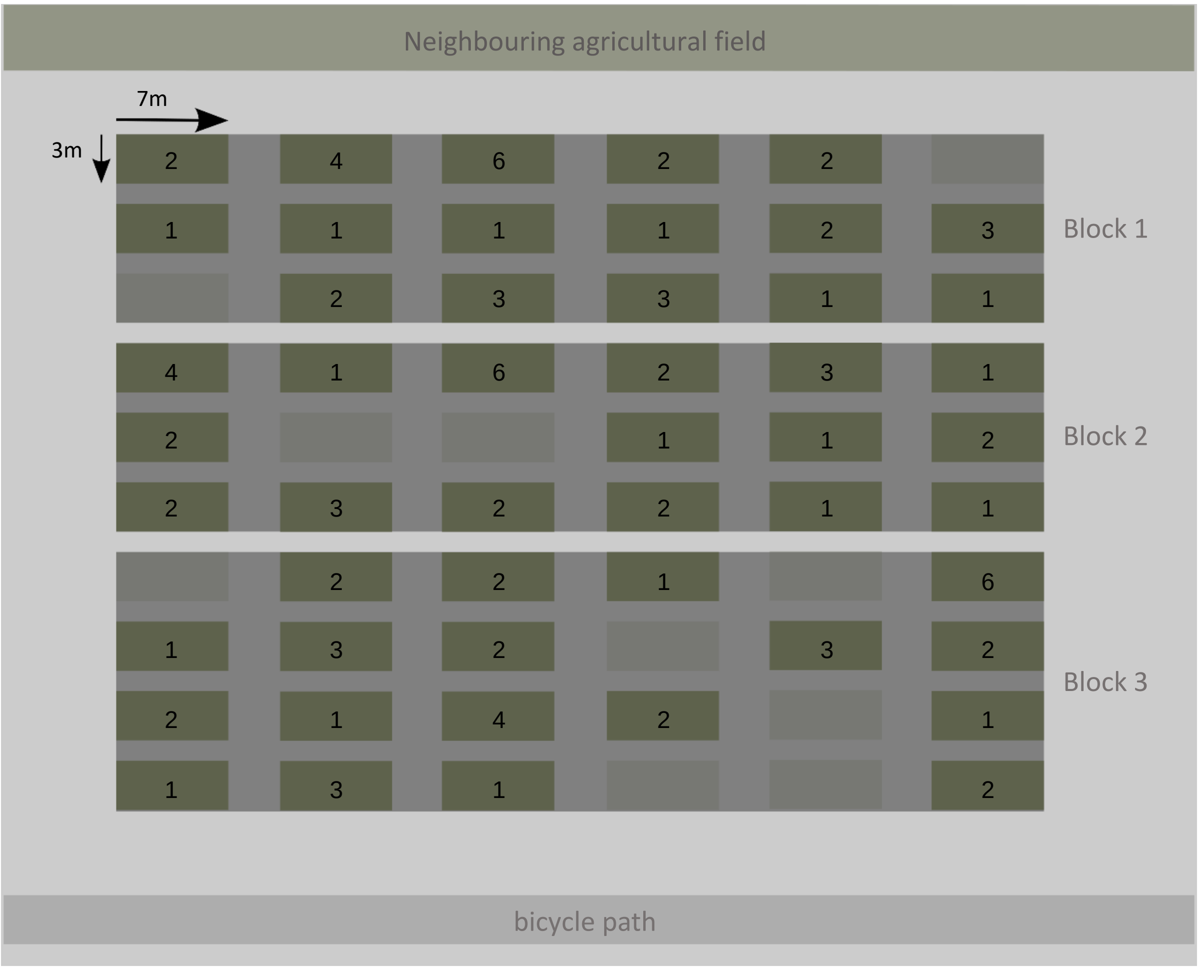

Figure 6: Experimental design of the LegacyNet field in Freising with blocks. Small green areas represent the individual plots. The dark-grey-colored plots are plant communities that were not used in this study. The grey rectangles indicate the three blocks, representing the slope of the field and the distance to the bicycle path in the south and neighbouring agricultural fields in the north.

2.3 Data Collection and Analysis Process

2.3.1 Data collection in LegacyNet

The first data collection was carried out in August 2020 by harvesting. Before each harvest, Sebastian T. Meyer and I estimated the cover of each sown plant species and the cover of weeds for each plot in % (Fig. 7). I collected two more ecosystem functions during the harvests (plant production and invasion resistance), while others were collected by students (e.g. predation, mammal activity, water availability, arthropods, and soil nitrogen). With the help of the Chair of Plant Nutrition, each plot was mowed, and the mown biomass was weighed (Fig. 7). A barcode assigned to the plot was scanned in the driver's cab, and the mown biomass was weighed directly before it was ejected by the tractor. Employees from the Chair of Terrestrial Ecology took a sample of the mown biomass for each plot by grabbing ten hands full of the mown plants. The samples for each plot were sorted by species, dried, and weighted within the following days (further information in Chapter 3). These data represent the ecosystem functions of plant production and invasion resistance. Harvesting was carried out twice in 2020 and four times in 2021 until the grassland phase ended. For the harvests, I took care of the planning, including organising the people needed for help, the materials for the fieldwork, and the transportation of materials. Furthermore, I was responsible for conducting the correct data collection methods, as defined by the LegacyNet Directors, as harvesting was part of an international network of experiments (Brophy, Finn et al. 2024).

Figure 7: Impressions of the field work in LegacyNet. a) The tractor provided by the Chair of Plant Nutrition has a special design, where the mown biomass was weighted directly before it was ejected by the tractor. b) the mown stripes can be seen in the middle of each plot. Next to each plot, there are piles of grass and plastic bags containing the grab samples of each plot. c) With Sebastian T. Meyer, I estimated plant cover (for each sown plant species and weeds) for each plot in % before each harvest.

Several other ecosystem functions were measured within student projects between 2020 and 2022 (e.g. Measurements for predation in 2020 and measurements on soil nitrogen in 2022) (further information in Chapter 3). While I was one contact person to help with logistics, material, documentation, and storage, the students were responsible for taking care of their samples. Over the years, many samples were collected, and I took care of the proper labelling, storage, and documentation of the samples.

2.3.2 Collection and procession of data from the Jena Experiment

Since the start of the Jena Experiment in 2002, multiple EFs have been measured (Weisser, Roscher et al. 2017). As I was interested in the effects over time and the relationship among EFs, I needed to collect data repeatedly measured over the years. Especially for analysing the relationships among EFs, I needed to define the data of interest to include in my analysis. With a small subset of data, measured continuously in all years, including plant biomass and -cover, I analysed the type of relationship (synergy vs. trade-offs) and the minimum number of data points needed to correctly identify the type of relationship. This pre-analysis showed that the type of relationship was correctly identified when measured within five years, independent of which years were chosen. Consequently, I decided to use all EFs that have been measured in the Jena Experiment, which:

- were measured in at least five years, whereas it did not matter which years
- were measured in all plots of the main experiment
- were measured at least once per plot and year

As soon as I identified the appropriate EFs, I had a collection of individual datasets but needed to adjust them to conclude everything into one dataset. First, I needed to define the seasons according to the meteorological seasons of the Northern Hemisphere. If the same EF was measured multiple times per season and year, the data needed to be accumulated to one measurement per year and season, which was done by averaging the raw data per plot, year, and season. Second, I excluded all plots that were either removed during the experiment or differed in treatment, e.g., bare ground, succession with and without mowing (Fig. 4). Third, I renamed the ecosystem functions to make them clearer and unified the data format. Lastly, I grouped the EFs into classes (Invasion resistance, Consumer, Plant nutrients, Plant productivity, Soil microbes, Soil nitrogen, Soil carbon, and soil properties) to identify potential patterns and to underline the similarities between individual EFs. With this dataset, I could start my analysis.

2.3.3 Preparation of data for the statistical analysis

To thoroughly investigate individual EFs and their relationships and to calculate multifunctionality, I employed various statistical transformations to ensure the robustness and validity of the results. Given the non-normal distribution of the data from the Jena Experiment and LegacyNet, I utilised different data transformation methods to adapt the data for normality. For the data from the Jena Experiment in the second Chapter, I used the boxcox-transformation to adapt normality. This transformation was advantageous because it determines specific constants (lambda-values λ and λ_2) for each EF separately to achieve normal distribution (refer to Chapter 2 for more details). For the data from the ΔBEF Experiment (Jena Experiment) and from LegacyNet, I used the log transformation to achieve a normal distribution (Chapters 1 and 3). Additionally, I used the minmax-transformation for the data from the main Experiment (Jena Experiment) (Chapter 2) and the data from LegacyNet (Chapter 3) to rescale the variables to a common scale between 0 and 1. This is beneficial when dealing with varying data scales. However, for the data from the ΔBEF Experiment (Jena Experiment), I opted not to transform the range of values to maintain the comparability of the pathogen damage across different functional groups.

Furthermore, for statistical reasons, I standardised the data from the ΔBEF Experiment (Jena Experiment) to centre the values around 0 with a standard deviation of 1. This standardisation was crucial for calculating linear mixed-effect models without an intercept, allowing the inclusion of sown proportions of all functional groups as explanatory variables (detailed in Chapter 1).

I aligned the data for direction to investigate the relationships among EFs (Chapter 2) and calculate multifunctionality (Chapter 3). Using their inverse, I transformed measurements deemed “undesirable” from a human perspective, so higher values represented a desirable state (Byrnes, Gamfeldt et al. 2014, Meyer, Ptacnik et al. 2018). With the transformed and normalised data, I proceeded with detailed statistical analyses to answer my hypothesis.

2.3.4 Statistical Analysis

The basis for all analysis: Linear mixed models

Linear mixed models were used to investigate the effects of diversity on various ecosystem functions. Therefore, I used this statistical analysis throughout all chapters, investigating how species- and functional group richness drove the pathogen damage of plant communities and individual functional groups (Chapter 1), several individual EFs (Chapters 2 and 3), and multifunctionality (Chapter 3). Accounting for random effects enabled me to analyse continuous data with nested or repeated measurements within groups. While random effects are assumed to have a random or non-systematic effect on the dependent variable, fixed effects are variables that are considered to have a systematic effect on the outcome variable. A linear model without random effects calculates significance levels by comparing the explained variance against the unexplained variance (residuals). A mixed effect model, however, tests the dependent variable not against the unexplained variance but against the explained variance of the random effect and, therefore, accounts for any effects caused by repeated measurements (Schmid, Baruffol et al. 2017). Additionally, understanding the mathematical principles behind calculations involving random and fixed effects allowed me to explore the drivers of ecosystem function relationships by performing a decomposition of covariances (see below). Overall, linear mixed-effect models are a powerful statistical tool for analysing complex data and can provide valuable insights into the relationship between variables of interest.

Analysis of plant species and their interactions affecting ecosystem functions: Diversity-interaction models

Diversity interaction (DI) models are mathematical models used to understand how diversity affects interactions between individual species or functional groups. I used this analysis to investigate how individual plant species, functional groups, and proportions within plant communities influenced ecosystem functions and multifunctionality (Chapter 3). Diversity interaction models are a regression-based approach for modelling the BEF relationship by considering species identities and relative abundances in communities (Kirwan, Connolly et al. 2009, Connolly, Bell et al. 2013, Dooley, Isbell et al. 2015, Moral, Connolly et al. 2022). In the DI model, the dependent variable can be any ecosystem function or index (such as multifunctionality), and the predictors are the species proportions. Compared to linear mixed effect models, DI models capture not only species-specific identity effects but also the interactions between species proportions or functional group proportions. These models attempt to capture the complexity of real-world situations where plants represent different functional groups and interact with each other in various ways. By exploring how diverse plant species interact with one another, these models can help us better understand the benefits and challenges of biodiversity and find ways to leverage it for positive outcomes.

Analysis of relationships among ecosystem functions: Correlations

Correlations were used to assess the relationship between two variables, as I did in Chapter 2. They quantify the strength and direction of relationships, aiding researchers in understanding patterns and making informed decisions based on data. The Pearson correlation coefficient is appropriate for investigating the relationships between ecosystem functions representing continuous variables. A positive correlation indicates that both variables change in the same direction (synergy), whereas a negative correlation indicates opposite changes (trade-off). In my study, I used correlations to investigate the relationships among EFs and their variability over time by calculating a standard deviation over correlation coefficients from different time points (Chapter 2).

Analysis of the drivers of relationships among ecosystem functions: Decomposition of covariances

Traditional linear models effectively explain the variation in a single dependent variable. However, conventional linear models fall short when examining relationships between two variables influenced by independent variables. Covariance decomposition offers a solution, allowing us to understand how an independent variable may influence two variables simultaneously, leading to a positive relationship. In the first step of the decomposition, the Preservation of the Sum of Squares (SS) for each EF pair (Chapter 2) was obtained using general linear models. In the second step, the (Mean) Sums of Products for each EF pair were calculated, and F-rations and significances needed to be estimated. However, because of a random effect structure, not all terms could be tested against

"Residuals". To determine the appropriate test statistics, I needed the concept of expected mean squares, which defines how the expected values of the variation between groups (like treatments) differ from the expected value of the variation within each group. The specific fixed factor influences this difference; one is tested and used to calculate significance. In the final step, the percentage per driver per EF pair was calculated, and EF pairs were separated into synergies and trade-offs. To test whether the results of this analysis accurately reflect the effects, a simulated dataset (provided by Sebastian T. Meyer) was used.

Excursion: Limitations of other attempts to analyse the drivers of relationships among ecosystem functions

Several challenges arose during the analyses, and some attempts to analyse the drivers of relationships among ecosystem functions (EFs) were unsuccessful, revealing the complexities and limitations inherent in ecological data and methodologies. One attempt was to use structural equation models (SEM), as these enable examining direct and indirect relationships among multiple variables (Shipley 2016). However, the number of data points was not sufficient to use this method for my research.

Another approach was to develop a new methodology to isolate explained effects - such as the effect of year on a variable - from the data. For example, a dataset that did not contain the variability explained by year was created. By comparing the correlations derived from the original dataset and the revised dataset, the stability of the correlations before and after the removal of explained effects could be quantified. However, several challenges were encountered, particularly the lack of defined effect sizes and p-values, which are essential for a robust analysis.

An additional approach was to use the concept of asynchronity. Asynchrony refers to the occurrence of EFs at different times within an ecosystem, therefore representing relationship dynamics (Wilcox, Tredennick et al. 2017, Huang, Liu et al. 2020). However, due to incomplete data on EFs across the years in the Jena Experiment, it was only possible to calculate asynchrony for specific EFs at particular times. Consequently, it did not fully meet the intended objectives, and correlations emerged as a more suitable method for capturing the relationships among EFs.

2.4. Overview of examined ecosystem functions

To investigate multiple ecosystem functions, this research systematically investigated a spectrum of ecological processes. These ecosystem functions were selected based on their ability to represent various processes throughout the ecosystem, offering a holistic understanding of the ecological dynamics within the studied system, covering plant health, nutrient cycling, soil characteristics, and interactions among different trophic levels (table 4).

Table 4: Overview of the chapters dedicated to analysing the ecosystem functions in grasslands. Besides the ecosystem function, an abbreviation (if present within the individual Chapter) and the unit of measurement are listed.

Chapter	Ecosystem function	Abbreviation of ecosystem function in the chapter	Unit of measurement
1	Community Pathogen damage		The mean percentage of individual leaf damage within a taxon is weighted by percent biomass.
1	Pathogen damage per functional group		The mean percentage of individual leaf damage within a functional group is weighted by percent biomass.
2	Shoot biomass	ShootBM	Biomass target material [g/m^2]
2	Plant height	PlantHeight	Plant height was measured [m]
2	LAI (leaf area index)	LAI	leaf area index measured as leaf area/ground area, [m^2/m^2]
2	Plant Cover	PlantCover	Cover target [%]
2	Bare ground Cover	BareGround$^{(-1)}$	Cover bare Ground [%]
2	Root biomass	RootBM	Standing root biomass was calculated [g/m^2]
2	Plant phosphorus	PlantP	Phosphorus concentration [%] of target plants
2	Plant calcium	PlantCa	Calcium concentration [%] of target plants
2	Plant potassium	PlantK	Potassium concentration [%] of target plants
2	Plant sodium	PlantNa	Sodium concentration [%] of target plants
2	Plant magnesium	PlantMg	Magnesium concentration [%] of target plants
2	Plant carbon	PlantC	C content of the sown species community [%]
2	Plant nitrogen	PlantN	N content of the sown species community [%]
2	Microbial biomass	MicrobeBM	Soil microbial carbon biomass [µg Cmic/ g soil$_{dryweight}$]
2	Basal respiration	SoilResp	Basal respiration was measured in [ml/ g/ h]
2	Predation	Predation	Bite marks on dummy caterpillars [%]
2	Herbivory	Herbivory	Herbivory damage [%]
2	Invader species richness	WeedSPr$_w^{-1}$	Invader species richness
2	Cover of weeds	WeedCover^{-1}	Cover of weeds [%]
2	Biomass of weeds	WeedBM^{-1}	Biomass weeds, estimated in [g/m^2]
2	Species richness of weeds	WeedSPr$_{nw}^{-1}$	Species richness of weeds
2	Dissolved organic carbon	SoilDOC	Carbon, organic, dissolved [mg/l]
2	Dissolved inorganic carbon	SoilDIC	Carbon, inorganic, dissolved [mg/l]
2	Organic carbon content in the soil	SoilC$_{org}$	Organic Carbon content in the soil [g/kg]

Chapter	**Ecosystem function**	**Abbreviation of ecosystem function in the chapter**	**Unit of measurement**
2	Inorganic carbon content in the soil	$SoilC_{inorg}$	Inorganic carbon content in the soil [g/kg]
2	Water content in the soil	SoilH2O	Soil water content [mass %] was measured as the difference between fresh weight and dry weight
2	Soil density	$SoilDensity^{-1}$	density of bulk soil [g/cm^3]
2	Ammonium in the soil	SoilNH4	ammonium content
2	Nitrate in the soil	SoilNO3	nitrate content
2	Mineral nitrogen in soil	$SoilN_{min}$	mineral nitrogen content (sum of ammonium and nitrate) in N [mg]/ dry soil [kg]
2	Total soil nitrogen	SoilN	Total nitrogen content in soil [g/kg]
3	Plant production		Average of standing root biomass [g/m^2]; shoot biomass [$g_{dryweight}/ g_{community\_freshweight}$]; total cover of plant species [%]; average plant height per community [cm]
3	Invasion resistance		Average of weed biomass in [$g_{dryweight}/ g_{community\_freshweight}$] (Inverse); cover of weeds in % (Inverse); the number of weed species (Inverse); the number of weed individuals (Inverse)
3	Predation		Average of Predation by rodents [%]; Predation by insects [%]
3	Mammal activity		Average of Mammal activity in June and in August [%]
3	Water availability		Average of Water content in plants in % [$g_{dry}/(g_{fresh}/100$]; Water content in soil in % [$g_{dry}/(g_{fresh}/100$]
3	Arthropods		Average number of arthropod taxa; arthropod abundance.
3	Soil nitrogen		Mineral nitrogen in the soil [kg/ha]

3. Chapter overview

This thesis contains three chapters of two published research articles and one manuscript ready for submission. In the following, all chapters are summarised, and the authors´ contributions in each chapter will be presented. The complete chapters are attached in the Appendix.

Chapter 1: Grasses and plant diversity determine the foliar pathogen damage of grassland plant communities of different community histories

Laura Argens, Maximilian Bröcher, Nico Eisenhauer, Liesje Mommer, Anne Ebeling, Sebastian T. Meyer
In preparation

This study investigated various factors influencing pathogen infection in grasslands, including the impact of plant community composition, diversity, grassland age, and community history on pathogen damage in grasslands. Understanding the underlying drivers of pathogen infection is crucial for maintaining stable grasslands. Therefore, I investigated whether pathogen damage decreases with species richness, whether grassland history plays a role, and whether the pathogen damage depends on functional group identity.

The data was collected in the Jena Experiment, a long-term biodiversity experiment where species richness and functional group richness were varied independently. The ΔBEF Experiment was established in 2016 to investigate the impact of aboveground and belowground assembly processes on diversity effects on ecosystem functions. Subplots were established with different plant and soil histories. Species-level foliar pathogen damage was estimated and used to calculate pathogen damage at the community and functional group levels.

The study found that higher plant species richness increased community pathogen damage. In contrast, functional group richness did not significantly affect community pathogen damage but decreased the pathogen damage of legumes. The extent of pathogen community damage varied with the plant community's functional group composition. Grass-dominated plant communities experienced more pathogen damage than other plant communities. Regarding pathogen damage in individual functional groups, grasses showed the highest pathogen damage, followed by legumes, tall herbs, and small herbs. Community pathogen damage decreased significantly over the years, with pathogen damage in grasses and small herbs showing the strongest decrease. There were no significant community history effects; neither was the plant- nor soil history. In conclusion, the study reveals the importance of considering plant groups' ecological roles and interactions in influencing ecosystem pathogen dynamics. It is necessary to maintain balanced, functionally diverse grasslands for ecosystem management strategies to enhance ecosystem resilience to pathogen damage.

Authors´ contributions

NE, AE, and STM were responsible for the project administration. NE and AE designed the experiment. MB, AE, and STM handled the data acquisition and curation. LA formatted the data and calculated the composite measures for further analysis. LA conducted the statistical analyses and prepared all the figures. STM supervised the statistical analysis. LA wrote the manuscript. All authors reviewed and edited the manuscript.

Chapter 2: Relationships between ecosystem functions vary among years and plots and are driven by plant species richness

Laura Argens, Wolfgang W. Weisser, Anne Ebeling, Nico Eisenhauer, Markus Lange, Yvonne Oelmann, Christiane Roscher, Holger Schielzeth, Bernhard Schmid, Wolfgang Wilcke, Sebastian T. Meyer

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This study investigated the variability in pairwise relationships between 31 ecosystem functions (EFs) measured repeatedly for 5-19 years in the Jena Experiment, covering various components of the ecosystem, to understand how much of the variability in EF relationships is driven by temporal factors such as years and seasons, as well as plot identity and species richness. The study aimed to determine whether pairs of EFs differ in their relationship with replicated measurements and what factors contribute to the relationships among EFs.

Positive correlations (indicating synergies) and negative correlations (indicating trade-offs) between different EFs were found. For example, a synergy was found between plant productivity and invasion resistance, and a trade-off was found between root biomass and soil nutrient concentrations. Furthermore, this study showed that EF relationships are highly variable over time.

Different drivers of the relationships between EFs were tested: year, season, species richness, and plot identity, whereas plot identity consisted of the identity of plant communities and abiotic factors. Results showed that species richness and plot identity explained the largest covariance fraction. The contribution of individual drivers could have antagonistic or synergistic effects, irrespective of whether the relationship was a synergy or a trade-off between the EFs. For synergies, most of the covariance was explained by species richness, while for trade-offs, most of the covariance was explained by plot identity. However, not all EFs were positively influenced by species richness; some were even driven into a trade-off. For trade-offs, herbs and legumes have already explained half of the effect of plot identity, whereas, for synergies, plot identity mainly consists of the impact of the presence of grasses and herbs. For example, the proportion of grasses impacted both synergies and trade-offs, with driving EFs on average more into a trade-off than towards a synergy (-1.8%, compared to 1.4% toward synergies, whereas the sign indicates whether the EFs are driven into a trade-off or a synergy). Year and season caused positive and negative covariances, with low average percentages explained by year and season.

In conclusion, the study revealed that correlations among EFs were variable over time, underscoring the necessity for repeated measurements to ensure accurate assessments of EF relationships. I identified species richness and plot identity as key drivers of EF correlations, with synergies promoted by species richness and trade-offs influenced by plot identity. These findings suggest that promoting biodiversity and managing species composition can enhance EF multifunctionality in grasslands, which could be important in guiding future land management strategies.

Authors´ contributions

WWW, AE, and NE were responsible for the project administration. WWW, AE, and NE designed the experiment, while AE, ML, YO, CR, WW, and STM planned the data acquisition and handled the data curation. LA formatted the data and calculated composite measures. LA conducted the statistical analyses and prepared all the figures. HS, BS, and STM Supervised the statistical analysis. LA wrote the manuscript. All authors reviewed and edited the manuscript.

Chapter 3: Functional group richness increases multifunctionality in intensively managed grasslands

Laura Argens, Caroline Brophy, Wolfgang W. Weisser, Sebastian T. Meyer

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This study investigated the provision of EFs in grassland leys. These EFs are highly important from a production-focused perspective (e.g., plant productivity and invasion resistance), as well as for sustainability (e.g., soil nitrogen, water availability) and nature protection (e.g., arthropod and mammal activity). By integrating ecosystem functions (EFs) into a multifunctionality index, I quantified the ecosystem's capacity to simultaneously provide multiple functions. I investigated the influence of species richness, functional group richness, the proportion of functional groups, and individual plant species on multifunctionality. Additionally, we examined how these factors affect individual EFs.

The study found that multifunctionality increased with species and functional group richness. An increase in multifunctionality was mainly caused by plant productivity and invasion resistance. Furthermore, multifunctionality was highest in legume-herb mixtures, whereas it was low in grass-monocultures and mixtures, including grasses in high proportions. Adding grasses to legume-herb mixtures gradually decreased multifunctionality. While all six species positively affected multifunctionality, the two species showing the highest impact on multifunctionality were *Trifolium repens* and *Chicorium intybus*. Plant communities consisting of grasses were less productive than herb or legume communities or their mixtures. Invasion resistance was highest for mixtures between grasses and herbs, while invasion resistance was low in plant communities that included legumes. Legumes and herbs were highly beneficial for water availability. Whereas legumes showed higher levels of water availability than herbs and grasses, grasses showed the lowest levels of water content. Legumes were highly healthy for soil nitrogen, while grasses showed the lowest soil nitrogen levels. Soil nitrogen was highest in communities of *Trifolium repens*, followed by *Trifolium pratense*. Furthermore, plant species interact and, therefore, affect individual EFs differently. A positive interaction among species means that the mixture of these two species results in a higher level of ecosystem functioning than expected based on each species' contributions. I showed that grasses and herbs positively interacted regarding invasion resistance and water availability. While adding species of complementary functional groups was shown to have positive effects, adding species of the same functional group affected different EFs positively. For example, water availability was increased by the interaction between *T. repens* and *T. pratense*.

In conclusion, the study found that different plant species and -combinations drive different ecosystem functions. Increasing plant diversity in intensively managed grassland leys can enhance multifunctionality, benefiting both agro-economics and sustainability. The findings highlight the importance of incorporating different functional groups, such as legumes and herbs, to promote productivity and conservation efforts in agricultural systems. Overall, the research underscores the potential of biodiversity to improve the performance of intensively managed agricultural landscapes, offering valuable insights for sustainable land management practices.

Authors´ contributions

LA, CB, and STM were responsible for the project administration, whereas CB and STM monitored the project regarding the international project, LA was responsible for the documentation and coordination of the team helping with the fieldwork. CB and STM designed the experiment. LA and STM were responsible for the data acquisition and curation. LA formatted the data and calculated the composite measures. LA conducted the statistical analyses and prepared all the figures. CB and STM supervised the statistical analysis. LA wrote the manuscript. All authors reviewed and edited the manuscript.

4. Discussion

4.1 Overview of findings

To further understand the effects of biodiversity on ecosystem functioning, my research provided insights outlined in the following key points:

Due to ~30 years of research, it is well known that biodiversity is crucial for the functioning of ecosystems, shifting the focus of biodiversity research towards implementing biodiversity benefits in agriculture. To face the challenges of current monitoring and assessment protocols, I explored the reported inconsistencies in ecosystem functions and their relationships by investigating their inherent variability. In Chapter 2, it was shown that individual EFs, as well as EF relationships, were highly variable over time. Individual EFs measured over multiple years showed a high unexplained variation; approximately one-third of EFs measured over numerous seasons, and nearly half of the variation in EFs measured within a single season remained unexplained (Chapter 2). For EF relationships, a high variability over time was shown (Chapter 2). These findings provide the basis for a nuanced discussion on the implications of such variability and its impact on our understanding of ecosystem dynamics (section 4.2).

To develop sustainable land use practices, my research aimed to bridge the gap between biodiversity effects on individual EFs and multifunctionality by investigating the impact of biodiversity on individual EFs and the relationships among EFs. Species- and functional group richness emerged as positive drivers of individual EFs, such as plant productivity, invasion resistance, and reducing pathogen damage of individual functional groups (especially legumes) (Chapters 1, 2, and 3). However, it was shown that individual functional groups, or even individual plant species, were essential for specific ecosystem functions. For example, legumes were beneficial for the nitrogen content in the soil, and *Lolium perenne* caused high invasion resistance (Chapter 3). However, they could also negatively affect other EFs, e.g., increasing the proportion of grasses diminished plant productivity, water content, and soil nitrogen (Chapter 3). These results indicated underlying EF relationships, further investigated in Chapter 2. Indeed, a synergy could be shown between plant productivity and invasion resistance, whereas root biomass and soil nutrient concentrations were shown to be in a trade-off (Chapter 2). To offer a better comprehension of the positive influence of biodiversity on ecosystem functioning, synergies, and trade-offs and how they were affected by species richness were investigated in Chapter 2. Species richness was shown to drive synergies among EFs. However, species richness did not only positively affect EF relationships, as some EFs were negatively influenced and, therefore, driven into a trade-off (Chapter 2). The biodiversity and the identity of functional groups could affect EF-relationships: The proportion of grasses was shown to influence synergies and trade-offs, with trade-offs being, on average, more pronounced (-1.8%, compared to 1.4% toward synergies) (Chapter 2). These findings indicate a complex dynamic between biodiversity and ecosystem functioning, where species richness drove synergies among ecosystem functions and introduced trade-offs. Still, time showed the variability of these relationships among EFs. This opens the discussion on our ability to understand and predict the continuous provision of EFs in a changing environment and suggests a nuanced approach in practical land management to maintain sustainable ecosystems (section 4.3).

Although our understanding of the positive effects of biodiversity on multifunctionality primarily originates from extensive biodiversity experiments, my research extended this knowledge by specifically investigating how biodiversity influenced multifunctionality under intensive management. It was found that multifunctionality increased with functional group and species richness. Furthermore, because various functional groups drove different ecosystem functions, specific plant communities resulted in high or low multifunctionality. Grass monocultures and mixtures with a high proportion of grasses showed low multifunctionality (Chapter 3). Since different plant species enhanced different EFs, biodiversity increased the complexity of ecosystems and likely the adaptability, stability, and resilience under environmental disturbances. This can lead to approaches incorporating biodiversity into intensively managed grasslands, but it still presents some challenges discussed in section 4.4.

Lastly, developing and implementing policies and regulations play an essential role in the success of sustainable land use practices. This involves addressing the challenges identified in my research and integrating findings into practical guidelines for policymakers and land managers. This is discussed in sections 4.4.3 and 4.5.

4.2 The advantages of long-term measurements of ecosystem functioning

One limitation in ecosystem function research is the variability of ecosystem functions and the lack of knowledge about critical shifts, where ecosystem functioning is no longer provided. Long-term measurements of ecosystem functions are essential in advancing our understanding of EFs and are indispensable to forming robust monitoring and assessment protocols. Exploring the variability of individual EFs, as shown in Chapter 2, is critical. I showed that the unexplained variation of individual EFs was high: One-third of the variation for EFs measured in several seasons and almost half for EFs measured in just one season was unexplained (Chapter 2). The variability of individual EFs depends on the specific EFs under investigation (Chapter 2), which was documented by many studies (Carpenter, Mooney et al. 2009, Cardinale, Duffy et al. 2012, Gaglio, Aschonitis et al. 2020, Qiu, Carpenter et al. 2020, van der Plas, Schröder-Georgi et al. 2020). It was shown, for example, that disease incidence is highly variable across space and time, while much of the variability appeared to be influenced by climatic and environmental variables (Jarosz and Davelos 1995). One goal would be to detect and define critical shifts in EFs across different biodiversity levels and spatiotemporal scales for maintaining functional ecosystems (Correia and Lopes 2023). Therefore, long-term measurements under various environmental conditions are needed.

One challenge for developing suitable management methods is the limited understanding of trade-offs within ecosystems, hindering the ability to define an optimum level of ecosystem functioning. The optimum would be a multifunctional ecosystem combining production and sustainability goals. Therefore, understanding the relationships among EFs is important in identifying the trade-offs between EFs that restrict the provision of multifunctionality. Chapter 2 highlights the variable nature of these relationships over time, supporting studies conducted by Cardinale, Duffy et al. (2012) and (Lee and Lautenbach 2016). This emphasises the need for long-term measurements of individual ecosystem functions and the reliable identification of trade-offs among ecosystem functions. Like individual EFs, critical transitions of these EF relationships reflecting the interactions within and among species could point toward unstable shifts in the ecosystem (Correia and Lopes 2023). Moreover, recognising these critical points would allow for more targeted conservation methods to ensure the multifunctionality of our ecosystems (Correia and Lopes 2023).

The consistent monitoring of ecosystem functioning is also crucial for understanding and managing ecosystem dynamics effectively. It was demonstrated that the biodiversity effects on various EFs strengthen over time (Griffin, O'Gorman et al. 2009, Isbell, Calcagno et al. 2011, Cardinale, Duffy et al. 2012, Reich, Tilman et al. 2012, Guerrero-Ramírez, Craven et al. 2017). This emphasises the importance of old grasslands and holds implications for sustainable agricultural practices as the positive effects of diverse plant communities are passed on over time. One way to maintain the stability of agricultural land is by making use of such legacy effects. While they are already used in crop rotations, more long-term measurements could enable us to detect and incorporate legacy effects into management methods. Indeed, ongoing investigations in the global analysis of LegacyNet explore the potential legacy effects of multispecies mixtures in crop rotation systems (Brophy, Finn et al. 2024). The positive impact of rotation systems in land use and management has been known for centuries; therefore, including legumes as cover crops in crop rotation in intensive farming is common (Ringler 1995). Including biodiversity in intensive agriculture could be crucial, especially when this hosts the possibility that the advantages are even bigger later than the implementation time due to the legacy effects.

In summary, the variability of individual EFs, dynamic relationships among EFs, and the detection of legacy effects underscore the indispensable role of long-term measurements. These insights are crucial for advancing scientific understanding and profoundly affect sustainable land use practices. Advanced research methods, such as those from food-web analysis (Hines, van der Putten et al. 2015, Eisenhauer, Schielzeth et al. 2019), can enhance our understanding of trade-offs between ecosystem functions, identify vulnerable species and habitats, and contribute to more informed and sustainable land management practices.

4.3 Ecology of biodiversity components

The components of biodiversity, including species- and functional group richness, genetic variation, ancestry, and species traits, collectively play a crucial role in the functioning of our planet's ecosystems. While the impact of biodiversity has been extensively studied for many years, this research aimed to provide a deeper understanding by exploring how different components of biodiversity influence individual ecosystem functions, synergies and trade-offs amongst them, and multifunctionality. Additionally, by considering both aboveground and belowground accumulation processes, I hope to better understand how the biodiversity components impact various ecosystem functions.

4.3.1 Examination of the components of biodiversity

Individual plant species are often investigated for specific processes, such as nutrient cycling (Hobbie 1992), the ecological impact of invasive species (Vilà, Espinar et al. 2011), and increasingly in defining suitable plant species for agricultural production (Malézieux, Crozat et al. 2009). Chapter 3 demonstrated how individual plant species impact multifunctionality and specific ecosystem functions. Diverse plant species exhibited unique effects on individual EFs, exemplified by the lowest plant productivity in the presence of *Lolium perenne* while showcasing heightened invasion resistance. Species identity plays an essential role in the effect of biodiversity. While species richness is one of the most investigated diversity indices (Morris, Caruso et al. 2014), studies suggest that species identity can be more important than species richness in some ecosystem functions (De Deyn, Raaijmakers et al. 2004, Abalos, De Deyn et al. 2014, Burns, Anacker et al. 2015).

The identity of functional groups aggregates species together, based on their functional traits, influencing the performance, fitness, and ecological niche of plant species (Díaz and Cabido 2001, Cadotte, Cardinale et al. 2008, Cadotte, Carscadden et al. 2011, Ebeling, Pompe et al. 2014), and, therefore, ecosystem functioning. My research revealed that various functional groups drive different ecosystem functions, potentially leading to trade-offs among EFs in monocultures or species mixtures dominated by a single functional group, resulting in reduced multifunctionality. For instance, an increasing proportion of grasses was associated with decreased plant productivity, water content, and soil nitrogen but increased invasion resistance (Chapter 3), indicating that a higher proportion of grasses strengthens trade-offs. This was further supported by my investigation of multifunctionality, which was consistently low in grass monocultures and mixtures with a high proportion of grasses (Chapter 3). In Chapter 2, I observed that the proportions of grasses influenced both synergies and trade-offs, with trade-offs being, on average, more pronounced (-1.8%, compared to 1.4% toward synergies). These findings align with broader trends in the field, highlighting the critical role of plant functional groups in shaping ecosystem properties and processes (Mouillot, Villéger et al. 2011, Eisenhauer, Schielzeth et al. 2019). Past research on functional groups has predominantly focused on explaining the effects of biodiversity (Roscher, Schumacher et al. 2012) or the impact of biodiversity loss on ecosystem functioning (Cardinale, Duffy et al. 2012). For example, specific functional traits were explored when species with particular traits, such as slower growth rates and longer lifespans, were lost at higher rates (Díaz, Fargione et al. 2006, Laureto, Cianciaruso et al. 2015). The focus shifts increasingly towards traits affecting coexistence, resource use, and ecosystem processes (Eisenhauer, Schielzeth et al. 2019). I showed that individual functional groups are essential for specific ecosystem functions and confirmed that different species [from different functional groups] are needed for ecosystem functioning through time (Isbell, Calcagno et al. 2011).

Instead of looking at individual species and functional groups, a more comprehensive perspective can be obtained by examining species and functional group richness. This approach helps to understand the interactions and properties that shape ecosystem dynamics and overall functioning (Díaz and Cabido 2001, Tilman, Reich et al. 2001, Cardinale, Srivastava et al. 2006). I showed that an increase in species richness leads to an increase in individual EFs, such as plant productivity, invasion resistance, and community pathogen damage (Chapter 1, Chapter 2, Chapter 3) and synergies among EFs (Chapter 2). However, not all EFs were positively influenced by species richness; some were even driven into a trade-off (Chapter 2). Despite this, a clear positive relationship existed between species richness and multifunctionality (Chapter 3). During the last decades, numerous studies have found that an increase in species richness leads to an increase in various ecosystem functions (Hooper, Chapin et al. 2005, Balvanera, Pfisterer et al. 2006, Weisser, Roscher et al. 2017, Cappelli, Pichon et al. 2022). The importance of species richness is particularly evident in the face of biodiversity loss. However, its relevance is regularly debated in naturally assembled communities at larger spatial scales (van der Plas 2019). Biodiversity experiments contain greater variance in their compositional features compared to naturally assembled plant communities, ensuring the reliability of their findings (Jochum, Fischer et al. 2020). Recent research confirmed the importance of species richness in real-world communities by investigating various EFs across different ecosystem types in Tanzania. The study found that the diversity effect explained even more variation in ecosystem functions when environmental heterogeneity was considered (Albrecht, Peters et al. 2021). Consequently, my findings are essential for understanding the relationships between species richness and ecosystem functioning and emphasise the importance of conserving biodiversity in natural plant communities.

Next to species richness, the number of different functional groups (functional group richness) present in a community is an important measure of diversity. Functional group richness could emphasise differences among coexisting plants more than species richness, accentuating diverse ecological roles and interactions among plant groups (Díaz and Cabido 2001, Chapin 2003). I could show a significant positive effect of functional group richness on individual EFs, such as plant productivity and invasion resistance (Chapter 3), reduced pathogen damage of legumes (Chapter 1), and multifunctionality (Chapter 3). The positive effects of functional group richness can be addressed to similar processes as the effects of species richness: Complementary resource use refers to the ability of a plant community to use different resources or access resources at different times. When the functional group richness increases, the complementary resource use within the plant community gets enhanced. Moreover, increasing the functional group richness increases the likelihood of a highly productive or efficient species in the community, called the selection effect. Both processes result in enhanced ecosystem functioning (Loreau and Hector 2001). Previously, functional group richness is critical for ecosystem functioning (Mouillot, Villéger et al. 2011), even for animal groups (Gagic, Bartomeus et al. 2015). As I could define specific interactions among functional groups and EFs, and functional group richness solely explained parts of EFs (Chapter 1, Chapter 3), my study underscores the importance of maintaining a diverse range of functional groups in plant communities to conserve ecosystem functions and services. For targeted management, our research emphasises identifying trait-service clusters (Bello, Lavorel et al. 2010) or identifying which functional groups are associated with what ecosystem functions and -services.

While our study delved into certain aspects of plant communities affecting ecosystem functions, it is important to acknowledge that many unexplored facets remain. Plant communities can encompass various factors beyond associated species or functional groups, as indicated by the variable “plot identity” in Chapter 2. Plot identity accounted for approximately 21.3% of the variation in individual EFs. Notably, for specific EFs like plant nutrients, plot identity explained even more variation, reaching up to 38% (Chapter 2). This variable could be assigned to various components, from abiotic factors to ecological components of plant communities: The genetic diversity within plant species can significantly impact ecosystem functioning, contributing to enhanced productivity and nutrient cycling (Semchenko, Saar et al. 2017). Interactions among individual plant species or functional groups (as shown in Chapter 3) could be contained in the identity effect of plant communities when they are not separately tested (like in Chapter 2). There is still much to unravel about how plant communities influence these interactions. In the context of trade-offs, most covariance was driven by plot identity (Chapter 2), suggesting that other variables within a plant community, such as negative interactions, play crucial roles in driving trade-offs. These insights contribute to the growing understanding of the relationships between plant functional groups, biodiversity, and ecosystem functioning.

4.3.2 Complex interactions behind biodiversity

As discussed, the various components of biodiversity, including identity effects of plant species and functional groups, species- and functional group richness, and genetic diversity, shape dynamics within plant communities (Correia and Lopes 2023). These dynamics are based on ecological principles such as competition, facilitation, and complementarity within plant communities. My research found indicators for various ecological principles and interactions among plant species or functional groups. Competition is caused when resources, such as nutrients, water, or sunlight, are shared between species (Tilman 1994). My results indicated competition when the relationships among EFs were investigated (Chapter 2), where plant productivity and invasion resistance were in a synergy, suggesting competition for resources between the resident plant community and the potential invading plant species. Competition for nutrients was also indicated by the trade-off between root biomass and soil nutrient concentrations (Chapter 2). Competition can lead to weaker ecosystem functioning. This was suggested by our finding that EF relationships are highly variable over time (Chapter 2), meaning that the availability of resources such as water and light fluctuates, either strengthening or weakening competition among plant species. Additionally, ecosystem functioning can be limited by competition because plants can be more susceptible to diseases (Gilbert and Parker 2010), which was indicated by our finding that pathogen damage increases with plant species richness (Chapter 1). Consequently, competition can weaken ecosystem functioning by representing ecological constraints, causing limited multifunctionality. These ecological constraints should be well-known so that management practices can be developed considering these constraints.

The opposite of competition is complementarity, which can weaken trade-offs (Weisser, Roscher et al. 2017) and highlight the coexistence of species caused by complementary resource use (Connell and Slatyer 1977, Temperton, Hobbs et al. 2004). I found indications for complementarity in Chapter 3, showing high water content in the soil in the combination of *Trifolium repens* and *Trifolium pratense*, likely due to a complementary rooting system. Also, functional groups can interact complementary, like grasses and herbs have shown positive interactions causing high invasion resistance and increasing water availability (Chapter 3) due to complementary traits concerning leaves and roots (Craine, Froehle et al. 2001, Freschet, Roumet et al. 2021). Complementary traits empower plants to utilise spatial resources effectively (Barry, Mommer et al. 2019). Another positive interaction among plants is facilitation, meaning one species exhibits beneficial traits for other plants by providing resources or shelter (Connell and Slatyer 1977). This was shown in Chapter 3 between herbs and legumes, where legumes caused high soil nitrogen and herbs likely acquired nitrogen from deeper soil layers, enabling an increased provision of soil nitrogen for other plants (Loreau and Hector 2001, Fornara and Tilman 2009, Grace, Boland et al. 2018, Freschet, Roumet et al. 2021, Hamacher, Malisch et al. 2021). Detailed knowledge about complementary could be utilised in management to design high-functioning plant communities by combining species with complementary traits.

Overall, these interactions among plant species were dominated by shared or contradicted functional traits. This emphasises that certain species and functional groups, including genetic diversity and phylogenetic species diversity, can have a greater impact on the relationships between biodiversity and ecosystem functioning (Eisenhauer, Schielzeth et al. 2019). While competition can be hard to resolve, complementary traits can weaken competition among plant species and weaken trade-offs (Weisser, Roscher et al. 2017), resulting in higher ecosystem functioning. Furthermore, it was previously shown that resource partitioning is more critical than facilitation for ecosystem functioning (Naeem, Thompson et al. 1994), highlighting our finding of the importance of functional groups with their complementary traits. Additionally, resource use is most efficient in highly diverse communities, being more productive than with low biodiversity (van der Plas 2019, Correia and Lopes 2023, Dietrich, Eisenhauer et al. 2023). Consequently, functional traits become a fundamental concept in designing grasslands. This could be used to develop a practical strategy to reduce the conflict between agriculture and conservation efforts in grassland leys or to monitor the functioning of grasslands based on the present plant species, indicating certain levels of facilitation and complementarity.

4.3.3 Interaction between age and biodiversity within plant communities

Previous insights on plant species interactions and functional traits have highlighted how plant diversity affects ecosystem functioning. However, biodiversity is also essential for the long-term functioning of ecosystems (Cardinale, Duffy et al. 2012, Reich, Tilman et al. 2012, Meyer, Ebeling et al. 2016, Guerrero-Ramírez, Craven et al. 2017, Dietrich, Ebeling et al. 2024), e.g. by influencing the assembling processes of microorganisms in the soil (Eisenhauer, Reich et al. 2012, Grenzer, Kulmatiski et al. 2021, Schmid, van Moorsel et al. 2021, Maciá-Vicente, Francioli et al. 2023, Delavaux, Angst et al. 2024). By understanding all these ecosystem dynamics, we can develop effective strategies for managing grasslands that balance agricultural needs and conservation efforts. Therefore, I investigated pathogen damage to biodiversity and community age to further understand the effects of diverse plant communities on aboveground and belowground processes. One finding was the observed decreasing trend in pathogen damage as time progressed (Chapter 1). However, when I further investigated the role of community age, the decline of pathogen damage did not vary between different history treatments. This lack of differentiation suggests that neither belowground nor aboveground processes associated with specific histories significantly explained the observed decreasing trend in pathogen damage over time. Like my results in Chapter 1, Vogel, Ebeling et al. (2019) showed that the diversity-productivity relationship was stronger in old plant communities than in young communities. However, this cannot be explained by the age of the soil alone. While a gradual build-up of soil organisms and fungi over time was shown already multiple times (Grenzer, Kulmatiski et al. 2021, Schmid, van Moorsel et al. 2021, Maciá-Vicente, Francioli et al. 2023), it was not shown to solely explain the strengthening biodiversity-productivity relationship over time. The results in Chapter 1 also indicate that for the decreasing pathogen damage over time, the processes aboveground and belowground cannot be separated to explain the trend over time. Grenzer, Kulmatiski et al. (2021) found that plant growth is affected by plant-soil feedback for individual plant species but not for plant communities. It was concluded that this is due to the high difference in intrinsic growth rates among species. Similarly, high inherent variability between species or time points was indicated by my other chapters, where EFs different from pathogen damage were investigated. Furthermore, an intrinsic variability was shown when I compared the effect of individual plant species on EFs (Chapter 3), revealing that not only the particular plant species but also their interactions can greatly impact individual ecosystem functions. This means I might find differences in history treatments for the pathogen damage of individual plant species. Still, within plant communities, the intrinsic variability was too high to detect history treatments or opposing effects from individual plant species balance each other out.

While my findings indicate that pathogen damage changed over time and showed a relationship with biodiversity, the lack of differentiation in the history treatments does not diminish the potential impact of historical land use on ecosystem functioning in general. How the land has been used historically, and the presence of specific plant species can impact the structure and composition of aboveground and belowground communities (Dietrich, Ebeling et al. 2024). For instance, long-term high-diversity plant communities have facilitative components like decomposers, arbuscular mycorrhizal fungi, and rhizobacteria that can enhance plant growth (Reynolds, Packer et al. 2003, Ke and Wan 2020). On the other hand, species-poor plant communities are more likely to accumulate pathogens, such as nematodes, leading to antagonistic net soil effects (Eisenhauer, Reich et al. 2012). As a result, the historical land use can affect plant communities, with long-established grasslands supporting more plant species than areas that were previously used differently (Nerlekar and Veldman 2020). Our results of consistent biodiversity effects on pathogen damage across years (Chapter 1) underscore plant diversity's persistent and influential role in shaping the dynamics of plant-pathogen interactions within the studied ecosystem.

Moving forward, future research should prioritise disentangling the impact of plant- and soil history on ecosystem stability to ensure resilience under changing climates. As existing studies predict alterations in the abiotic factors defining specific biotopes under the future climate (Rubanschi, Meyer et al. 2023), practical management decisions will benefit from insights on whether to preserve current biotopes, considering both plant- and soil history or to establish plant communities in new sites with no soil history but potential plant history through appropriate seeding. Therefore, understanding the historical context of plant and soil interactions is crucial for comprehending the present-day biodiversity and ecological dynamics above and below ground for various ecosystem functions.

4.4 Management Approaches for Ultimate Multifunctionality

4.4.1 Challenges in achieving ultimate multifunctionality due to the interconnectedness of EFs

Multifunctionality refers to the capacity of ecosystems to provide multiple ecosystem functions and services simultaneously (Hector and Bagchi 2007). It encompasses the idea that ecosystems perform various ecological processes and support diverse organisms while delivering numerous benefits to humans, such as food production, water regulation, climate regulation, and biodiversity conservation (Millennium Ecosystem Assessment 2005). Ultimate multifunctionality, on the other hand, represents an idealised concept where ecosystems would optimally fulfil all possible EFs and ES simultaneously without any trade-offs or conflicts among different functions. It implies achieving the highest possible level of multifunctionality, where every potential ecosystem function is fully realised. While the idea of attaining ultimate multifunctionality is striving, as usual with idealised concepts, there are some challenges and limitations to consider:

Ultimate multifunctionality is an unattainable goal, influenced by subjective human perspectives and the inherent disparities among ecosystem functions. The quantification of multifunctionality is based on the assigned value for each ecosystem function, and while some functions may align in perspectives, others may not. For example, a farmer may value water content in soil and productivity but may not value high mammal activity as a positive aspect, prompting a reassessment of the multifunctionality index (as calculated in Chapter 3). Therefore, creating a comprehensive multifunctionality index that reflects the opinion of every stakeholder is unattainable. This leads to the realisation that adaptive management strategies tailored to specific objectives and stakeholder needs are necessary. The consequences for management practices resulting from these limitations include setting clear and specific goals that guide decision-making.

Other limitations why ultimate multifunctionality cannot be achieved lie within ecosystems' nature. Ecosystems are complex, and trade-offs exist among different EFs (as discussed in Chapter 2). While my research highlights that biodiversity is crucial in enhancing multifunctionality (chapter 3), it is essential to recognise that biodiversity also introduces trade-offs among functions, limiting the attainment of ultimate multifunctionality (Chapter 2). Therefore, achieving ultimate multifunctionality without compromising any other EF is challenging due to these inherent trade-offs. Trade-offs occur over time because some EFs, such as productivity, depend on a seasonal cycle. Ultimate multifunctionality would require consistent performance across diverse landscapes and changing environmental conditions, while in reality, ecosystem functions vary over time (as shown in Chapter 2). A nuanced and context-dependent management strategy is needed to address the inherent trade-offs and complexities associated with achieving ultimate multifunctionality in ecosystem management. Exploring the limitations of multifunctionality by comparing relationships among ecosystem functions across different land use types is crucial. Under intensive management, potential strengthening trade-offs and the increasing importance of specific plant traits for multifunctionality in agricultural landscapes should be investigated. These ecosystem management practices must balance maximising agricultural productivity and conserving biodiversity and ecosystem services.

4.4.2 Two contrasting approaches: Land sparing vs. Land sharing

Conserving biodiversity while maintaining agricultural production could be achieved through land sparing or land sharing. Positioned on a gradient, these strategies offer various options in between (Sidemo-Holm, Ekroos et al. 2021). Land sharing involves integrating conservation practices within agricultural landscapes, using different approaches to increase biodiversity, such as reducing pesticides and fertilisers and creating habitats on small land patches, as done in organic farming (Tscharntke, Grass et al. 2021, Bateman and Balmford 2023). This approach is beneficial for biodiversity, carbon sequestration, pollination, and livelihoods without requiring a reduction in agricultural land use to the extent of conservation reserves (Rosa-Schleich, Loos et al. 2019, Tscharntke, Grass et al. 2021). The growing adoption of organic farming in recent years is considered advantageous for species on farmlands (Bateman and Balmford 2023). However, critics argue that organic agriculture leads to declines in production (Tscharntke, Grass et al. 2021) and may not benefit organisms that require contiguous natural habitats (Bateman and Balmford 2023). Incorporating plant diversity in intensively managed grassland leys, as investigated in Chapter 3, can enhance multifunctionality and lead to a more sustainable landscape. However, a conversion from cropland to grassland leys involves temporarily removing land from arable production, which may lead to yield losses during the ley phase. Furthermore, a decrease in productivity would cause more food imports, resulting in declines in wildlife overseas (Bateman and Balmford 2023). Collas, Crastes dit Sourd et al. (2023) go even further, concluding that a land-sharing strategy harms conservation and food security globally by burdening food-exporting nations by compensating for lost domestic production in the name of conservation. Therefore, assessing the economic and ecological advantages of such practices over a prolonged period is essential. Further restrictions on agricultural land may increase pressure on production areas, adversely affecting biodiversity elsewhere (Bateman and Balmford 2023).

On the other hand, land sparing involves reducing the agricultural footprint by intensifying production on a smaller land area and preserving natural habitats. This approach requires creating large, separate areas of sustainably intensified agriculture and wilderness (Bateman and Balmford 2023). Rewilding such areas has proven beneficial for local endangered species (Bateman and Balmford 2023). However, it may not effectively conserve traditional agroecosystems and synanthropic species shaped by human land-use history (Grass, Batáry et al. 2021). Land-use history showed that extensively managed grasslands, which reflect traditional agroecosystems employing low-input agricultural practices, play an important role in conserving biodiversity and promoting ecosystem functioning (Sollenberger, Moura Kohmann et al. 2019). In the late 19th century, semi-natural grasslands dominated many landscapes and required livestock grazing or hay-cutting for their maintenance (Queiroz, Beilin et al. 2014). For example, appropriate grazing management has improved water regulation and carbon storage, prevented erosion, and enhanced pollinator diversity (Bengtsson, Bullock et al. 2019). Some endangered species even need specific management, whereas intensified management is a trade-off with biodiversity (Stoate, Baldi et al. 2009, Bengtsson, Bullock et al. 2019). Consequently, relying solely on land sparing may not effectively preserve endangered species. Nevertheless, the appropriate management practices can mitigate or avoid these trade-offs, which are important to identify. My research challenges the static trade-off assumption between biodiversity and agricultural production. The findings highlight the variable nature of trade-offs and synergies, influenced by external variables such as biodiversity and the presence of specific functional groups (Chapter 2). Specifically, the research demonstrated that incorporating multispecies mixtures, even within intensively managed systems, can enhance production and biodiversity (Chapter 3), resulting in a more multifunctional landscape. Therefore, intensively managed agricultural lands can achieve greater multifunctionality when biodiversity is embraced and integrated into management practices.

In summary, the dichotomy between land sparing and land sharing is not static but involves dynamic interactions influenced by various factors. A combined approach of land sparing and land sharing may be the most effective for preserving species (Bateman and Balmford 2023, Tälle, Öckinger et al. 2023). In Indonesia, a nuanced strategy that blends land sparing with selective agricultural intensification has shown promise in balancing trade-offs and enhancing food supply (Lusiana, van Noordwijk et al. 2012). My research further suggests that even within a land-sparing approach, solutions exist to mitigate the negative impacts of intensive agriculture. A study from Stroud (2019) gives hope that farmers are also interested in applying practices to monitor the health of the soils and to adapt their management accordingly. During a study in England, farmers utilised earthworm presence to monitor the health of soils. 100% of the farmers would do the survey again, and 57% used it to adapt their soil management practices (Stroud 2019). Thus, adopting a flexible and context-specific approach is essential when navigating the complex trade-offs between conservation efforts and agricultural production (Fischer, Abson et al. 2014, Game, Meijaard et al. 2014). The European Union has recognised the harmful effects of intensive management, addressed through payment schemes such as agri-environmental subsidies (Bengtsson, Bullock et al. 2019, Hermoso, Carvalho et al. 2022). However, an approach to expand traditional grassland management practices is needed to conserve biodiversity, which in practical terms would require more drastic changes in the “greening” subsidies of the EU's Common Agricultural Policy (CAP) (Dengler and Tischew 2018, Hermoso, Carvalho et al. 2022).

This interconnected nature is reflected at a smaller scale, where achieving multifunctionality faces inherent limitations, as evidenced by various studies (Maes, Paracchini et al. 2012, Lefcheck, Byrnes et al. 2015, Meyer, Ptacnik et al. 2018, van der Plas 2019). Similar to complex relationships between ecosystem functions, understanding the interactions between SDGs is necessary. These interactions are crucial in informing decision-making processes (Scharlemann, Brock et al. 2020). Interconnectedness poses a major challenge in achieving all SDGs, as progress in one area influences the outcome in others. Recognising the interplay between SDGs is essential for devising comprehensive strategies that contribute synergistically to sustainable development objectives.

4.4.3 Interconnectedness of SDGs

The Sustainability Development Goals are highly interconnected, where economic growth and poverty reduction lead to the provision of essential services. However, expanding agricultural activities represents one approach to addressing hunger reduction. A potential conflict that may intensify is hunger and food insecurity, which could increase the pressure on food production and lead to further land degradation or biodiversity loss. Numerous studies have explored the interconnectedness of SDGs, revealing both synergies and trade-offs. An extensive meta-analysis identified 508 interlinkages between Goal 2 (Zero Hunger) and all other goals, with 31% indicating trade-offs, 60% revealing synergies, and 8% did not specify the connection (European Commission 1995 - 2024). Based on my work, I suggest that there are considerable opportunities for synergies between Zero Hunger and other goals like Life on Land or Sustainable Consumption. My work highlights that biodiversity drives synergies between plant production and soil properties, such as carbon and nitrogen content (Chapter 2) while enhancing plant production, water availability, and invasion resistance (Chapter 3). This suggests a potential weakening of trade-offs between these goals. However, the extent of this mitigation largely depends on how the Zero Hunger goal is pursued. If agricultural intensification continues to be the primary approach to achieving Zero Hunger, it could exacerbate these trade-offs. Therefore, it is crucial to consider a nuanced approach to ensure that achieving Zero Hunger does not compromise Goal 15 (Life on Land), emphasising the critical role of sustainable land use practices in achieving both goals. My research contributes to the practical implementation by exploring conflicts in grassland management and investigating approaches to enhance biodiversity, soil health, and water resource management. In the next step, it is crucial to strengthen the link between policy and management. In future scenarios, it is even more essential to comprehend the interdependence of social and economic limitations with ecological knowledge (Hooper, Chapin et al. 2005).

4.5 Specific Contributions of my research to the implementation of the Sustainable Development Goals

The Common Agricultural Policy (CAP) adopted by the European Union is a collective policy for member countries, focusing on economic, environmental, and social sustainability (e.g., by promoting jobs in farming and associated sectors, preservation of landscape and biodiversity, and ensuring the supply of affordable food) to tackle the trade-off between conservation effort and agricultural production (Landwirtschaft 2023). My research directly contributes to the environmental sustainability aspect of CAP by exploring and optimising conflicts in grassland, as discussed in Chapters 2 and 3. On a global scale, CAP aligns with several SDGs, including Responsible Consumption and Production (Goal 12), Life on Land (Goal 15), Zero Hunger (Goal 2), and Climate Action (Goal 13). Responsible Consumption and Production (Goal 12) encompasses sustainable resource management, waste reduction, and promotion of sustainable consumption, supporting rural economies. Similarly, Zero Hunger (Goal 2) addresses sustainable agriculture. My research revealed that legumes enhance nitrogen content, and grasses negatively impact water content in the soil (Chapter 3), offering insights into sustainable resource management, soil health improvement, and water use reduction. While the positive effects of legumes have been known for a long time, nowadays, they are used in short-term rotations as a winter cover crop (Power 1987, Ringler 1995, Graham and Vance 2003). The utilisation of legumes in agriculture is proposed to reduce the usage of N fertiliser and the high sequestration of carbon in soils, which would reduce the loading with chemicals in the soil and a reduction of emission of greenhouse gases (Power 1987, Graham and Vance 2003, Stagnari, Maggio et al. 2017), and even benefitting higher trophic levels, such as the abundance of earthworms (Schmidt, Clements et al. 2003, Milcu, Partsch et al. 2008, Singh, Cameron et al. 2021). My findings suggest incorporating legumes into multispecies mixtures for a broader positive impact, aligning with the promotion of reduced chemical use and environmental pollution under Goal 12.

Life on Land (Goal 15), which aims to halt biodiversity loss and promote sustainable use of terrestrial ecosystems, aligns with Goal 12. My study implicitly underscores the threat to ecosystem services provision, revealing that different plant species drive various ecosystem functions included in the multifunctionality index (Chapter 3). Moreover, I emphasise the complex interactions between plant species within a community, suggesting harsh consequences in the face of biodiversity loss. My research highlights that maintaining functional ecosystems requires biodiversity and diverse species from different functional groups in grassland ecosystems (Chapter 3). This confirms former findings, suggesting that different functional groups or trophic levels affect ecosystem functioning differently and that biodiversity loss would have various consequences on ecosystem functioning (Northfield, Snyder et al. 2010, Barnes, Jochum et al. 2018). Consequently, nature conservation efforts should promote functional diversity within plant communities. While the standard Agricultural Policy of the European Union addresses Life on Land by supporting natural habitats or protecting biodiversity, nationally, this works over programs promoting measures to maintain ecologically relevant habitats (e.g., VNP) or measures to protect species from the IUCN Red List of Threatened Species (e.g., LNPR) . However, biodiversity should be promoted whenever possible to ensure multifunctional landscapes and be urgently incorporated in agricultural areas.

Climate Action (Goal 13) addresses climate change impacts, and my research, as indicated in Chapter 2, emphasises the potential effects of future climate on individual ecosystem functions and relationships by showing their high variability over time. In the future, this variability might further increase under the influence of extreme events. Several studies showed that climate change could cause an intensification of extreme weather events, e.g., increased frequency and amplitude of temperature (Jentsch, Kreyling et al. 2007, Lima and Wethey 2012). Heat waves occurred with increasing frequency over large land areas around the world between 1950 and 2011 (Perkins-Kirkpatrick, Alexander et al. 2012). Like a constant average temperature increase, heat waves could severely impact ecosystems, exceeding their functioning (Jentsch, Kreyling et al. 2007). Within the last years, even Germany, considered a water-rich country, experienced water scarcity as droughts became more severe (Zink, Samaniego et al. 2016) with wide-ranging consequences, affecting agriculture, ecosystems, water supply, energy production, health, infrastructure, and tourism (Zink, Samaniego et al. 2016, Bastos, Ciais et al. 2020). Therefore, a change in management method is needed, as no machine or adaptation of fertiliser will solve this problem. For multiple biomes across the western hemisphere, even for marine, intertidal communities, it was shown that biodiverse plant communities are less sensitive to temperature variability (Oliveira, Moore et al. 2022, Mancuso, Giommi et al. 2023). Biodiversity was shown to reduce the variability of ecosystem functions over time (Loreau, Naeem et al. 2001, Eisenhauer, Schielzeth et al. 2019), acting as a buffer against environmental changes (Hong, Schmid et al. 2022, Mahecha, Bastos et al. 2022). Highlighting the importance of ecosystem resilience and stability, my findings on highly variable ecosystem functions (Chapter 2) underscore the need for adaptive management practices alongside those promoting resilient plant communities to address future climate challenges. As the human population and consumption continue to increase, there is a growing demand for applying the knowledge of biodiversity research to develop sustainable management practices for ecosystems, including agroecosystems (Isbell, Adler et al. 2017, Isbell, Gonzalez et al. 2017, Eisenhauer, Schielzeth et al. 2019), as highly diverse grasslands benefit soil, climate, and water and therefore representing the life insurance for agriculture.

5. Conclusion and Advocacy for Sustainable Land Use

Several steps are needed to develop a sustainable approach to agriculture and resolve the conflict between nature conservation and productivity in agriculture. First, robust monitoring and assessment protocols are required to quantify EFs consistently. I showed that long-term measurements are essential due to the high variability of individual ecosystem functions. Additionally, long-term measurements are required to understand the limitations of multifunctionality due to underlying relationships among EFs. Second, sustainable land use practices need to be developed. By exploring the impact of biodiversity on various ecosystem functions, my research suggests that incorporating diverse plant species, even in intensively managed systems, can lead to enhanced multifunctionality. This finding challenges the conventional notion of a static trade-off between biodiversity conservation and agricultural production and shows how much land sharing can be achieved. However, the economic viability of this approach needs to be evaluated.

Additionally, my research implied that differences between newly established grasslands and old-growth grasslands exist concerning their ecosystem functioning, emphasising the importance of historical factors in shaping the biodiversity-ecosystem-functioning relationship. Lastly, the development and implementation of policies and regulations play an essential role in the success of sustainable land use practices. My research found that incorporating diverse plant species, such as legumes, into multispecies mixtures in intensively managed systems can positively impact sustainable resource management, soil health improvement, water use reduction, and reduced chemical use. These benefits directly support Goal 12 (Responsible Consumption and Production). My study also highlights the importance of biodiversity in promoting functional diversity within plant communities, which contributes to the goals of halting biodiversity loss (Life on Land, Goal 15) and promoting sustainable use of terrestrial ecosystems (Goal 12). Furthermore, my research on legume benefits for nitrogen content supports sustainable agriculture practices that enhance productivity while reducing environmental impacts, aligning with Goal 2 (Zero Hunger). Finally, my research emphasises ecosystem variability over time, underscoring the importance of adaptive management practices that align with Goal 13 (Climate Action) to address future climate challenges in agricultural systems. To balance nature conservation and agricultural productivity, we need a comprehensive approach that includes robust monitoring, sustainable land use practices, and supportive policies. Research like mine contributes valuable insights to help achieve these goals and promote sustainable agriculture.

References

Abalos, D., G. B. De Deyn, T. W. Kuyper and J. W. van Groenigen (2014). "Plant species identity surpasses species richness as a key driver of N2O emissions from grassland." Global Change Biology **20**(1): 265-275.

Albrecht, J., M. K. Peters, J. N. Becker, C. Behler, A. Classen, A. Ensslin, S. W. Ferger, F. Gebert, F. Gerschlauer, M. Helbig-Bonitz, W. J. Kindeketa, A. Kühnel, A. V. Mayr, H. K. Njovu, H. Pabst, U. Pommer, J. Röder, G. Rutten, D. Schellenberger Costa, N. Sierra-Cornejo, A. Vogeler, M. G. R. Vollstädt, H. I. Dulle, C. D. Eardley, K. M. Howell, A. Keller, R. S. Peters, V. Kakengi, C. Hemp, J. Zhang, P. Manning, T. Mueller, C. Bogner, K. Böhning-Gaese, R. Brandl, D. Hertel, B. Huwe, R. Kiese, M. Kleyer, C. Leuschner, Y. Kuzyakov, T. Nauss, M. Tschapka, M. Fischer, A. Hemp, I. Steffan-Dewenter and M. Schleuning (2021). "Species richness is more important for ecosystem functioning than species turnover along an elevational gradient." Nature Ecology & Evolution **5**(12): 1582-1593.

Balvanera, P., A. B. Pfisterer, N. Buchmann, J.-S. He, T. Nakashizuka, D. Raffaelli and B. Schmid (2006). "Quantifying the evidence for biodiversity effects on ecosystem functioning and services." Ecology Letters **9**(10): 1146-1156.

Bardgett, R. D., J. M. Bullock, S. Lavorel, P. Manning, U. Schaffner, N. Ostle, M. Chomel, G. Durigan, E. L. Fry, D. Johnson, J. M. Lavallee, G. Le Provost, S. Luo, K. Png, M. Sankaran, X. Hou, H. Zhou, L. Ma, W. Ren, X. Li, Y. Ding, Y. Li and H. Shi (2021). "Combatting global grassland degradation." Nature Reviews Earth & Environment **2**(10): 720-735.

Barnes, A. D., M. Jochum, J. S. Lefcheck, N. Eisenhauer, C. Scherber, M. I. O’Connor, P. de Ruiter and U. Brose (2018). "Energy flux: the link between multitrophic biodiversity and ecosystem functioning." Trends in ecology & evolution **33**(3): 186-197.

Barry, K. E., L. Mommer, J. van Ruijven, C. Wirth, A. J. Wright, Y. Bai, J. Connolly, G. B. De Deyn, H. de Kroon, F. Isbell, A. Milcu, C. Roscher, M. Scherer-Lorenzen, B. Schmid and A. Weigelt (2019). "The Future of Complementarity: Disentangling Causes from Consequences." Trends Ecol Evol **34**(2): 167-180.

Bastos, A., P. Ciais, P. Friedlingstein, S. Sitch, J. Pongratz, L. Fan, J. P. Wigneron, U. Weber, M. Reichstein, Z. Fu, P. Anthoni, A. Arneth, V. Haverd, A. K. Jain, E. Joetzjer, J. Knauer, S. Lienert, T. Loughran, P. C. McGuire, H. Tian, N. Viovy and S. Zaehle (2020). "Direct and seasonal legacy effects of the 2018 heat wave and drought on European ecosystem productivity." Science Advances **6**(24): eaba2724.

Bateman, I. and A. Balmford (2023). "Current conservation policies risk accelerating biodiversity loss." Nature **618**(7966): 671-674.

Bazzichetto, M., M. G. Sperandii, C. Penone, P. Keil, E. Allan, J. Lepš, D. Prati, M. Fischer, R. Bolliger and M. Gossner (2023). "Functional components of biodiversity mediate stability of grasslands under extreme drought."

Bello, F., S. Lavorel, S. Diaz, R. Harrington, J. Cornelissen, R. Bardgett, M. Berg, P. Cipriotti, C. Feld, D. Hering, P. Silva, S. Potts, L. Sandin, J. P. Sousa, J. Storkey, D. Wardle and P. Harrison (2010). "Towards an assessment of multiple ecosystem processes and services via functional traits." Biodiversity and Conservation **19**.

Bengtsson, J., J. M. Bullock, B. Egoh, C. Everson, T. Everson, T. O'Connor, P. J. O'Farrell, H. G. Smith and R. Lindborg (2019). "Grasslands—more important for ecosystem services than you might think." Ecosphere **10**(2): e02582.

Brooker, R. W., F. T. Maestre, R. M. Callaway, C. L. Lortie, L. A. Cavieres, G. Kunstler, P. Liancourt, K. Tielbörger, J. M. J. Travis, F. Anthelme, C. Armas, L. Coll, E. Corcket, S. Delzon, E. Forey, Z. Kikvidze, J. Olofsson, F. Pugnaire, C. L. Quiroz, P. Saccone, K. Schiffers, M. Seifan, B. Touzard and R. Michalet (2008). "Facilitation in Plant Communities: The Past, the Present, and the Future." Journal of Ecology **96**(1): 18-34.

Brophy, C., J. Finn and C. S. Malisch. (2024). "LegacyNet - An international network of experiments." from https://legacynet.scss.tcd.ie/index.php.

Burns, J. H., B. L. Anacker, S. Y. Strauss and D. J. Burke (2015). "Soil microbial community variation correlates most strongly with plant species identity, followed by soil chemistry, spatial location and plant genus." AoB PLANTS **7**.

Buzhdygan, O. Y., S. T. Meyer, W. W. Weisser, N. Eisenhauer, A. Ebeling, S. R. Borrett, N. Buchmann, R. Cortois, G. B. De Deyn and H. de Kroon (2020). "Biodiversity increases multitrophic energy use efficiency, flow and storage in grasslands." Nature Ecology & Evolution **4**(3): 393-405.

Byrnes, J. E. K., L. Gamfeldt, F. Isbell, J. S. Lefcheck, J. N. Griffin, A. Hector, B. J. Cardinale, D. U. Hooper, L. E. Dee, J. Emmett Duffy and R. Freckleton (2014). "Investigating the relationship between biodiversity and ecosystem multifunctionality: challenges and solutions." Methods in Ecology and Evolution **5**(2): 111-124.

Cadotte, M. W., B. J. Cardinale and T. H. Oakley (2008). "Evolutionary history and the effect of biodiversity on plant productivity." Proceedings of the National Academy of Sciences **105**(44): 17012-17017.

Cadotte, M. W., K. Carscadden and N. Mirotchnick (2011). "Beyond species: functional diversity and the maintenance of ecological processes and services." Journal of Applied Ecology **48**(5): 1079-1087.

Cappelli, S. L., N. A. Pichon, T. Mannall and E. Allan (2022). "Partitioning the effects of plant diversity on ecosystem functions at different trophic levels." Ecological Monographs **92**(3): e1521.

Cardinale, B. J., J. E. Duffy, A. Gonzalez, D. U. Hooper, C. Perrings, P. Venail, A. Narwani, G. M. Mace, D. Tilman, D. A. Wardle, A. P. Kinzig, G. C. Daily, M. Loreau, J. B. Grace, A. Larigauderie, D. S. Srivastava and S. Naeem (2012). "Biodiversity loss and its impact on humanity." Nature **486**(7401): 59-67.

Cardinale, B. J., K. L. Matulich, D. U. Hooper, J. E. Byrnes, E. Duffy, L. Gamfeldt, P. Balvanera, M. I. O'Connor and A. Gonzalez (2011). "The functional role of producer diversity in ecosystems." American Journal of Botany **98**(3): 572-592.

Cardinale, B. J., D. S. Srivastava, J. Emmett Duffy, J. P. Wright, A. L. Downing, M. Sankaran and C. Jouseau (2006). "Effects of biodiversity on the functioning of trophic groups and ecosystems." Nature **443**(7114): 989-992.

Carpenter, S. R., H. A. Mooney, J. Agard, D. Capistrano, R. S. DeFries, S. Díaz, T. Dietz, A. K. Duraiappah, A. Oteng-Yeboah and H. M. Pereira (2009). "Science for managing ecosystem services: Beyond the Millennium Ecosystem Assessment." Proceedings of the National Academy of Sciences **106**(5): 1305-1312.

Cavender-Bares, J., K. H. Kozak, P. V. A. Fine and S. W. Kembel (2009). "The merging of community ecology and phylogenetic biology." Ecology Letters **12**(7): 693-715.

Chapin, F. S., 3rd (2003). "Effects of plant traits on ecosystem and regional processes: a conceptual framework for predicting the consequences of global change." Ann Bot **91**(4): 455-463.

Collas, L., R. Crastes dit Sourd, T. Finch, R. Green, N. Hanley and A. Balmford (2023). "The costs of delivering environmental outcomes with land sharing and land sparing." People and Nature **5**(1): 228-240.

Commission, E. "Common agricultural policy funds." Retrieved 06.01.2024, from https://agriculture.ec.europa.eu/common-agricultural-policy/financing-cap/cap-funds.

Connell, J. H. and R. O. Slatyer (1977). "Mechanisms of Succession in Natural Communities and Their Role in Community Stability and Organization." The American Naturalist **111**(982): 1119-1144.

Connolly, J., T. Bell, T. Bolger, C. Brophy, T. Carnus, J. A. Finn, L. Kirwan, F. Isbell, J. Levine and A. Lüscher (2013). "An improved model to predict the effects of changing biodiversity levels on ecosystem function." Journal of Ecology **101**(2): 344-355.

Correia, A. M. and L. F. Lopes (2023). "Revisiting Biodiversity and Ecosystem Functioning through the Lens of Complex Adaptive Systems." Diversity **15**(8): 895.

Cousins, S. A., A. G. Auffret, J. Lindgren and L. Tränk (2015). "Regional-scale land-cover change during the 20th century and its consequences for biodiversity." Ambio **44**: 17-27.

Craine, J., J. Froehle, D. Tilman, D. Wedin and F. S. Chapin Iii (2001). "The relationships among root and leaf traits of 76 grassland species and relative abundance along fertility and disturbance gradients." Oikos **93**: 274-285.

Cutress, D. (2022). "Land sparing and land sharing - considerations for farming with nature." from https://businesswales.gov.wales/farmingconnect/news-and-events/technical-articles/land-sparing-and-land-sharing-considerations-farming-nature.

De Deyn, G. B., C. E. Raaijmakers, J. Van Ruijven, F. Berendse and W. H. Van Der Putten (2004). "Plant species identity and diversity effects on different trophic levels of nematodes in the soil food web." Oikos **106**(3): 576-586.

Delavaux, C. S., J. K. Angst, H. Espinosa, M. Brown, D. F. Petticord, J. W. Schroeder, K. Broders, E. A. Herre, J. D. Bever and T. W. Crowther (2024). "Fungal community dissimilarity predicts plant–soil feedback strength in a lowland tropical forest." Ecology **105**(1): e4200.

Dengler, J. and S. Tischew (2018). Grasslands of Western and Northern Europe - between intensification and abandonment**:** 27-63.

Díaz, S. and M. Cabido (2001). "Vive la différence: plant functional diversity matters to ecosystem processes." Trends in Ecology & Evolution **16**(11): 646-655.

Díaz, S., J. Fargione, F. S. Chapin III and D. Tilman (2006). "Biodiversity loss threatens human well-being." PLoS biology **4**(8): e277.

Dietrich, P., A. Ebeling, S. Meyer, A. E. Asato, M. Bröcher, G. Gleixner, Y. Huang, C. Roscher, B. Schmid, A. Vogel and N. Eisenhauer (2024). "Plant diversity and community age stabilize ecosystem multifunctionality." Global Change Biology **30**: e17225.

Dietrich, P., N. Eisenhauer and C. Roscher (2023). "Linking plant diversity–productivity relationships to plant functional traits of dominant species and changes in soil properties in 15-year-old experimental grasslands." Ecology and Evolution **13**(3): e9883.

Dooley, Á., F. Isbell, L. Kirwan, J. Connolly, J. A. Finn, C. Brophy and Y. Buckley (2015). "Testing the effects of diversity on ecosystem multifunctionality using a multivariate model." Ecology Letters **18**(11): 1242-1251.

Dudley, N., L. Eufemia, I. Petersen, M. Fleckenstein, J. Campari, M. E. Periago, F. O. Minarro, F. O. Miñarro, C. Siqueira, J. F. Timmers, S. Rincón, K. Musálem, E. Rendón, D. C. Forero, M. Kauffman, L. Miaro, A. Burns, Z. Ge, O. Pereladova, C. Buyanaa, A. Serdyuk, K. Thapa, A. de Valença, S. Doornbos and I. McConnel (2020). Grassland and Savannah ecosystems, WWF Deutschland.

Ebeling, A., S. Pompe, J. Baade, N. Eisenhauer, H. Hillebrand, R. Proulx, C. Roscher, B. Schmid, C. Wirth and W. W. Weisser (2014). "A trait-based experimental approach to understand the mechanisms underlying biodiversity–ecosystem functioning relationships." Basic and Applied Ecology **15**(3): 229-240.

Eisenhauer, N., P. B. Reich and S. Scheu (2012). "Increasing plant diversity effects on productivity with time due to delayed soil biota effects on plants." Basic and Applied Ecology **13**(7): 571-578.

Eisenhauer, N., H. Schielzeth, A. D. Barnes, K. Barry, A. Bonn, U. Brose, H. Bruelheide, N. Buchmann, F. Buscot, A. Ebeling, O. Ferlian, G. T. Freschet, D. P. Giling, S. Hättenschwiler, H. Hillebrand, J. Hines, F. Isbell, E. Koller-France, B. König-Ries, H. de Kroon, S. T. Meyer, A. Milcu, J. Müller, C. A. Nock, J. S. Petermann, C. Roscher, C. Scherber, M. Scherer-Lorenzen, B. Schmid, S. A. Schnitzer, A. Schuldt, T. Tscharntke, M. Türke, N. M. van Dam, F. van der Plas, A. Vogel, C. Wagg, D. A. Wardle, A. Weigelt, W. W. Weisser, C. Wirth and M. Jochum (2019). "A multitrophic perspective on biodiversity-ecosystem functioning research." Adv Ecol Res **61**: 1-54.

Ellis, E. C., K. Klein Goldewijk, S. Siebert, D. Lightman and N. Ramankutty (2010). "Anthropogenic transformation of the biomes, 1700 to 2000." Global ecology and biogeography **19**(5): 589-606.

European Commission. (1995 - 2024). "SDG interlinkages visualization tool - Goal level." from https://knowsdgs.jrc.ec.europa.eu/interlinkages/goals.

Felipe-Lucia, M. R., S. Soliveres, C. Penone, M. Fischer, C. Ammer, S. Boch, R. S. Boeddinghaus, M. Bonkowski, F. Buscot, A. M. Fiore-Donno, K. Frank, K. Goldmann, M. M. Gossner, N. Hölzel, M. Jochum, E. Kandeler, V. H. Klaus, T. Kleinebecker, S. Leimer, P. Manning, Y. Oelmann, H. Saiz, P. Schall, M. Schloter, I. Schöning, M. Schrumpf, E. F. Solly, B. Stempfhuber, W. W. Weisser, W. Wilcke, T. Wubet and E. Allan (2020). "Land-use intensity alters networks between biodiversity, ecosystem functions, and services." Proceedings of the National Academy of Sciences **117**(45): 28140-28149.

Fischer, J., D. J. Abson, V. Butsic, M. J. Chappell, J. Ekroos, J. Hanspach, T. Kuemmerle, H. G. Smith and H. von Wehrden (2014). "Land Sparing Versus Land Sharing: Moving Forward." Conservation Letters **7**(3): 149-157.

Fischer, M., O. Bossdorf, S. Gockel, F. Hänsel, A. Hemp, D. Hessenmöller, G. Korte, J. Nieschulze, S. Pfeiffer, D. Prati, S. Renner, I. Schöning, U. Schumacher, K. Wells, F. Buscot, E. K. V. Kalko, K. E. Linsenmair, E.-D. Schulze and W. W. Weisser (2010). "Implementing large-scale and long-term functional biodiversity research: The Biodiversity Exploratories." Basic and Applied Ecology **11**(6): 473-485.

Foley, J. A., R. DeFries, G. P. Asner, C. Barford, G. Bonan, S. R. Carpenter, F. S. Chapin, M. T. Coe, G. C. Daily, H. K. Gibbs, J. H. Helkowski, T. Holloway, E. A. Howard, C. J. Kucharik, C. Monfreda, J. A. Patz, I. C. Prentice, N. Ramankutty and P. K. Snyder (2005). "Global Consequences of Land Use." Science **309**(5734): 570-574.

Foley, J. A., N. Ramankutty, K. A. Brauman, E. S. Cassidy, J. S. Gerber, M. Johnston, N. D. Mueller, C. O'Connell, D. K. Ray, P. C. West, C. Balzer, E. M. Bennett, S. R. Carpenter, J. Hill, C. Monfreda, S. Polasky, J. Rockström, J. Sheehan, S. Siebert, D. Tilman and D. P. M. Zaks (2011). "Solutions for a cultivated planet." Nature **478**(7369): 337-342.

Fornara, D. A. and D. Tilman (2009). "Ecological mechanisms associated with the positive diversity–productivity relationship in an N-limited grassland." Ecology **90**(2): 408-418.

Freschet, G. T., C. Roumet, L. H. Comas, M. Weemstra, A. G. Bengough, B. Rewald, R. D. Bardgett, G. B. De Deyn, D. Johnson, J. Klimešová, M. Lukac, M. L. McCormack, I. C. Meier, L. Pagès, H. Poorter, I. Prieto, N. Wurzburger, M. Zadworny, A. Bagniewska-Zadworna, E. B. Blancaflor, I. Brunner, A. Gessler, S. E. Hobbie, C. M. Iversen, L. Mommer, C. Picon-Cochard, J. A. Postma, L. Rose, P. Ryser, M. Scherer-Lorenzen, N. A. Soudzilovskaia, T. Sun, O. J. Valverde-Barrantes, A. Weigelt, L. M. York and A. Stokes (2021). "Root traits as drivers of plant and ecosystem functioning: current understanding, pitfalls and future research needs." New Phytologist **232**(3): 1123-1158.

Gagic, V., I. Bartomeus, T. Jonsson, A. Taylor, C. Winqvist, C. Fischer, E. M. Slade, I. Steffan-Dewenter, M. Emmerson, S. G. Potts, T. Tscharntke, W. Weisser and R. Bommarco (2015). "Functional identity and diversity of animals predict ecosystem functioning better than species-based indices." Proc Biol Sci **282**(1801): 20142620.

Gaglio, M., V. Aschonitis, G. Castaldelli and E. A. Fano (2020). "Land use intensification rather than land cover change affects regulating services in the mountainous Adige river basin (Italy)." Ecosystem Services **45**: 101158.

Game, E. T., E. Meijaard, D. Sheil and E. McDonald-Madden (2014). "Conservation in a wicked complex world; challenges and solutions." Conservation Letters **7**(3): 271-277.

Garland, G., S. Banerjee, A. Edlinger, E. Miranda Oliveira, C. Herzog, R. Wittwer, L. Philippot, F. T. Maestre and M. G. A. van der Heijden (2021). "A closer look at the functions behind ecosystem multifunctionality: A review." Journal of Ecology **109**(2): 600-613.

Gilbert, G. S. and I. M. Parker (2010). "Rapid evolution in a plant-pathogen interaction and the consequences for introduced host species." Evol Appl **3**(2): 144-156.

Gordon, L. J., G. D. Peterson and E. M. Bennett (2008). "Agricultural modifications of hydrological flows create ecological surprises." Trends in Ecology & Evolution **23**(4): 211-219.

Grace, C., T. M. Boland, H. Sheridan, S. Lott, E. Brennan, R. Fritch and M. B. Lynch (2018). "The effect of increasing pasture species on herbage production, chemical composition and utilization under intensive sheep grazing." Grass and Forage Science **73**(4): 852-864.

Graham, P. H. and C. P. Vance (2003). "Legumes: Importance and Constraints to Greater Use." Plant Physiology **131**(3): 872-877.

Grass, I., P. Batáry and T. Tscharntke (2021). Chapter Six - Combining land-sparing and land-sharing in European landscapes. Advances in Ecological Research. D. A. Bohan and A. J. Vanbergen, Academic Press. **64:** 251-303.

Grenzer, J., A. Kulmatiski, L. Forero, A. Ebeling, N. Eisenhauer and J. Norton (2021). "Moderate plant–soil feedbacks have small effects on the biodiversity–productivity relationship: A field experiment." Ecology and Evolution **11**(17): 11651-11663.

Griffin, J., E. O'Gorman, M. Emmerson, S. Jenkins, A. Klein, M. Loreau and A. Symstad (2009). Biodiversity and the stability of ecosystem functioning.

Guerrero-Ramírez, N., D. Craven, P. Reich, J. Ewel, F. Isbell, J. Koricheva, J. Parrotta, H. Auge, H. Erickson, D. Forrester, A. Hector, J. Joshi, F. Montagnini, C. Palmborg, D. Piotto, C. Potvin, C. Roscher, J. Ruijven, D. Tilman and N. Eisenhauer (2017). "Diversity-dependent temporal divergence of ecosystem functioning in experimental ecosystems." Nature Ecology & Evolution **1**: 1639-1642.

Hamacher, M., C. S. Malisch, T. Reinsch, F. Taube and R. Loges (2021). "Evaluation of yield formation and nutritive value of forage legumes and herbs with potential for diverse grasslands due to their concentration in plant specialized metabolites." European Journal of Agronomy **128**: 126307.

Hasan, S. S., L. Zhen, M. G. Miah, T. Ahamed and A. Samie (2020). "Impact of land use change on ecosystem services: A review." Environmental Development **34**: 100527.

Hector, A. and R. Bagchi (2007). "Biodiversity and ecosystem multifunctionality." Nature **448**(7150): 188-190.

Hector, A., M. Loreau, B. Schmid, C. Beierkuhnlein, M. Caldeira, M. Diemer, P. Dimitrakopoulos, J. A. Finn, H. Freitas, P. Giller, J. Good, R. Harris, P. Högberg, K. Huss-Danell, J. V. B. Joshi, A. Jumpponen, C. Körner, P. Leadley, A. Minns and J. Lawton (2002). Biodiversity manipulation experiments: studies replicated at multiple sites**:** 36-46.

Hector, A., B. Schmid, C. Beierkuhnlein, M. Caldeira, M. Diemer, P. Dimitrakopoulos, J. Finn, H. Freitas, P. Giller, J. Good, R. H. Harris, P. Högberg, K. Huss-Danell, J. Joshi, A. Jumpponen, C. Körner, P. Leadley, M. Loreau, A. Minns and J. Lawton (1999). "Plant Diversity and Productivity Experiments in European Grasslands." Science **286**: 1123-1127.

Hermoso, V., S. Carvalho, S. Giakoumi, D. Goldsborough, S. Katsanevakis, S. Leontiou, V. Markantonatou, B. Rumes, I. Vogiatzakis and K. Yates (2022). "The EU Biodiversity Strategy for 2030: Opportunities and challenges on the path towards biodiversity recovery." Environmental Science & Policy **127**: 263-271.

Hines, J., W. H. van der Putten, G. B. De Deyn, C. Wagg, W. Voigt, C. Mulder, W. W. Weisser, J. Engel, C. Melian, S. Scheu, K. Birkhofer, A. Ebeling, C. Scherber and N. Eisenhauer (2015). Chapter Four - Towards an Integration of Biodiversity–Ecosystem Functioning and Food Web Theory to Evaluate Relationships between Multiple Ecosystem Services. Advances in Ecological Research. G. Woodward and D. A. Bohan, Academic Press. **53:** 161-199.

Hobbie, S. E. (1992). "Effects of plant species on nutrient cycling." Trends in ecology & evolution **7**(10): 336-339.

Hong, P., B. Schmid, F. De Laender, N. Eisenhauer, X. Zhang, H. Chen, D. Craven, H. J. De Boeck, Y. Hautier, O. L. Petchey, P. B. Reich, B. Steudel, M. Striebel, M. P. Thakur and S. Wang (2022). "Biodiversity promotes ecosystem functioning despite environmental change." Ecology Letters **25**(2): 555-569.

Hooper, D. U., E. C. Adair, B. J. Cardinale, J. E. Byrnes, B. A. Hungate, K. L. Matulich, A. Gonzalez, J. E. Duffy, L. Gamfeldt and M. I. O’Connor (2012). "A global synthesis reveals biodiversity loss as a major driver of ecosystem change." Nature **486**(7401): 105-108.

Hooper, D. U., F. S. Chapin, J. Ewel, A. Hector, P. Inchausti, S. Lavorel, J. H. Lawton, D. Lodge, M. Loreau and S. Naeem (2005). "Effects of biodiversity on ecosystem functioning: a consensus of current knowledge." Ecological monographs **75**(1): 3-35.

Huang, M., X. Liu and S. Zhou (2020). "Asynchrony among species and functional groups and temporal stability under perturbations: Patterns and consequences." Journal of Ecology **108**(5): 2038-2046.

Isbell, F., P. R. Adler, N. Eisenhauer, D. Fornara, K. Kimmel, C. Kremen, D. K. Letourneau, M. Liebman, H. W. Polley and S. Quijas (2017). "Benefits of increasing plant diversity in sustainable agroecosystems." Journal of ecology **105**(4): 871-879.

Isbell, F., V. Calcagno, A. Hector, J. Connolly, W. S. Harpole, P. B. Reich, M. Scherer-Lorenzen, B. Schmid, D. Tilman, J. van Ruijven, A. Weigelt, B. J. Wilsey, E. S. Zavaleta and M. Loreau (2011). "High plant diversity is needed to maintain ecosystem services." Nature **477**(7363): 199-202.

Isbell, F., D. Craven, J. Connolly, M. Loreau, B. Schmid, C. Beierkuhnlein, T. M. Bezemer, C. Bonin, H. Bruelheide, E. de Luca, A. Ebeling, J. N. Griffin, Q. Guo, Y. Hautier, A. Hector, A. Jentsch, J. Kreyling, V. Lanta, P. Manning, S. T. Meyer, A. S. Mori, S. Naeem, P. A. Niklaus, H. W. Polley, P. B. Reich, C. Roscher, E. W. Seabloom, M. D. Smith, M. P. Thakur, D. Tilman, B. F. Tracy, W. H. van der Putten, J. van Ruijven, A. Weigelt, W. W. Weisser, B. Wilsey and N. Eisenhauer (2015). "Biodiversity increases the resistance of ecosystem productivity to climate extremes." Nature **526**(7574): 574-577.

Isbell, F., A. Gonzalez, M. Loreau, J. Cowles, S. Díaz, A. Hector, G. M. Mace, D. A. Wardle, M. I. O'Connor and J. E. Duffy (2017). "Linking the influence and dependence of people on biodiversity across scales." Nature **546**(7656): 65-72.

Janssen, P. J. D., M. D. Lambreva, N. Plumeré, C. Bartolucci, A. Antonacci, K. Buonasera, R. N. Frese, V. Scognamiglio and G. Rea (2014). "Photosynthesis at the forefront of a sustainable life." Frontiers in Chemistry **2**.

Jarosz, A. M. and A. L. Davelos (1995). "Effects of disease in wild plant populations and the evolution of pathogen aggressiveness." New Phytologist **129**(3): 371-387.

Jentsch, A., J. Kreyling and C. Beierkuhnlein (2007). "A new generation of climate-change experiments: events, not trends." Frontiers in Ecology and the Environment **5**(7): 365-374.

Jochum, M., M. Fischer, F. Isbell, C. Roscher, F. van der Plas, S. Boch, G. Boenisch, N. Buchmann, J. A. Catford, J. Cavender-Bares, A. Ebeling, N. Eisenhauer, G. Gleixner, N. Hölzel, J. Kattge, V. H. Klaus, T. Kleinebecker, M. Lange, G. Le Provost, S. T. Meyer, R. Molina-Venegas, L. Mommer, Y. Oelmann, C. Penone, D. Prati, P. B. Reich, A. Rindisbacher, D. Schäfer, S. Scheu, B. Schmid, D. Tilman, T. Tscharntke, A. Vogel, C. Wagg, A. Weigelt, W. W. Weisser, W. Wilcke and P. Manning (2020). "The results of biodiversity–ecosystem functioning experiments are realistic." Nature Ecology & Evolution.

Kampa, M. and E. Castanas (2008). "Human health effects of air pollution." Environmental Pollution **151**(2): 362-367.

Ke, P.-J. and J. Wan (2020). "Effects of soil microbes on plant competition: a perspective from modern coexistence theory." Ecological Monographs **90**(1): e01391.

Kiester, A. R. (2013). Species Diversity, Overview. Encyclopedia of Biodiversity (Second Edition). S. A. Levin. Waltham, Academic Press**:** 706-714.

Kirwan, L., J. Connolly, C. Brophy, O. H. Baadshaug, G. Belanger, A. Black, T. Carnus, R. P. Collins, J. Čop and I. Delgado (2014). "The Agrodiversity Experiment: three years of data from a multisite study in intensively managed grasslands."

Kirwan, L., J. Connolly, J. A. Finn, C. Brophy, A. Lüscher, D. Nyfeler and M. T. Sebastià (2009). "Diversity–interaction modeling: estimating contributions of species identities and interactions to ecosystem function." Ecology **90**(8): 2032-2038.

Landwirtschaft, B. f. E. u. (2023). GAP-Strategieplan für die Bundesrepublik Deutschland.

Laureto, L. M. O., M. V. Cianciaruso and D. S. M. Samia (2015). "Functional diversity: an overview of its history and applicability." Natureza & Conservação **13**(2): 112-116.

Lee, H. and S. Lautenbach (2016). "A quantitative review of relationships between ecosystem services." Ecological Indicators **66**: 340-351.

Lefcheck, J. S., J. E. Byrnes, F. Isbell, L. Gamfeldt, J. N. Griffin, N. Eisenhauer, M. J. Hensel, A. Hector, B. J. Cardinale and J. E. Duffy (2015). "Biodiversity enhances ecosystem multifunctionality across trophic levels and habitats." Nature communications **6**(1): 1-7.

Lima, F. P. and D. S. Wethey (2012). "Three decades of high-resolution coastal sea surface temperatures reveal more than warming." Nature Communications **3**(1): 704.

Loreau, M. and A. Hector (2001). "Partitioning selection and complementarity in biodiversity experiments." Nature **412**(6842): 72-76.

Loreau, M., S. Naeem, P. Inchausti, J. Bengtsson, J. P. Grime, A. Hector, D. U. Hooper, M. A. Huston, D. Raffaelli, B. Schmid, D. Tilman and D. A. Wardle (2001). "Biodiversity and ecosystem functioning: current knowledge and future challenges." Science **294**(5543): 804-808.

Lusiana, B., M. van Noordwijk and G. Cadisch (2012). "Land sparing or sharing? Exploring livestock fodder options in combination with land use zoning and consequences for livelihoods and net carbon stocks using the FALLOW model." Agriculture, Ecosystems & Environment **159**: 145-160.

Maciá-Vicente, J. G., D. Francioli, A. Weigelt, C. Albracht, K. E. Barry, F. Buscot, A. Ebeling, N. Eisenhauer, J. Hennecke, A. Heintz-Buschart, J. van Ruijven and L. Mommer (2023). "The structure of root-associated fungal communities is related to the long-term effects of plant diversity on productivity." Molecular Ecology **32**(13): 3763-3777.

Maes, J., M. Paracchini, G. Zulian, M. Dunbar and R. Alkemade (2012). "Synergies and trade-offs between ecosystem service supply, biodiversity, and habitat conservation status in Europe." Biological conservation **155**: 1-12.

Mahecha, M. D., A. Bastos, F. J. Bohn, N. Eisenhauer, H. Feilhauer, H. Hartmann, T. Hickler, H. Kalesse-Los, M. Migliavacca and F. E. Otto (2022). "Biodiversity loss and climate extremes—study the feedbacks." Nature **612**(7938): 30-32.

Malézieux, E., Y. Crozat, C. Dupraz, M. Laurans, D. Makowski, H. Ozier-Lafontaine, B. Rapidel, S. De Tourdonnet and M. Valantin-Morison (2009). "Mixing plant species in cropping systems: concepts, tools and models: a review." Sustainable agriculture: 329-353.

Mancuso, F. P., C. Giommi, M. C. Mangano, L. Airoldi, B. Helmuth and G. Sarà (2023). "Evenness, biodiversity, and ecosystem function of intertidal communities along the Italian coasts: Experimental short-term response to ambient and extreme air temperatures." Science of The Total Environment **858**: 160037.

Manning, P., J. Loos, A. D. Barnes, P. Batáry, F. J. J. A. Bianchi, N. Buchmann, G. B. De Deyn, A. Ebeling, N. Eisenhauer, M. Fischer, J. Fründ, I. Grass, J. Isselstein, M. Jochum, A. M. Klein, E. O. F. Klingenberg, D. A. Landis, J. Lepš, R. Lindborg, S. T. Meyer, V. M. Temperton, C. Westphal and T. Tscharntke (2019). Transferring biodiversity-ecosystem function research to the management of ‘real-world’ ecosystems. Advances in Ecological Research. N. Eisenhauer, D. A. Bohan and A. J. Dumbrell, Academic Press. **61:** 323-356.

Manning, P., F. van der Plas, S. Soliveres, E. Allan, F. T. Maestre, G. Mace, M. J. Whittingham and M. Fischer (2018). "Redefining ecosystem multifunctionality." Nat Ecol Evol **2**(3): 427-436.

Meyer, S. T., A. Ebeling, N. Eisenhauer, L. Hertzog, H. Hillebrand, A. Milcu, S. Pompe, M. Abbas, H. Bessler, N. Buchmann, E. De Luca, C. Engels, M. Fischer, G. Gleixner, A. Hudewenz, A.-M. Klein, H. de Kroon, S. Leimer, H. Loranger, L. Mommer, Y. Oelmann, J. M. Ravenek, C. Roscher, T. Rottstock, C. Scherber, M. Scherer-Lorenzen, S. Scheu, B. Schmid, E.-D. Schulze, A. Staudler, T. Strecker, V. Temperton, T. Tscharntke, A. Vogel, W. Voigt, A. Weigelt, W. Wilcke and W. W. Weisser (2016). "Effects of biodiversity strengthen over time as ecosystem functioning declines at low and increases at high biodiversity." Ecosphere **7**(12): e01619.

Meyer, S. T., R. Ptacnik, H. Hillebrand, H. Bessler, N. Buchmann, A. Ebeling, N. Eisenhauer, C. Engels, M. Fischer, S. Halle, A. M. Klein, Y. Oelmann, C. Roscher, T. Rottstock, C. Scherber, S. Scheu, B. Schmid, E. D. Schulze, V. M. Temperton, T. Tscharntke, W. Voigt, A. Weigelt, W. Wilcke and W. W. Weisser (2018). "Biodiversity-multifunctionality relationships depend on identity and number of measured functions." Nat Ecol Evol **2**(1): 44-49.

Milcu, A., S. Partsch, C. Scherber, W. W. Weisser and S. Scheu (2008). "Earthworms and legumes control litter decomposition in a plant diversity gradient." Ecology **89**(7): 1872-1882.

Millennium Ecosystem Assessment (2005). Ecosystems and human well-being, Island press Washington, DC:.

Mittelbach, G. G. and B. J. McGill (2019). Community ecology, Oxford University Press.

Moral, R. d. A., J. Connolly, R. Vishwakarma and C. Brophy (2022). DImodels: Diversity-Interactions (DI) Models. R package.

Morison, J. I. and M. D. Morecroft (2006). "Plant growth and climate change."

Morris, E. K., T. Caruso, F. Buscot, M. Fischer, C. Hancock, T. S. Maier, T. Meiners, C. Müller, E. Obermaier, D. Prati, S. A. Socher, I. Sonnemann, N. Wäschke, T. Wubet, S. Wurst and M. C. Rillig (2014). "Choosing and using diversity indices: insights for ecological applications from the German Biodiversity Exploratories." Ecol Evol **4**(18): 3514-3524.

Mouillot, D., S. Villéger, M. Scherer-Lorenzen and N. W. H. Mason (2011). "Functional Structure of Biological Communities Predicts Ecosystem Multifunctionality." PLOS ONE **6**(3): e17476.

Naeem, S. (1998). "Species redundancy and ecosystem reliability." Conservation biology **12**(1): 39-45.

Naeem, S., L. J. Thompson, S. P. Lawler, J. H. Lawton and R. M. Woodfin (1994). "Declining biodiversity can alter the performance of ecosystems." Nature **368**(6473): 734-737.

Nations, U. "The 17 Goals." Retrieved 06.01.2024, from https://sdgs.un.org/goals.

Nerlekar, A. N. and J. W. Veldman (2020). "High plant diversity and slow assembly of old-growth grasslands." Proceedings of the National Academy of Sciences **117**(31): 18550-18556.

Northfield, T. D., G. B. Snyder, A. R. Ives and W. E. Snyder (2010). "Niche saturation reveals resource partitioning among consumers." Ecology Letters **13**(3): 338-348.

Oliveira, B. F., F. C. Moore and X. Dong (2022). "Biodiversity mediates ecosystem sensitivity to climate variability." Communications Biology **5**(1): 628.

Pattberg, P. and K. Bäckstrand (2023). "Enhancing the achievement of the SDGs: lessons learned at the half-way point of the 2030 Agenda." International Environmental Agreements: Politics, Law and Economics **23**(2): 107-114.

Perkins-Kirkpatrick, S., L. Alexander and J. Nairn (2012). "Increasing frequency, intensity and duration of observed global heatwaves and warm spells." Geophysical Research Letters **39**: 20714.

Perrings, C., C. Folke and K.-G. Mäler (1992). "The ecology and economics of biodiversity loss: the research agenda." Ambio: 201-211.

Petermann, J. S. and O. Y. Buzhdygan (2021). "Grassland biodiversity." Current Biology **31**(19): R1195-R1201.

Plutino, M., E. Bianchetto, A. Durazzo, M. Lucarini, L. Lucini and I. Negri (2022). "Rethinking the Connections between Ecosystem Services, Pollinators, Pollution, and Health: Focus on Air Pollution and Its Impacts." International Journal of Environmental Research and Public Health **19**(5): 2997.

Power, J. F. (1987). "Legumes: Their potential role in agricultural production." American Journal of Alternative Agriculture **2**(2): 69-73.

Prangel, E., L. Kasari-Toussaint, L. Neuenkamp, N. Noreika, R. Karise, R. Marja, N. Ingerpuu, T. Kupper, L. Keerberg, E. Oja, M. Meriste, A. Tiitsaar, M. Ivask and A. Helm (2023). "Afforestation and abandonment of semi-natural grasslands lead to biodiversity loss and a decline in ecosystem services and functions." Journal of Applied Ecology **60**(5): 825-836.

Qiu, J., S. R. Carpenter, E. G. Booth, M. Motew and C. J. Kucharik (2020). "Spatial and temporal variability of future ecosystem services in an agricultural landscape." Landscape Ecology **35**(11): 2569-2586.

Queiroz, C., R. Beilin, C. Folke and R. Lindborg (2014). "Farmland abandonment: threat or opportunity for biodiversity conservation? A global review." Frontiers in Ecology and the Environment **12**(5): 288-296.

Reich, P. B., D. Tilman, F. Isbell, K. Mueller, S. E. Hobbie, D. F. Flynn and N. Eisenhauer (2012). "Impacts of biodiversity loss escalate through time as redundancy fades." Science **336**(6081): 589-592.

Resolution, G. A. (2015). "Transforming our world: the 2030 Agenda for Sustainable Development." UN Doc. A/RES/70/1 (September 25, 2015).

Reynolds, H. L., A. Packer, J. D. Bever and K. Clay (2003). "Grassroots ecology: plant–microbe–soil interactions as drivers of plant community structure and dynamics." Ecology **84**(9): 2281-2291.

Ringler, A. (1995). Landschaftspflegekonzept Bayern. 1. Einführung-Ziele der Landschaftspflege in Bayern, Bayerisches Staatsministerium für Landesentwicklung und Umweltfragen.

Ritchie, H. R., Max. (2019). "Land Use." from https://ourworldindata.org/land-use.

Rodriguez, J. P., T. D. Beard Jr, E. M. Bennett, G. S. Cumming, S. J. Cork, J. Agard, A. P. Dobson and G. D. Peterson (2006). "Trade-offs across space, time, and ecosystem services." Ecology and Society **11**(1).

Rosa-Schleich, J., J. Loos, O. Mußhoff and T. Tscharntke (2019). "Ecological-economic trade-offs of Diversified Farming Systems – A review." Ecological Economics **160**: 251-263.

Roscher, C., J. Schumacher, J. Baade, W. Wilcke, G. Gleixner, W. W. Weisser, B. Schmid and E.-D. Schulze (2004). "The role of biodiversity for element cycling and trophic interactions: an experimental approach in a grassland community." Basic and Applied Ecology **5**(2): 107-121.

Roscher, C., J. Schumacher, M. Gubsch, A. Lipowsky, A. Weigelt, N. Buchmann, B. Schmid and E.-D. Schulze (2012). "Using plant functional traits to explain diversity–productivity relationships." PloS one **7**(5): e36760.

Rubanschi, S., S. T. Meyer, C. Hof and W. W. Weisser (2023). "Modelling potential biotope composition on a regional scale revealed that climate variables are stronger drivers than soil variables." Diversity and Distributions **29**(4): 492-508.

Sánchez-Bayo, F. and K. A. G. Wyckhuys (2019). "Worldwide decline of the entomofauna: A review of its drivers." Biological Conservation **232**: 8-27.

Scharlemann, J. P. W., R. C. Brock, N. Balfour, C. Brown, N. D. Burgess, M. K. Guth, D. J. Ingram, R. Lane, J. G. C. Martin, S. Wicander and V. Kapos (2020). "Towards understanding interactions between Sustainable Development Goals: the role of environment–human linkages." Sustainability Science **15**(6): 1573-1584.

Scherber, C., N. Eisenhauer, W. W. Weisser, B. Schmid, W. Voigt, M. Fischer, E.-D. Schulze, C. Roscher, A. Weigelt and E. Allan (2010). "Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment." Nature **468**(7323): 553-556.

Schmid, B., M. Baruffol, Z. Wang and P. A. Niklaus (2017). "A guide to analyzing biodiversity experiments." Journal of Plant Ecology **10**(1): 91-110.

Schmid, M. W., S. J. van Moorsel, T. Hahl, E. De Luca, G. B. De Deyn, C. Wagg, P. A. Niklaus and B. Schmid (2021). "Effects of plant community history, soil legacy and plant diversity on soil microbial communities." Journal of Ecology **109**(8): 3007-3023.

Schmidt, O., R. O. Clements and G. Donaldson (2003). "Why do cereal–legume intercrops support large earthworm populations?" Applied Soil Ecology **22**(2): 181-190.

Semchenko, M., S. Saar and A. Lepik (2017). "Intraspecific genetic diversity modulates plant–soil feedback and nutrient cycling." New Phytologist **216**(1): 90-98.

Shipley, B. (2016). Cause and correlation in biology: a user's guide to path analysis, structural equations and causal inference with R, Cambridge university press.

Sidemo-Holm, W., J. Ekroos and H. G. Smith (2021). "Land sharing versus land sparing—What outcomes are compared between which land uses?" Conservation Science and Practice **3**(11): e530.

Singh, J., E. Cameron, T. Reitz, M. Schädler and N. Eisenhauer (2021). "Grassland management effects on earthworm communities under ambient and future climatic conditions." European Journal of Soil Science **72**(1): 343-355.

Slade, E. M., R. Bagchi, N. Keller and C. D. Philipson (2019). "When Do More Species Maximize More Ecosystem Services?" Trends in Plant Science **24**(9): 790-793.

Sollenberger, L., M. Moura Kohmann, J. Dubeux Jr and M. Silveira (2019). "Grassland Management Affects Delivery of Regulating and Supporting Ecosystem Services." Crop Science **59**.

Stagnari, F., A. Maggio, A. Galieni and M. Pisante (2017). "Multiple benefits of legumes for agriculture sustainability: an overview." Chemical and Biological Technologies in Agriculture **4**(1): 2.

Stange, M., R. D. H. Barrett and A. P. Hendry (2021). "The importance of genomic variation for biodiversity, ecosystems and people." Nature Reviews Genetics **22**(2): 89-105.

Stoate, C., A. Baldi, P. Beja, N. Boatman, I. Herzon, A. Van Doorn, G. De Snoo, L. Rakosy and C. Ramwell (2009). "Ecological impacts of early 21st century agricultural change in Europe–a review." Journal of environmental management **91**(1): 22-46.

Stroud, J. L. (2019). "Soil health pilot study in England: Outcomes from an on-farm earthworm survey." PLoS One **14**(2): e0203909.

Tälle, M., E. Öckinger, T. Löfroth, L. B. Pettersson, H. G. Smith, M. Stjernman and T. Ranius (2023). "Land sharing complements land sparing in the conservation of disturbance-dependent species." Ambio **52**(3): 571-584.

Temperton, V., R. Hobbs, T. Nuttle and S. Halle (2004). ASSEMBLY RULES AND RESTORATION ECOLOGY Bridging the Gap Between Theory and Practice New from Island Press The Science and Practice of Ecological Restoration Series.

The Jena Experiment. (2024). "ΔBEF Experiment." from https://the-jena-experiment.de/index.php/bef-experiment/.

The World Counts. (2024). "The World Counts - World Population." Retrieved 20.03.2024, from https://www.theworldcounts.com/populations/world/people.

Tilman, D. (1994). "Competition and Biodiversity in Spatially Structured Habitats." Ecology **75**(1): 2-16.

Tilman, D. and J. A. Downing (1994). "Biodiversity and stability in grasslands." Nature **367**(6461): 363-365.

Tilman, D., F. Isbell and J. M. Cowles (2014). "Biodiversity and Ecosystem Functioning." Annual Review of Ecology, Evolution, and Systematics **45**(1): 471-493.

Tilman, D., P. B. Reich and F. Isbell (2012). "Biodiversity impacts ecosystem productivity as much as resources, disturbance, or herbivory." Proceedings of the National Academy of Sciences **109**(26): 10394-10397.

Tilman, D., P. B. Reich, J. Knops, D. Wedin, T. Mielke and C. Lehman (2001). "Diversity and productivity in a long-term grassland experiment." Science **294**(5543): 843-845.

Tilman, D., P. B. Reich and J. M. Knops (2006). "Biodiversity and ecosystem stability in a decade-long grassland experiment." Nature **441**(7093): 629-632.

Trenberth, K. E. (2011). "Changes in precipitation with climate change." Climate research **47**(1-2): 123-138.

Truchy, A., D. G. Angeler, R. A. Sponseller, R. K. Johnson and B. G. McKie (2015). Linking Biodiversity, Ecosystem Functioning and Services, and Ecological Resilience. Ecosystem Services - From Biodiversity to Society, Part 1**:** 55-96.

Tscharntke, T., I. Grass, T. C. Wanger, C. Westphal and P. Batáry (2021). "Beyond organic farming - harnessing biodiversity-friendly landscapes." Trends in Ecology & Evolution **36**(10): 919-930.

United Nations (2023). The sustainable development goals report 2023: Special edition, United Nations: Department of Economic and Social Affairs.

van der Plas, F. (2019). "Biodiversity and ecosystem functioning in naturally assembled communities." Biol Rev Camb Philos Soc **94**(4): 1220-1245.

van der Plas, F., T. Schröder-Georgi, A. Weigelt, K. Barry, S. Meyer, A. Alzate, R. L. Barnard, N. Buchmann, H. de Kroon, A. Ebeling, N. Eisenhauer, C. Engels, M. Fischer, G. Gleixner, A. Hildebrandt, E. Koller-France, S. Leimer, A. Milcu, L. Mommer, P. A. Niklaus, Y. Oelmann, C. Roscher, C. Scherber, M. Scherer-Lorenzen, S. Scheu, B. Schmid, E.-D. Schulze, V. Temperton, T. Tscharntke, W. Voigt, W. Weisser, W. Wilcke and C. Wirth (2020). "Plant traits alone are poor predictors of ecosystem properties and long-term ecosystem functioning." Nature Ecology & Evolution.

Vilà, M., J. L. Espinar, M. Hejda, P. E. Hulme, V. Jarošík, J. L. Maron, J. Pergl, U. Schaffner, Y. Sun and P. Pyšek (2011). "Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems." Ecology letters **14**(7): 702-708.

Vogel, A., A. Ebeling, G. Gleixner, C. Roscher, S. Scheu, M. Ciobanu, E. Koller-France, M. Lange, A. Lochner, S. T. Meyer, Y. Oelmann, W. Wilcke, B. Schmid and N. Eisenhauer (2019). Chapter Seven - A new experimental approach to test why biodiversity effects strengthen as ecosystems age. Advances in Ecological Research. N. Eisenhauer, D. A. Bohan and A. J. Dumbrell, Academic Press. **61:** 221-264.

Wagg, C., C. Roscher, A. Weigelt, A. Vogel, A. Ebeling, E. de Luca, A. Roeder, C. Kleinspehn, V. M. Temperton, S. T. Meyer, M. Scherer-Lorenzen, N. Buchmann, M. Fischer, W. W. Weisser, N. Eisenhauer and B. Schmid (2022). "Biodiversity–stability relationships strengthen over time in a long-term grassland experiment." Nature Communications **13**(1): 7752.

Waldén, E. (2018). Restoration of semi-natural grasslands: Impacts on biodiversity, ecosystem services and stakeholder perceptions, Department of Physical Geography, Stockholm University.

Weed, A. S., M. P. Ayres and J. A. Hicke (2013). "Consequences of climate change for biotic disturbances in North American forests." Ecological Monographs **83**(4): 441-470.

Weisser, W. W., C. Roscher, S. T. Meyer, A. Ebeling, G. Luo, E. Allan, H. Beßler, R. L. Barnard, N. Buchmann and F. Buscot (2017). "Biodiversity effects on ecosystem functioning in a 15-year grassland experiment: Patterns, mechanisms, and open questions." Basic and Applied Ecology **23**: 1-73.

Whitfield, K. and G. Fanjul. (2021). "Sustainable Development Goals." Retrieved 14.04.2024, 2024, from https://www.isglobal.org/en/-/sdgs-and-global-health.

Wikipedia. (2021). "Dans-la-prairie-by-Claude." Retrieved 20.04.2024, 2024, from https://de.wikipedia.org/wiki/Datei:Dans-la-prairie-by-Claude-001.jpg#file.

Wilcox, K. R., A. T. Tredennick, S. E. Koerner, E. Grman, L. M. Hallett, M. L. Avolio, K. J. La Pierre, G. R. Houseman, F. Isbell and D. S. Johnson (2017). "Asynchrony among local communities stabilises ecosystem function of metacommunities." Ecology letters **20**(12): 1534-1545.

Wu, D., C. Xu, S. Wang, L. Zhang and S. Kortsch (2023). "Why are biodiversity—ecosystem functioning relationships so elusive? Trophic interactions may amplify ecosystem function variability." Journal of Animal Ecology **92**(2): 367-376.

Zink, M., L. Samaniego, R. Kumar, S. Thober, J. Mai, D. Schäfer and A. Marx (2016). "The German drought monitor." Environmental Research Letters **11**(7): 074002.

Appendix: Chapter 1

Grasses and plant diversity determine the foliar pathogen damage of grassland plant communities of different community histories

The article is available upon request (please get in touch with laura.argens@tum.de).

Appendix: Chapter 2

Relationships between ecosystem functions vary among years and plots and are driven by plant species richness

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Appendix: Chapter 3

Functional group richness increases multifunctionality in intensively managed grasslands

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