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Eco-evolutionary dynamics in grasslands during land use change: consequences for plant-microbe interactions and ecosystem function

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Abstract

1. Land use change can cause the loss of plant species and functional diversity, but whether it drives eco-evolutionary changes within plant species is unclear.

2. Semi-natural grasslands are particularly threatened by land use change, including management intensification on productive soils and abandonment on marginal land. As such, they serve as an excellent system for exploring if and how land use change causes evolutionary changes within plant populations and what their wider consequences could be.

3. Here we synthesise what is known about land use impacts at the plant community and ecosystem level, build predictions on potential evolutionary responses and review empirical evidence available to date. We predict that land use intensification and abandonment may cause genetic and functional shifts in grassland plant populations, disrupt plant-microbial associations and create eco-evolutionary feedbacks that impact wider ecosystem processes. Evolutionary responses to land use may also undermine the adaptive potential of plant species to future climate change.

4. *Synthesis*: This review highlights the lack of studies on eco-evolutionary dynamics in ecosystems under land use change, despite their potential importance for the functioning and stability of plant and soil communities and the ecosystem processes that they maintain.

Introduction

Land use change is a major factor driving biodiversity loss and the erosion of functioning in ecosystems worldwide (Laliberté et al., 2010; Allan et al., 2015; Felipe-Lucia et al. 2020). In plant communities, shifts in land use affect ecological dynamics by modifying the availability of key resources (such as soil nutrients; reviewed by Suding et al., 2005; Schils et al., 2022), changing the area and connectivity of habitats (reviewed by Eriksson et al., 2002; Cousins, 2009), and altering species composition (reviewed by Gerstner et al., 2017). While it is well known that land use change has major impacts on the diversity and composition of plant (Kull & Zobel, 1991; reviewed by Suding et al., 2005; Schils et al., 2022) and soil communities (de Vries et al., 2012a, 2012b; Tsiafouli et al., 2015), it is only recently that evidence has emerged to suggest that long-term land use change can also generate evolutionary shifts within plant populations (Odat et al., 2004; Helm et al., 2009; Pluess, 2013; Völler et al., 2013, 2017; Aavik et al., 2019). Moreover, land use change may also disrupt the plant-microbial interactions that underlie key soil functions, such as carbon and nutrient cycling (Donnison et al., 2000; Legay et al., 2014; Thion et al., 2016; Huang et al., 2019; Pichon et al., 2020). Despite these advances, the prevalence and wider consequences of eco-evolutionary changes in plant and microbial systems during land use change for biodiversity and ecosystem functioning remain unknown.

Semi-natural grasslands are unique biodiversity hotspots that provide essential ecosystem services, such as sustaining soil fertility and water quality (Heidenreich, 2009; Bengtsson et al., 2019; Lange et al., 2021) and mitigating the effects of climate change (De Deyn et al., 2011; O'Mara, 2012; Bengtsson et al., 2019). These ecosystems are particularly threatened by recent changes in land use (Strijker, 2005; Silva et al., 2008; Sollenberger et al., 2019) and can therefore serve as model systems to explore the potential impact of land use change on eco-evolutionary dynamics within plant species as well as its wider consequences for ecosystem functions and resilience to climate change. Semi-natural grasslands have been shaped by centuries of human activity; typically, they have been grazed by livestock at low intensities and/or cut for hay (which is used for fodder; Bignal & McCracken, 1996; Eriksson et al., 2002). These practices maintain high plant species richness in environments that would otherwise be dominated by trees and/or shrubs (Wilson et al., 2012; Habel et al., 2013; Nerlekar & Veldman, 2020).

Though semi-natural grasslands were once widespread, the area of these ecosystems has declined dramatically during the last century (especially in Europe, where they are of high conservation value; Poschlod & WallisDeVries, 2002; Ramankutty et al., 2008; Janišová et al., 2011). Vast areas of semi-natural grasslands on fertile soils have been subject to land use intensification (Estel et al., 2018), boosting productivity at the expense of plant species richness and ecosystem services (Diekmann et al., 2019). At the other extreme, grazing and/or mowing has been progressively abandoned on less fertile or poorly accessible grasslands, leading to plant community turnover (Poschlod & WallisDeVries, 2002; Poschlod et al., 2005; Strijker, 2005; Habel et al., 2013) and loss of below-ground biodiversity (Schrama et al., 2023) and soil multi-functionality (Peco et al., 2017).

Here, we synthesize recent advances in our knowledge about land use intensification and abandonment in semi-natural grasslands. In doing so, our goal is to illustrate the potential for land use change to drive eco-evolutionary shifts in plant populations and their interactions with associated soil microbes. We also aim to highlight potentially important consequences for ecosystem functioning and the resilience of grasslands to future environmental change. First, we discuss how land use intensification and abandonment may generate genetic and functional changes in grassland plant populations. We then apply what is known about land use impacts on plant communities to make predictions about the potential directions of evolutionary change within plant populations. Next, we consider how this may disrupt plant-microbe associations, including with those microbes responsible for carbon and nutrient cycling. We then discuss how land use change may cause eco-evolutionary feedbacks that affect the adaptive potential of grassland plant populations to future perturbations, such as extreme weather events expected with climate change. With this review, we aim to inform future research and increase fundamental understanding of the eco-evolutionary responses of plant species to land use change.

Predicting the impacts of land use change on genetic diversity and functional traits within plant species

Plants are known for their potential to locally adapt to natural variation in environmental conditions (reviewed by Hoeksema & Forde, 2008; Leimu & Fischer, 2008; Oduor et al., 2016; Rúa et al., 2016) as well as respond rapidly to the selective pressures imposed by global change factors (Lortie & Hierro, 2021; Delavaux et al., 2022; Santangelo et al., 2022). During land use intensification in grasslands, changes in resource availability are driven by the application of inorganic fertilisers and/or manures (Fig. 1). Following nutrient enrichment, plant growth and vegetation height increase and communities shift away from nutrient limitation and towards light limitation (Vojtech et al., 2007; Hautier et al., 2009; Borer et al., 2014; Eskelinen et al., 2022). Higher intensity of grazing and/or mowing may occur alongside fertilisation. During grassland abandonment, cessation of grazing and/or mowing (Fig. 1) also results in increased vegetation height and light limitation and is accompanied by litter accumulation and the encroachment of woody species over time (reviewed by Ratajczak et al., 2012). In both intensified and abandoned grasslands, these environmental changes may impose new selective pressures and generate evolutionary changes in plant populations (Fig. 1).

Empirical studies in semi-natural grasslands suggest that land use intensification and abandonment can result in: i) genetic differentiation among plant populations (Snaydon & Davies, 1982; Völler et al., 2017); ii) changes in genetic diversity within or among populations (Odat et al., 2004; Silvertown et al., 2009; Stöcklin et al., 2009; Busch & Reisch, 2016); and/or iii) shifts in plant traits/phenotypes among populations (Snaydon, 1970; Snaydon & Davies, 1972; Davies & Snaydon, 1974, 1976; Lindborg et al., 2005; Völler et al., 2012, 2013). However, for almost every aspect of the response of grassland plants to land use change, our knowledge of how communities react exceeds our awareness of the changes that occur within species (Fig. 2 & Table S1). Furthermore, for some important plant traits that could be affected by land use change, such as root exudation and disease resistance, few or no studies currently exist, highlighting the need for additional research.

Genetic diversity within plant populations during land use change

In semi-natural grasslands, declines in plant genetic diversity during land use change are expected to occur due to reduced local population sizes (reviewed by Honnay & Jacquemyn, 2007) in parallel with habitat loss and fragmentation at the landscape level (reviewed by Picó & van Groenendael, 2007). Land use intensification reduces the local population sizes of grassland specialist species adapted to low soil nutrient levels (reviewed by Suding et al., 2005; Laliberté et al., 2010; Habel et al., 2013; Dengler et al., 2014; Schils et al., 2022) as these species are replaced by populations of fast-growing species that are better able to utilize nutrient additions (Craine et al., 2001; Louault et al., 2005; van Diggelen et al., 2005; Díaz et al., 2007; Doležal et al., 2018). Similarly, abandonment reduces the local population sizes of grassland specialists as they are replaced by encroaching species (Bakker et al., 1980; Willems, 1983; Lindborg et al., 2005; Johansson et al., 2008; Lehtilä et al., 2016), resulting in genetic bottlenecks and increasing the effect of genetic drift (Busch &

Reisch, 2016; Lehmair et al., 2020). In regions where grassland management has been abandoned at a landscape scale, loss of connectivity impedes gene flow between populations, further reducing within-population genetic diversity (Prentice et al., 2006; Honnay et al., 2007; Helm et al., 2009; Aavik et al., 2019; Lehmair et al., 2020; Pagel et al., 2020; Reinula et al., 2021).

Few empirical studies have quantified changes in population genetic diversity in response to land use change, rendering predictions challenging (reviewed by Pluess, 2013). While negative effects on genetic variation have been found in some populations undergoing intensification or abandonment (relative to extensively managed counterparts; Busch & Reisch, 2016), positive effects on genetic and phenotypic diversity have been reported in others (for intensification effects see Silvertown et al., 2009; Völler et al., 2013; abandonment effects in Träger et al. 2021).

The effect of specific land use changes on genetic diversity within species could depend on species' traits. Slow-growing species typically experience strong declines in population size during land use change (which may reduce genetic diversity), while populations of fast-growing species should remain stable or increase; however, evidence is scarce to test this relationship. The speed of genetic diversity loss may also vary among species, with annual and short-lived plants reacting quicker than long-lived perennials (Epps & Keyghobadi, 2015; Reinula et al., 2021), potentially increasing variability in population-level responses to land use change.

Empirical evidence demonstrates that there is generally no correlation between grassland species richness and genetic diversity of specialist grassland plants (Odat et al., 2010; Reisch & Schmid, 2019; Reisch & Hartig, 2020). This could occur if the effects of land use change on plant populations *versus* species richness are driven by different factors and/or occur at different spatial and temporal scales. Population genetic diversity is predominantly influenced by population size and habitat connectivity as well as environmental selection (Leimu et al., 2006). In contrast, species richness at a grassland site is largely defined by macroevolutionary processes that led to a particular set of species being adapted to its' given environmental conditions; a set which is then modified by local dispersal and species interactions (i.e., species pool theory; Taylor, 1990; Zobel, 1997, 2016). In addition, species richness may respond to habitat loss and management abandonment with considerable time lags, leading to extinction debt (Hanski & Ovaskainen, 2002; reviewed by Eriksson et al., 2002; Cousins, 2009; Kuussaari et al., 2009; Saran et al., 2019). Reductions in genetic diversity are likely to occur more rapidly (although lagged responses have also been observed, e.g., Münzbergova et al., 2013; Aavik et al., 2019). Thus, we cannot rely on community-level observations of species loss to predict changes in species' genetic diversity. To make generalisations, additional studies that quantify genetic variation in plant populations under land use change are needed.

Heritable shifts in functional traits within plant populations undergoing land use change

Land use change can cause directional shifts in a wide range of plant phenotypic traits (Fig. 2). However, our knowledge and mechanistic understanding of intraspecific trait shifts under land use change is limited. This is because trait patterns observed in the field may be caused by genetic effects as well as epigenetic effects (Richards, 2011; Jablonka, 2017; Cavalli & Heard, 2019), which can be heritable (e.g., maternal effects; Roach & Wulff, 1987) or transient, such as in the case of phenotypic plasticity (i.e., the ability of a genotype to produce variable phenotypes; reviewed by Sultan, 2000; Callaway et al., 2003; Fig. 1). Below we present predictions regarding potential evolutionary trait shifts in response to land use change based on what we know about trait changes at the plant community level. We also review existing evidence at the population level. We predict that land use change can result in functional shifts within two broad categories of traits: (1) traits related to resource acquisition *versus* defence and (2) reproductive traits. While shifts in traits related to resource acquisition and tissue defence can alter ecological interactions with consequences for ecosystem functions, changes in reproductive traits could be important for population persistence by determining the rate of generation of new genetic variants and hence adaptive potential.

(1) Evolutionary shifts in traits related to resource acquisition and defence

The plant economics spectrum describes a range of variation in plant growth strategies where plants can either maximize growth rate and resource acquisition (characterized by high specific leaf area and high tissue nitrogen content) or invest in tissue protection (resulting in increased tissue density; Wright et al, 2004; Weigelt et al., 2021); this is also known as the growth-defence trade-off (Coley et al., 1985; reviewed by Smakowska et al., 2016; Monson et al., 2021). Plant height forms another key axis of variation in plant growth strategies, reflecting competitive ability for light and dispersal potential (Díaz et al., 2016).

Light limitation in the dense vegetation characterizing fertilised and abandoned grasslands causes shifts in plant species composition along these trait axes. Intensive land use favors the dominance of tall plant species with resource-acquisitive traits, such as fast growth, higher nitrogen content, and reduced tissue dry matter content and longevity (Fig. 2; reviewed by Díaz et al., 2007; Craine et al., 2001; Garnier et al., 2007; Johnson et al., 2008; Chollet et al., 2014; Neyret et al., 2024). The encroachment of woody species after grassland abandonment also favors tall species with strategies of either shade avoidance or tolerance (Wahlman & Milberg, 2002; Kahmen & Poschlod, 2004; van Diggelen et al., 2005; Saar et al., 2012; Joyce, 2014; Neuenkamp et al., 2016; Nielsen et al., 2021).

Based on these community-level observations, we predict that plant genotypes with traits enhancing competitive ability for light (such as increased stature, high tissue nitrogen content, high specific leaf area, and fast resource acquisition) should become more dominant within plant species following land use intensification or abandonment (Fig. 2). Shifts towards more competitive traits should occur alongside reduced tissue protection (i.e., reduced leaf and root dry matter content), and hence higher susceptibility to abiotic and biotic stress. To date, the only study examining heritable changes in response to land use intensification in the form of controlled application of lime and fertilisers found support for enhanced competitive ability in fertilised populations expressed as increased plant height and biomass (Snaydon & Davies, 1972). However, limited heritable changes in height and biomass were detected in studies where fertilisation was accompanied by more intense mowing, which may have counteracted selection for higher stature and fast growth (Völler et al., 2013, 2017).

(2) Evolutionary shifts in reproductive traits

In grassland communities, intensified mowing favors early-flowering species (van Diggelen et al., 2005) while fertilisation and frequent mowing leads to reduced seed regeneration potential (Klaus et al., 2018). This suggests that land-use intensification can impose a selective pressure towards earlier-flowering and reduced seed reproduction within species. In agreement with this prediction, mowing and grazing intensification caused heritable shifts in flowering phenology away from the time of biomass removal in *Bromus hordeaceous* (Völler et al., 2013). More intense grazing reduced reproductive allocation (i.e., seed reproduction, seed mass, or seed number) in *B. hordeaceous* and four other grassland species (Völler et al., 2017). On the contrary, fertilisation alone caused a heritable shift towards higher allocation to seed production in *Anthoxanthum odoratum* (Snaydon & Davies, 1972).

In abandoned grasslands, loss of grazer disturbance and increased litter accumulation also imposes selection on reproductive traits by reducing seed regeneration sites (reviewed by Pluess, 2013; Joyce, 2014; Jessen et al., 2023). This favors species with higher seed mass (Kahmen et al., 2002, Kahmen & Poschlod, 2004; Wehn et al., 2017), perennial growth (Pykälä, 2005; Johansson et al., 2011; but see Kahmen et al., 2002; Pluess, 2013), and clonal reproduction (Willems, 1983; Kahmen et al., 2002; Johansson et al., 2011; Weiss & Jeltsch, 2015; but see Pluess, 2013; Joyce, 2014). In addition, impaired pollen and seed dispersal in abandoned landscapes further reduce the advantages of sexual reproduction and favors short-distance dispersal (Johansson et al., 2011; Jacquemyn et al., 2012; Saar et al., 2012). However, the limited evidence available at the population level is mixed, as land use abandonment has been associated with reduced flowering frequency, seed number, seed mass and regeneration success in some studies (Musche et al., 2008; Fischer et al., 2011), but not in others (Lindborg et al., 2005).

Predicting evolutionary change in plant-microbe interactions and plant-soil feedbacks during land use change

The environmental changes and habitat fragmentation that accompany land use transitions can shift plant-microbe interactions and modify soil microbial community composition and function (Fig. 3; Bissett et al., 2011; Lauber et al., 2013; Tsiafouli et al., 2015; Mony et al., 2020, 2022). Shifts in soil microbial communities are caused by simultaneous changes in light and nutrient availability (de Vries et al., 2012a) and plant community composition (Johnson et al., 2003), as well as altered pathways of resource input to soil from plant litter and animal wastes (Schrama et al., 2023). We predict that land use change can also impose selective pressure on plant-microbial interactions and i) disrupt mutualistic associations with key soil microbes, such as arbuscular mycorrhizal (AM) fungi; ii) increase pathogen pressure; and iii) modify plant-soil feedbacks.

Disruption of mutualistic plant-microbial associations during land use change

Arbuscular mycorrhizal fungi colonize the roots of the majority of grassland plant species and provide a range of benefits to plant hosts, including increased nutrient uptake, pathogen protection, and abiotic stress resistance, in exchange for plant-assimilated carbon compounds (Smith & Read, 2008; reviewed by Delavaux et al., 2017). Nutrient enrichment and shading can increase the costs and decrease the benefits of being mycorrhizal to the point that such symbiosis can be considered parasitic for plants (Johnson et al., 2010, 2015). It can therefore be predicted that high soil nutrient availability in fertilised grasslands and carbon limitation caused by shading in abandoned grasslands can render carbon investment into AM fungi less beneficial and favour plant genotypes with weaker reliance on AM fungal associations for nutrient supply (Fig. 3; Johnson et al., 2008, 2010; Revillini et al., 2016). In addition, the encroachment of shrub and/or tree species that associate with ectomycorrhizal (EM) fungal species can lead to further declines in soil AM fungal abundance (Kalucka & Jagodziński, 2017; Neuenkamp et al., 2018) and potentially increase the selection pressure for genotypes with weaker AM fungal dependence.

However, evolutionary shifts in plant-AM fungal associations under land use change may be complicated by additional impacts of defoliation (grazing or mowing) on carbon allocation to AM fungi (which are known to be highly variable; Gehring & Whitham, 2002; Barto & Rillig, 2010), dependency of fertilization effects on soil N:P ratios (Miller et al., 2012) and multifunctionality of AM fungal benefits to the plant. In a global survey of grassland experiments, fertilisation did not affect root AM fungal colonization rates but led to declines in soil hyphal densities (Lekberg et al., 2021). This suggests that fertilisation may shift the function of AM fungi from nutrient provision via extensive soil hyphal networks to defensive function (which is associated with more hyphae residing in roots than soil). It can therefore be predicted that land use change can promote the spread of plant genotypes with either reduced strength or higher plasticity in AM fungal associations, either in terms of regulating the degree of root colonization or carbon allocation, or switching the mutualist's function from nutrition to defence (Zobel et al., 2024).

In addition to AM fungal associations, plants can engage in mutualistic interactions with a diverse community of free-living microbiota via root exudation (Narula et al., 2009). Moderate defoliation by grazers is known to increase root exudation, which can stimulate rates of nitrogen mineralization, plant nutrient uptake, and leaf tissue regrowth immediately following defoliation (Hamilton & Frank, 2001; Hamilton et al., 2008; Wilson et al., 2018; Panchal et al., 2022). However, intense grazing can cause carbon limitation and reduce carbon flow into soil microbial biomass (Medina-Roldán & Bardgett, 2011). Therefore, we predict that grazing abandonment or intensified grazing may favor plant genotypes with reduced root exudation, potentially further disrupting mutualistic relationships and modifying nutrient cycling.

Patterns of plant disease during land use change

Recent studies suggest that both land use intensification and abandonment can increase pathogen pressure on grassland plants (Fig. 2). Fertilisation has been shown to increase the relative abundance of soil fungal pathogens across a wide range of grasslands (Lekberg et al., 2021), and increased plant susceptibility to fungal disease in response to N fertilisation is also widely known in agricultural crops (Walters & Bingham, 2007; Veresoglou et al., 2013). Grazing manipulation studies also show increased foliar pathogen loads in ungrazed grasslands (Wennström & Ericson, 1991; Tian et al., 2009; Zhang et al., 2020; but see Daleo et al., 2009). Increases in plant size and leaf surface area (such as in fertilised grasslands) and longer exposure of leaves to pathogens (as in ungrazed plants) could also increase infection rates from foliar pathogens (Eck et al., 2022).

Though wild plant populations typically contain high levels of diversity in the genes that confer disease resistance (Burdon & Jarosz, 1991; Thrall, 2001; Laine, 2004), the loss of genetic diversity within plant populations due to land use change could compromise this diversity and increase plant disease susceptibility. Furthermore, declines in plant species richness (which could reduce dilution effects; Ostfeld & Keesing, 2012), in parallel with community-level and population-level shifts towards fast growth at the expense of defence, could also increase plant infection risk (Mitchell et al., 2002; Cappelli et al., 2020; reviewed by Laine, 2023). Hence, we can predict that these populations are likely to experience increased selection for pathogen resistance due to higher pathogen densities in fertilised or abandoned grasslands. As a result, selection imposed by changes in the abiotic environment (i.e., nutrient and light availability) towards faster-growing plants with enhanced competitive ability could be counteracted by selective pressure imposed by biotic agents such as pathogens, making predictions about net evolutionary outcomes challenging.

Shifts in plant-soil feedbacks during land use change and potential for eco-evolutionary feedbacks

Mutualistic and antagonistic soil microbes also drive plant-soil feedbacks, which regulate plant community composition and ecosystem functioning in grasslands (Bever et al., 1997; reviewed by Kulmatiski et al., 2008; Crawford et al., 2019). Plant-soil feedback is either positive or negative when plant-driven changes in soil microbial community composition or nutrient conditions either improve or reduce the performance of subsequent conspecific plants in those soils. Species characterized by traits related to fast growth and/or low reliance on mycorrhizal fungi tend to suffer from negative plant-soil feedbacks (Lemmermeyer et al., 2015; Cortois et al., 2016; Semchenko et al., 2018; Xi et al., 2021), which should limit their dominance in local communities and enhance species co-existence. However, it has been shown that plant-soil feedbacks can be modified by fertilisation and land use intensity in a species-specific way (Manning et al., 2008; Harrison & Bardgett, 2010; Heinze et al., 2015a; in ’t Zandt et al., 2019). Furthermore, some fast-growing grass species have been shown to exhibit more positive growth responses to soil biota from intensively managed sites compared to biota from extensively managed sites, probably contributing to their increasing dominance under land use intensification (Heinze et al., 2015a, 2015b). The underlying mechanisms remain unknown but could be related to the ability of fast-growing plant species to modulate microbial symbiosis to their advantage despite increases in pathogen abundance and declines in mycorrhizal fungal abundance associated with fertilisation (Lekberg et al., 2021; Zobel et al., 2024). It can be predicted that similar changes may occur within plant populations where plant-soil feedback may select for genotypes with more flexible relationships with symbiotic soil organisms. In abandoned grasslands, empirical studies on plant-soil feedback are scarce, but declines in mutualistic associations and increases in pathogen pressure could lead to similar shifts in plant-soil feedback as in intensively managed grasslands.

In addition, eco-evolutionary feedback with soil saprotrophs could be a possible mechanism by which fast-growing plant genotypes may spread during land use intensification. Under intensive land use, elevated soil nutrient conditions could drive evolutionary shifts towards tissues with high nutrient content but low longevity, further enhancing nutrient cycling and resulting in positive feedback to plant growth (Baxendale et al., 2014; Van Nuland et al., 2017).

Consequences of evolutionary responses to land use change for the adaptive potential of grassland plant species during global change

The loss of genetic diversity and/or shifts in functional traits within plant species during land use change could negatively affect species' persistence and adaptive potential (Koch et al., 2014; Nordstrom et al., 2023). Besides the inherent challenges caused by reductions in population size alongside shifts in dispersal and reproductive traits, land-use change may affect population persistence by changing the rate of generation of new genetic variants, further affecting adaptive potential. Theoretically, these processes may force species into an extinction vortex and accelerate the loss of populations through increased genetic drift, inbreeding, and fixation of maladaptive genetic variants (Nordstrom et al., 2023). In addition, shifts in resource acquisition and/or defensive traits during land use change could further restrict the ability of populations to persist and adapt in the face of extreme weather events (e.g., droughts; Lehner et al., 2006; Büntgen et al., 2021; IPPC 2021), species invasions (Bradley et al., 2010), and disease outbreaks (Anderson et al., 2004; Chakraborty & Newton, 2011; Eastburn et al., 2011; Elad & Pertot, 2014), which are predicted to become more frequent with global change (Fig. 3). Below, we focus on severe drought events as an example of the interactive effects of land use and climate change and identify potential eco-evolutionary feedbacks that can be expected.

The frequency and severity of droughts are expected to increase in many regions (Trnka et al., 2011; Xu et al., 2019, IPCC, 2021; Treydte et al., 2024) and can lead to rapid collapse of plant populations (Godfree et al., 2011). It has been demonstrated that grassland plant communities dominated by fast-growing species are less resistant to drought stress than those dominated by slow-growing species (Oram et al., 2023) but may recover faster after droughts (Hoover et al., 2014; Stampfli et al., 2018; Williams & de Vries, 2020). Superior recovery after droughts could be due to efficient utilization of the nutrient flushes that follow droughts (Oliveira et al., 2021) or the recruitment of beneficial microbes that aid in drought recovery via root exudation (Williams & de Vries, 2020; de Vries et al., 2023).

It is currently unknown how evolutionary changes within plant species in response to land use change may affect population resilience to drought. Based on community-level observations, we can predict that competitive exclusion of stress-tolerant genotypes by resource-acquisitive genotypes could impair species' drought resistance, but could result in faster regrowth after drought. In addition, plant species richness has been shown to moderate the impact of drought on plant productivity (Vogel et al., 2012; Isbell et al., 2015; Wagg et al., 2017; Souther et al., 2020). As genetic diversity within plant species has been shown to produce a similar buffering effect (Reusch et al., 2005; Prieto et al., 2015), declines in genetic diversity because of land use change could further compromise grassland drought resilience.

Drought resistance could be further diminished if genetic or functional shifts within grassland populations in response to land use change disrupt plant-microbial interactions, particularly associations with AM fungi, which are known to enhance drought tolerance (Remke et al., 2021; Puy et al., 2022; but see Bauer et al., 2020). Moreover, changes in plant carbon allocation to the microbial species involved in nitrogen and carbon cycling can also modify grassland responses to drought (Fuchslueger et al., 2016; Karlowsky et al., 2018; Kübert et al., 2019; Chomel et al., 2022; Oram et al., 2023). For example, intensive management favours opportunistic and resilient bacterial taxa over drought-sensitive taxa with poor recovery after drought (Lavellee et al. 2024), which may reinforce selection for plant genotypes with fast recovery but low resistance to drought. In summary, land use intensification and cessation of traditional management in grasslands may increase the sensitivity of plant populations to drought via reductions in plant genetic diversity, changes in functional trait composition and disruption of microbial associations.

Consequences of evolutionary responses to land use change for grassland ecosystem functioning

Faced with escalating climatic perturbations, it is critical to consider the evolutionary consequences of long-term land use change as a threat to ecosystem functioning (Mooney et al., 2009; Montoya & Raffaelli, 2010). Predictions can be made based on community-level observations and knowledge of the role of plant genetic diversity in ecosystem functioning. Plant species richness and functional diversity within plant communities have consistently been shown to enhance grassland productivity (Hooper et al., 2005; Cardinale et al., 2007; Clark et al., 2012; van ’t Veen et al., 2020) as well as stability (Tilman et al., 2006a; Hallett et al., 2017). While less is known about the role of plant genetic diversity, there is a general trend for genotypic and trait diversity to also increase productivity and stability (reviewed in Reusch et al., 2005; Cook-Patton et al., 2011; Whitlock, 2014; Abbott et al., 2017) and complement species diversity in maintaining ecosystem functioning (Prieto et al., 2015). It can hence be predicted that declines in plant genetic and functional diversity due to land use change can compromise ecosystem functioning.

Simultaneous changes in plant species and microbial communities in response to land use intensification and abandonment are also known to change carbon storage and nutrient cycling (e.g., Neyret et al., 2024). Higher nutrient levels and increased quality and quantity of plant-derived substrates (e.g., litter N content) associated with intensive grassland management can cause soil food webs to shift from fungal dominance to communities dominated by fast-propagating bacteria (Bardgett & McAlister, 1999; Leff et al., 2015). Cessation of grazing has been shown to reduce the diversity of below-ground communities, their metabolic activity, and the capacity of soils to maintain multiple functions (Schmitt et al., 2010; Peco et al., 2017; Schrama et al., 2023). As microbial diversity and network complexity are positively correlated with ecosystem functioning in grasslands (Wagg et al., 2019), land use intensification and abandonment have been shown to have detrimental effects on soil nutrient retention (de Vries et al., 2011), carbon storage (Tilman et al., 2006b; De Deyn et al., 2008; de Vries et al., 2012a; Allan et al., 2015; Ward et al., 2016; Sollenberger et al., 2019; Felipe-Lucia et al., 2020; Pichon et al., 2020), and ecosystem multifunctionality (Luo et al., 2023).

The importance of population-level responses to land use change in driving shifts in carbon and nutrient cycling is currently unknown. However, studies on genotypic variation in plant-soil interactions show that genotypes can differ in traits related to soil functions and that genotypic diversity can modify nutrient and carbon cycling via litter decomposition dynamics and root exudation (Schweitzer et al., 2005; Micallef et al., 2009; Wang et al., 2014; Semchenko et al., 2017, 2021). In addition, as AM fungi stabilize soil carbon via storage in mycelial tissue and formation of fungal necromass and soil aggregates (which protect carbon from microbial decomposition; Wilson et al., 2009; Morris et al., 2019; Hawkins et al., 2023), potential evolutionary shifts towards lower reliance on mycorrhizal symbiosis within plant populations could have a detrimental effect on soil carbon storage. Thus, we can predict that declines in genetic and functional diversity within plant populations, the displacement of resource-conservative genotypes by resource-acquisitive genotypes, and disruption of co-evolved relationships between plants and their microbial mutualists under changing land use could all undermine the ecosystem services provided by grasslands.

Conclusions

Understanding how anthropogenic change affects the biodiversity and functioning of plant communities as well as the evolution and ecology of the species within them is a central challenge in biology (Griffin et al., 2009; Bennett et al., 2015; Newbold et al., 2015; Oliver et al., 2015; Smith et al., 2019; Paudel et al., 2021). Existing knowledge about how land use change alters plant communities can be applied to understand the broader potential for land use change to drive eco-evolutionary shifts in plant populations and their interactions with associated microbes. Indirect evidence suggests that land use change may generate genetic and functional changes in grassland plant populations, which could disrupt plant-microbe associations, including with those microbes responsible for nutrient cycling and other key ecosystem functions. Plant evolutionary responses to land use change may then create eco-evolutionary feedbacks that further erode the functioning of grassland ecosystems and the adaptive potential of plant populations to future perturbations, especially under climate change. Empirical evidence for eco-evolutionary dynamics is extremely limited and requires more attention alongside investigation of community-level responses. In particular, several aspects linking population-level processes to ecosystem functions remain practically unexplored (Fig. 2).

Several major challenges have impeded advancement, including difficulties characterizing evolutionary change and linking genetic changes to plant-microbial interactions and ecosystem functions. Until recently, estimates of genetic diversity relied on neutral genetic markers, which can be a weak predictor of functional diversity within plant populations (Holderegger et al., 2006; Whitlock, 2014; Teixeira & Huber, 2021). However, advances in the rapidly developing field of landscape genomics hold great potential for detecting loci of adaptive relevance in non-model plants (Dauphin et al., 2023). In addition, our mechanistic understanding of plant-microbe and soil interactions has burgeoned in recent decades, e.g., on the multiple roles of mycorrhizae in nutrient cycling and defence (Delavaux et al., 2017) and the role of plant-soil feedback in vegetation dynamics (Gundale & Kardol, 2021; Semchenko et al., 2022). These advances offer a promising avenue for exploring eco-evolutionary dynamics under global change and linking them to species adaptive potential and ecosystem function.

Figures

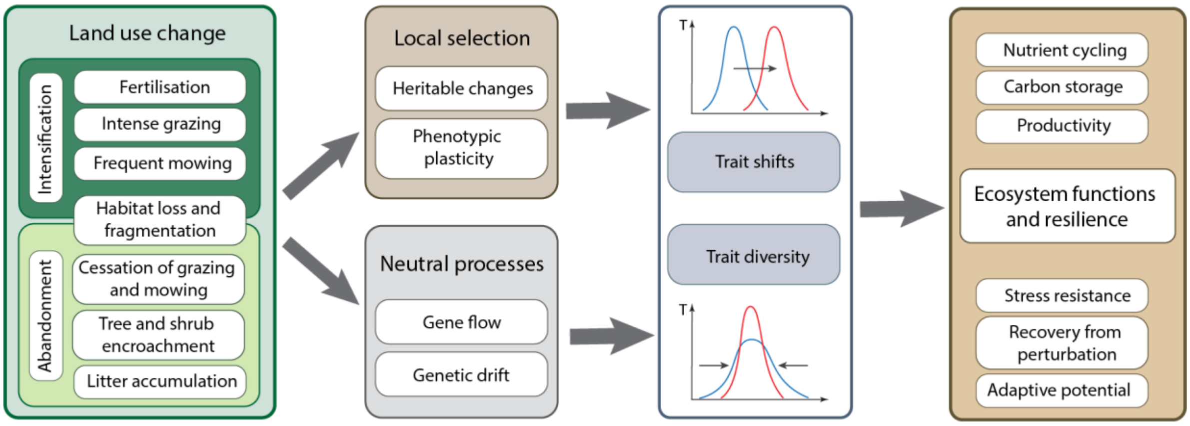

Figure 1: Processes underlying the impact of land use change in grasslands on ecosystem functions and resilience via evolutionary change in plant populations. The vast majority of historical semi-natural grasslands in Europe have been transformed by two main forms of land use change: i) intensification characterized by the application of fertilisers and more intense mowing/grazing; and ii) abandonment characterized by the cessation of grazing and mowing, leading to tree and shrub encroachment. Both intensification and abandonment can also result in the loss and fragmentation of habitat area with suitable growth conditions for grassland specialist species. These environmental changes can impose local selective pressure on plant populations – individuals with phenotypic trait values that are a better fit to changing conditions can gain a fitness advantage, leading to trait value shifts within populations and changes in trait diversity or variability. Changes in trait value or composition can occur either via phenotypic plasticity (i.e., the ability of a genotype to produce multiple phenotypes depending on environmental conditions) or via heritable shifts within populations (i.e., changes in allele frequencies, mutations, heritable epigenetic changes). Changes in population size and connectivity to other populations during habitat fragmentation can also change trait diversity and modify population responses to selection due to genetic drift (i.e., the random loss of genetic variation and/or fixation of maladaptive genetic variants) and changes in gene flow (i.e., the exchange of genetic variants between populations). The combined effect of land use change on intraspecific trait diversity and composition can in turn modify ecosystem processes (e.g., nutrient cycling, carbon storage and productivity) and resilience to further perturbations.

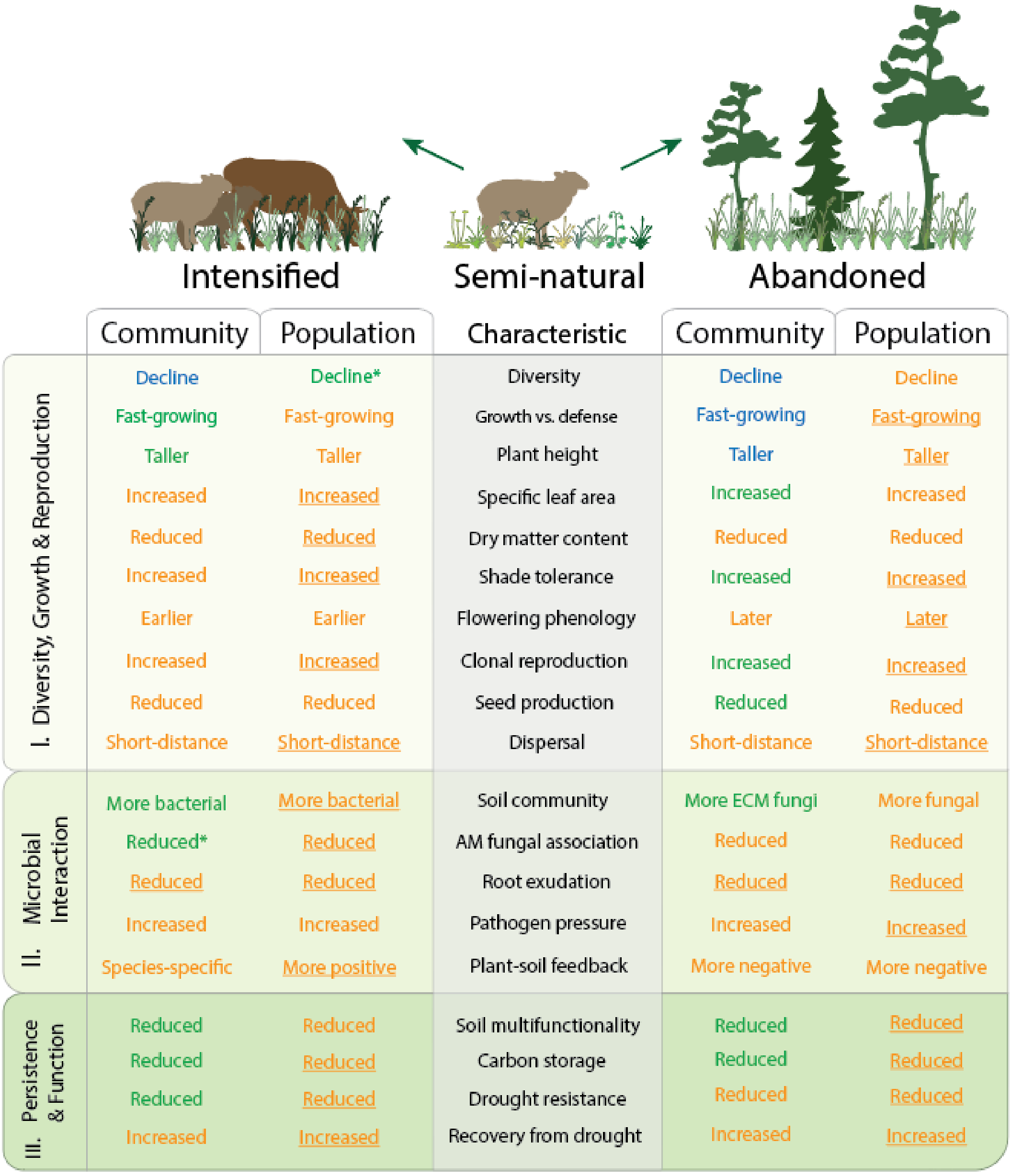

Figure 2: Current knowledge about the effects of land use intensification and abandonment on characteristics of grassland plant communities *versus* populations. For each characteristic (in the central column), we list the predicted direction of change due to land use intensification (leftmost two columns) and abandonment (rightmost two columns) at both the community and population level. Predictions are color-coded to reflect how much focus has been placed on them in the literature: blue indicates well-studied topics (> 10 studies), green indicates somewhat-studied topics (5 – 10 studies), and orange indicates less-studied topics (0 – 4 studies). Underscored predictions indicate that there are no studies to date that explicitly test this prediction. To allow comparison of biodiversity between communities and populations, here, ‘diversity’ refers to all of species, genetic, and/or functional diversity. For characteristics quantified at the population-level, included studies could reflect either genetic or epigenetic change, or phenotypic plasticity. Predictions are primarily based on theoretical consideration, while empirical studies generally report variable outcomes. Asterisks indicate cases in which theoretical predictions assume a decline in the characteristic, but empirical studies indicate that that the opposite might be true. See Table S1 for a non-exhaustive list of studies informing these predictions.

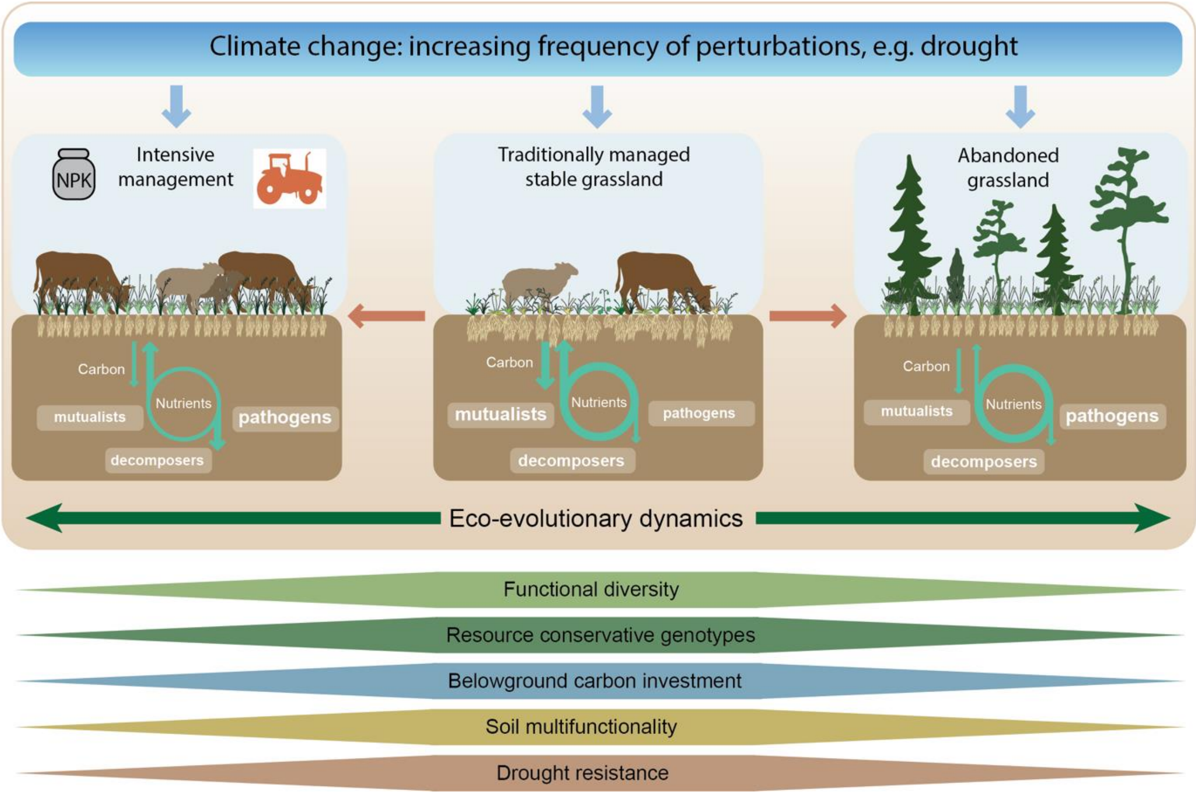

Figure 3. Predicted eco-evolutionary changes in grassland plant populations in response to land use and global change. Increased nutrient supply due to fertilisation in intensively managed grasslands and increased shading due to cessation of management in abandoned grasslands may select for competitive genotypes with low investment of carbon to mutualistic mycorrhizal fungi and root exudates, resulting in a shift from beneficial to pathogenic interactions with soil communities. Intensive management may enhance nutrient cycling with potential declines in nutrient retention, while abandoned grasslands may experience slowed nutrient cycling due to litter accumulation and invasion by ECM trees. The decline in plant functional diversity, the disruption of co-evolved plant-soil interactions and the displacement of resource-conservative strategies by competitive strategies with low stress tolerance can cascade to impair wider ecosystem processes, such soil carbon storage and nutrient retention, and ecosystem resilience to extreme weather events.

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Author Contributions

This research was conceptualized by MS and JLE. JLE and MS wrote the first draft of the manuscript. All authors contributed to and approved the final version of the manuscript.

Data Availability

This manuscript does not use data.

Supplementary Table 1: Literature on how land use intensification or abandonment affects various characteristics of semi-natural grassland plant communities or populations. This list includes published empirical studies, reviews, meta-analyses, special feature introductions, and book chapters that include focus on the topic of how land use intensification or abandonment affects semi-natural grassland. This list is not exhaustive; rather, it is intended as a resource and to highlight discrepancies in the amount of focus that has been placed on communities versus populations and on various topics. Various characteristics of semi-natural grassland plants (or their associated microbes or soil environments) are listed in approximately the same order as they appear in Fig. 2 and in which they are primarily discussed in our review. Most empirical studies appearing here explicitly test for the effect of intensification or abandonment on one or more of the listed characteristics in i) a field observational study (e.g., paired intensified or abandoned vs. extensively-managed grasslands), ii) a controlled experiment (e.g., with treatments mimicking land use intensification or abandonment), or iii) a theoretical model. Plant competition experiments with species that increase in abundance during intensification or abandonment versus grassland specialist species are also included. Reviews, meta-analyses, etc. appear in bold. Within a category, literature sources are listed chronologically.

Characteristic	**Intensification**		**Abandonment**	
	Community	*Population*	*Community*	*Population*
Diversity or composition (species, genetic, or functional)	1. During & Willems 1984 2. Kull & Zobel 1991 3. Austrheim et al. 1999 4. Cousins & Eriksson 2002 5. Fédoroff et al. 2005 6. van Diggelen et al. 2005 7. **Isselstein et al. 2005** 8. **Plantureux et al. 2005** 9. **Suding et al. 2005** 10. de Bello et al. 2006 11. Semelová et al. 2008 12. Niedrist et al. 2009 13. Oelmann et al. 2009 14. **Laliberté et al. 2010**	1. Snaydon & Davies 1982 2. Odat et al. 2004 3. Silvertown et al. 2009 4. **Pluess 2013** 5. Völler et al. 2013 6. Völler et al. 2017	1. Bakker et al. 1980 2. Willems 1983 3. During & Willems 1984 4. Kull & Zobel 1991 5. Milberg & Hansson 1993 6. Eriksson & Eriksson 1997 7. Austrheim et al. 1999 8. Hansson & Fogelfors 2000 9. **Pykälä 2000** 10. Cousins & Eriksson 2001 11. Kahmen et al. 2002 12. Moog et al. 2002 13. Wahlman & Milberg 2002	1. **Pluess 2013**

Characteristic	Intensification		Abandonment	
	Community	*Population*	*Community*	*Population*
	15. **Janišová et al. 2011** 16. Pakeman 2011 17. Reitalu et al. 2012 18. Bonanomi et al. 2013 19. **Habel et al. 2013** 20. Janeček et al. 2013 21. Allan et al. 2014 22. **Dengler et al. 2014** 23. Allan et al. 2015 24. Strebel & Bühler 2015 25. **Gossner et al. 2016** 26. Simons et al. 2017 27. Doležal et al. 2018 28. **Tälle et al. 2018** 29. Uchida et al. 2018 30. Čop & Eler 2019 31. **Diekmann et al. 2019** 32. Tonn et al. 2019 33. Buzhdygan et al. 2020 34. **Tianen et al. 2020** 35. Zarzycki & Kopeć 2020 36. Kuhn et al. 2021 37. Pakeman & Fielding 2021 38. Castillo-Garcia et al. 2022 39. **Schils et al. 2022**		14. Cousins & Eriksson 2002 15. Cousins & Lindborg 2004 16. Pykälä 2004 17. **Cousins & Eriksson 2005** 18. **Eriksson et al. 2005** 19. **Isselstein et al. 2005** 20. Pykälä 2005 21. Pykälä et al. 2005 22. de Bello et al. 2006 23. Poyry et al. 2006 24. Cousins et al. 2007 25. Raatikainen et al. 2007 26. Aavik et al. 2008 27. Cousins & Eriksson 2008 28. Johansson et al. 2008 29. Niedrist et al. 2009 30. Reitalu et al. 2010 31. **Janišová et al. 2011** 32. Vassilev et al. 2011 33. Ford et al. 2012 34. Reitalu et al. 2012 35. Bonanomi et al. 2013 36. Catorci et al. 2013 37. **Habel et al. 2013**	

Characteristic	Intensification		Abandonment	
	Community	*Population*	*Community*	*Population*
	40. Zhang et al. 2022		38. Janeček et al. 2013 39. Targetti et al. 2013 40. **Dengler et al. 2014** 41. **Joyce 2014** 42. Veen et al. 2014 43. Aldezabal et al. 2015 44. Strebel & Bühler 2015 45. Weiss & Jeltsch 2015 46. Stybnarova et al. 2016 47. Wehn et al. 2017 48. Doležal et al. 2018 49. Neuenkamp et al. 2018 50. Swacha et al. 2018 51. Uchida et al. 2018 52. **Valko et al. 2018** 53. Johansen et al. 2019 54. Peciña et al. 2019 55. Bohner et al. 2020 56. Uchida & Kamura 2020 57. Kuhn et al. 2021 58. Pakeman & Fielding 2021 59. Bonanomi et al. 2022 60. Gavrichkova et al. 2022 61. Prangel et al. 2023 62. Wipulasena et al. 2023	
Abundance or distribution	1. Cousins et al. 2003	1. Semelová et al. 2008	1. Eriksson et al. 2002	1. Bakker et al. 1980

Characteristic	Intensification		Abandonment	
	Community	*Population*	*Community*	*Population*
	2. **Janišová et al. 2011** 3. **Dengler et al. 2014** 4. Aune et al. 2018 5. Castillo-Garcia et al. 2022		2. **Poschlod & WallisdeVries 2002** 3. Cousins et al. 2003 4. **Eriksson et al. 2005** 5. Pykälä 2005 6. Prentice et al. 2006 7. **Janišová et al. 2011** 8. **Dengler et al. 2014** 9. Aune et al. 2018 10. Gavrichkova et al. 2022	2. Willems 1983 3. Lindborg et al. 2005 4. Herben et al. 2006 5. Mildén et al. 2007 6. Johansson et al. 2011 7. Veen et al. 2014 8. Lehtilä et al. 2016 9. Kose et al. 2019
Biomass or primary productivity	1. During & Willems 1984 2. van der Maarel & Titlyanova 1989 3. Kull & Zobel 1991 4. Cousins et al. 2003 5. Louault et al. 2005 **6. Suding et al. 2005** 7. Oelmann et al. 2009 8. **Pluess 2013** 9. De Keersmaecker et al. 2016 10. Völler et al. 2017 11. Zarzycki & Kopeć 2020 12. Van Sundert et al. 2021 13. Castillo-Garcia et al. 2022 14. **Schils et al. 2022** 15. Zhang et al. 2022	1. Snaydon 1970 2. Snaydon & Davies 1972 3. Davies & Snaydon 1974 4. Davies & Snaydon 1976 5. Bobbink & Willems 1991 6. Fischer et al. 2008 7. Fischer et al. 2011 8. Völler et al. 2013	1. During & Willems 1984 2. van der Maarel & Titlyanova 1989 3. Cousins et al. 2003 4. **Pluess 2013** 5. **Joyce 2014** 6. Weiss & Jeltsch 2015 7. Stybnarova et al. 2016 8. Doležal et al. 2018 9. Bohner et al. 2020 10. Gavrichkova et al. 2022 11. Prangel et al. 2023	1. Veen et al. 2014

Characteristic	Intensification		Abandonment	
	Community	*Population*	*Community*	*Population*
	16. **Wentao et al. 2023**			
Nutrient requirements, acquisition, or tissue content	1. van Diggelen et al. 2005 2. **Díaz et al. 2007** 3. Semelová et al. 2008 4. de Vries et al. 2012a 5. Doležal et al. 2018 6. Castillo-Garcia et al. 2022	1. Snaydon 1970 2. Davies & Snaydon 1973a 3. Davies & Snaydon 1973b	1. Willems 1983 2. Wahlman & Milberg 2002 3. Pykälä 2005 4. **Pluess 2013** 5. Targetti et al. 2013 6. **Joyce 2014** 7. Neuenkamp et al. 2016 8. Doležal et al. 2018 9. Karlowsky et al. 2018 10. Wehn et al. 2018 11. Gavrichkova et al. 2022	—
Plant height or growth form	1. Kull & Zobel 1991 2. Louault et al. 2005 **3. Suding et al. 2005** 4. van Diggelen et al. 2005 5. Semelová et al. 2008 6. Völler et al. 2017 7. Doležal et al. 2018	1. Snaydon & Davies 1972 2. Völler et al. 2013	1. Willems 1983 2. Kull & Zobel 1991 3. Kahmen et al. 2002 4. Luoto et al. 2003a 5. Luoto et al. 2003b 6. Cousins & Lindborg 2004 7. Kahmen & Poschlod 2004 8. Pykälä 2004 9. Johansson et al. 2011 10. Vassilev et al. 2011 11. **Pluess 2013** 12. **Joyce 2014** 13. Weiss & Jeltsch 2015 14. Wehn et al. 2017 15. Doležal et al. 2018 16. Bohner et al. 2020	—

Characteristic	Intensification		Abandonment	
	Community	*Population*	*Community*	*Population*
			17. Bonanomi et al. 2022	
Specific leaf area	1. Kull & Zobel 1991 2. Louault et al. 2005 3. **Pluess 2013**	—	1. Cousins & Lindborg 2004 **2. Pluess 2013** 3. Peco et al. 2017 4. Wehn et al. 2017 5. Wehn et al. 2018	1. Targetti et al. 2013
Leaf dry matter content	1. Louault et al. 2005	—	1. Wehn et al. 2017 2. Wehn et al. 2018	1. Targetti et al. 2013
Shade tolerance	1. van Diggelen et al. 2005 2. Nielsen et al. 2021	—	1. Wahlman & Milberg 2002 2. Cousins & Lindborg 2004 3. Pykälä 2005 4. Neuenkamp et al. 2016 5. Bohner et al. 2020 6. Nielsen et al. 2021	—
Flowering phenology	1. van Diggelen et al. 2005 2. Louault et al. 2005	1. Snaydon & Davies 1972 2. Völler et al. 2013 3. Völler et al. 2017	1. Kahmen et al. 2002 2. Kahmen & Poschlod 2004 3. Vassilev et al. 2011 4. Catorci et al. 2013	—
Clonality	1. Kull & Zobel 1991 2. **Suding et al. 2005** 3. **Wentao et al. 2023**	—	1. Willems 1983 2. Kahmen et al. 2002 3. Johansson et al. 2011 4. Catorci et al. 2013 5. **Pluess 2013** 6. **Joyce 2014** 7. Weiss & Jeltsch 2015	—

Characteristic	Intensification		Abandonment	
	Community	*Population*	*Community*	*Population*
Annual vs. perennial life cycle	1. **Suding et al. 2005** 2. van Diggelen et al. 2005 3. Uchida et al. 2018	1. Davies & Snaydon 1976	1. Kahmen et al. 2002 2. Pykälä 2005 3. Johansson et al. 2011 4. Uchida et al. 2018	—
Seed production, mass, or reproductive output	1. Louault et al. 2005 2. Völler et al. 2017 3. **Wentao et al. 2023**	1. Snaydon & Davies 1972 2. Fischer et al. 2011 3. Völler et al. 2013	1. Willems 1983 2. Eriksson & Eriksson 1997 3. Kahmen et al. 2002 4. Cousins & Lindborg 2004 5. Kahmen & Poschlod 2004 6. Fischer et al. 2008 7. **Pluess 2013** 8. Wehn et al. 2017	1. Lindborg et al. 2005 2. Musche et al. 2008
Seed dispersal	1. Cousins et al. 2003	—	1. Cousins et al. 2003 2. Johansson et al. 2011 3. Neuenkamp et al. 2016	—
Seed bank	1. Klaus et al. 2018	—	1. Milberg & Hansson 1993 2. Eriksson & Eriksson 1997	—
Seed germination or seedling survival	1. During & Willems 1984 2. Cousins et al. 2003 3. Klaus et al. 2018	—	1. Bakker et al. 1980 2. Willems 1983 3. Eriksson & Eriksson 1997 4. Cousins et al. 2003 5. Lindborg 2006 6. **Pluess 2013** 7. **Joyce 2014** **8. Valko et al. 2018**	1. Lindborg et al. 2005 2. Musche et al. 2010 3. Kose et al. 2019

Characteristic	Intensification		Abandonment	
	Community	*Population*	*Community*	*Population*
Soil community diversity or composition	1. Bardgett et al. 2001 2. de Vries et al. 2006 3. de Vries et al. 2012a 4. Liliensiek et al. 2012 5. Lemanski & Scheu 2015 6. **Gossner et al. 2016** 7. Fornara et al. 2020	—	1. Aldezabal et al. 2015 2. Karlowsky et al. 2018 3. Swacha et al. 2018 4. Bohner et al. 2020 5. Bonanomi et al. 2022 6. Fernández-Guisuraga et al. 2022 7. Wipulasena et al. 2023 8. Serrano et al. 2024	—
AM fungi or microbial mutualists	1. Johnson et al. 2003 2. **Suding et al. 2005** 3. Egerton-Warburton et al. 2007 4. Johnson et al. 2008 5. Antoninka et al. 2011 **6. Gossner et al. 2016** 7. Simons et al. 2017	—	1. Lumini et al. 2010 2. Karlowsky et al. 2018 3. Neuenkamp et al. 2018	1. Van Geel et al. 2021
Root exudation	—	—	—	—
Pathogen abundance or plant disease	**1. Veresoglou et al. 2013** **2. Gossner et al. 2016**	1. Snaydon & Davies 1972	1. Bonanomi et al. 2022	
Defoliation tolerance	1. Castillo-Garcia et al. 2022	1. Kirschbaum et al. 2021	1. Weiss & Jeltsch 2015	1. Musche et al. 2010 2. Kirschbaum et al. 2021
Plant-soil feedback	1. Harrison & Bardgett 2010 2. Castillo-Garcia et al. 2022	—	1. Ilmarinen & Mikola 2009	1. Medina-Roldán et al. 2012 2. Veen et al. 2014
Drought resistance	1. Hartmann et al. 2013 2. De Keersmaecker et al. 2016	—	1. Karlowsky et al. 2018	—

Characteristic	Intensification		Abandonment	
	Community	*Population*	*Community*	*Population*
	3. Carlsson et al. 2017 4. Stampfli et al. 2018 5. Kübert et al. 2019 6. Bharath et al. 2020 7. Ullah et al. 2020 8. Van Sundert et al. 2021 9. Chomel et al. 2022			
Soil nutrient composition or cycling	1. Austrheim et al. 1999 2. Semelová et al. 2008 3. de Vries et al. 2012a 4. **Soussana & Lemaire 2014** 5. Cui et al. 2020 6. Castillo-Garcia et al. 2022 7. **Schils et al. 2022** 8. Cui et al. 2023	1. Snaydon & Davies 1972	1. Austrheim et al. 1999 2. Ford et al. 2012 3. Karlowsky et al. 2018 4. Wehn et al. 2018 5. Johansen et al. 2019 6. Bohner et al. 2020 7. Gavrichkova et al. 2022 8. Serrano et al. 2024	—
Carbon storage	1. de Vries et al. 2013 2. **Soussana & Lemaire 2014** 3. Thorhallsdottir & Gudmundsson 2023 4. Cui et al. 2020 5. Fornara et al. 2020 6. **Schils et al. 2022**	—	1. Ford et al. 2012 2. Peco et al. 2017 3. Karlowsky et al. 2018 4. Peciña et al. 2019 5. Bohner et al. 2020 6. Gavrichkova et al. 2022 7. Prangel et al. 2023 8. Thorhallsdottir & Gudmundsson 2023	—

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