Using individual-based modeling to understand grassland diversity and resilience in the Anthropocene

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Abstract

The world's grassland systems are increasingly threatened by anthropogenic change. Susceptible to a variety of different stressors, from land-use intensification to climate change, understanding the mechanisms driving the maintenance of these systems' biodiversity and stability, and how these mechanisms may shift under human-mediated disturbance, is thus critical for successfully navigating the next century. Within this dissertation, I use an individual-based and spatially-explicit model of grassland community assembly (IBC-grass) to examine several processes, thought key to understanding their biodiversity and stability and how it changes under stress. In the first chapter of my thesis, I examine the conditions under which intraspecific trait variation influences the diversity of simulated grassland communities. In the second and third chapters of my thesis, I shift focus towards understanding how belowground herbivores influence the stability of these grassland systems to either a disturbance that results in increased, stochastic, plant mortality, or eutrophication.

Intraspecific trait variation (ITV), or variation in trait values between individuals of the same species, is fundamental to the structure of ecological communities. However, because it has historically been difficult to incorporate into theoretical and statistical models, it has remained largely overlooked in community-level analyses. This reality is quickly shifting, however, as a consensus of research suggests that it may compose a sizeable proportion of the total variation within an ecological community and that it may play a critical role in determining if species coexist. Despite this increasing awareness that ITV matters, there is little consensus of the magnitude and direction of its influence. Therefore, to better understand how ITV changes the assembly of grassland communities, in the first chapter of my thesis, I incorporate it into an established, individual-based grassland community model, simulating both pairwise invasion experiments as well as the assembly of communities with varying initial diversities. By varying the amount of ITV in these species' functional traits, I examine the magnitude and direction of ITV's influence on pairwise invasibility and community coexistence. During pairwise invasion, ITV enables the weakest species to more frequently invade the competitively superior species, however, this influence does not generally scale to the community level. Indeed, unless the community has low alpha- and beta- diversity, there will be little effect of ITV in bolstering diversity. In these situations, since the trait axis is sparsely filled, the competitively inferior may suffer less competition and therefore ITV may buffer the persistence and abundance of these species for some time.

In the second and third chapters of my thesis, I model how one of the most ubiquitous trophic interactions within grasslands, herbivory belowground, influences their diversity and stability. Until recently, the fundamental difficulty in studying a process within the soil has left belowground herbivory "out of sight, out of mind." This dilemma presents an opportunity for simulation models to explore how this understudied process may alter community dynamics. In the second chapter of my thesis, I implement belowground herbivory – represented by the weekly removal of plant biomass – into IBC-grass. Then, by introducing a pulse disturbance, modelled as the stochastic mortality of some percentage of the plant community, I observe how the presence of belowground

herbivores influences the resistance and recovery of Shannon diversity in these communities. I find that high resource, low diversity, communities are significantly more destabilized by the presence of belowground herbivores after disturbance. Depending on the timing of the disturbance and whether the grassland's seed bank persists for more than one season, the impact of the disturbance – and subsequently the influence of the herbivores – can be greatly reduced. However, because human-mediated eutrophication increases the amount of resources in the soil, thus pressuring grassland systems, our results suggest that the influence of these herbivores may become more important over time.

In the third chapter of my thesis, I delve further into understanding the mechanistic underpinnings of belowground herbivores on the diversity of grasslands by replicating an empirical mesocosm experiment that crosses the presence of herbivores above- and below-ground with eutrophication. I show that while aboveground herbivory, as predicted by theory and frequently observed in experiments, mitigates the impact of eutrophication on species diversity, belowground herbivores counterintuitively reduce biodiversity. Indeed, this influence positively interacts with the eutrophication process, amplifying its negative impact on diversity. I discovered the mechanism underlying this surprising pattern to be that, as the herbivores consume roots, they increase the proportion of root resources to root biomass. Because root competition is often symmetric, herbivory fails to mitigate any asymmetries in the plants' competitive dynamics. However, since the remaining roots have more abundant access to resources, the plants' competition shifts aboveground, towards asymmetric competition for light. This leads the community towards a low-diversity state, composed of mostly high-performance, large plant species. We further argue that this pattern will emerge unless the plants' root competition is asymmetric, in which case, like its counterpart aboveground, belowground herbivory may buffer diversity by reducing this asymmetry between the competitively superior and inferior plants.

I conclude my dissertation by discussing the implications of my research on the state of the art in intraspecific trait variation and belowground herbivory, with emphasis on the necessity of more diverse theory development in the study of these fundamental interactions. My results suggest that the influence of these processes on the biodiversity and stability of grassland systems is underappreciated and multidimensional, and must be thoroughly explored if researchers wish to predict how the world's grasslands will respond to anthropogenic change. Further, should researchers myopically focus on understanding central ecological interactions through only mathematically tractable analyses, they may miss entire suites of potential coexistence mechanisms that can increase the coviability of species, potentially leading to coexistence over ecologically-significant timespans. Individual-based modelling, therefore, with its focus on individual interactions, will prove a critical tool in the coming decades for understanding how local interactions scale to larger contexts, and how these interactions shape ecological communities and further predicting how these systems will change under human-mediated stress.

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1. General Introduction

1.1 An urgent need to understand grassland diversity and resilience

As human population growth increases the intensity of land use management (Vitousek 1997, Rockström et al. 2009, Steffen et al. 2015), the diversity of earth's grasslands is on the decline (Wesche et al. 2012, Harrison et al. 2015). The causes for this degradation are multidimensional and often interacting, and include not only land-use intensification (Allan et al. 2015, Gossner et al. 2016), but also eutrophication (Stevens et al. 2004, Dupré et al. 2010, Wesche et al. 2012), and climate change (Knapp et al. 2002, Zavaleta et al. 2003, Cantarel et al. 2013). To understand how grasslands will change in the Anthropocene—and predict their resilience to the stresses anticipated over the coming century—we must improve our understanding of how critical community assembly mechanisms mediate the diversity and resilience of these biological systems over time.

Basic research is therefore fundamentally necessary to successfully navigate the Anthropocene. By improving our understanding of how diverse grassland communities assemble, scientists may discover promising techniques to maintain their diversity and functioning despite global change. For example, as more knowledge accrues concerning how grassland arthropods respond to extreme-stressors, such as mowing and harvesting, conservationists and land-use managers have begun to introduce refuges into extensively managed agricultural areas (Humbert et al. 2012, Buri et al. 2013). However, the multidimensional challenges facing today's grasslands demand equally nuanced analyses. Ecological modeling thus has the potential to become an important tool for addressing these new challenges. By seamlessly incorporating aspects of ecological systems that have, historically, been too complex to explore with simple modeling techniques (e.g. spatial heterogeneity, local interactions, and individual variation), individual-based models (Huston et al. 1988, Grimm et al. 2006) may prove pivotal in clarifying our understanding of how ecosystems will change under human-mediated stress.

In this thesis, I use an individual-based and spatially-explicit grassland model (May et al. 2009) to investigate key outstanding questions facing community ecologists today. The model, developed to reflect how grassland communities assemble under various management regimes, has been parameterized to real data (Weiss et al. 2014) through the Biodiversity Exploratories framework (Fischer et al. 2010). Leveraging this tool, I relax several common ecological assumptions and demonstrate that their removal fosters a greater understanding of these grassland systems.

1.2 Relaxing simplifying assumptions to clarify ecological dynamics

Our understanding of biodiversity has long relied on highly simplified modeling approaches. For example, the most basic models in ecology, Lotka-Volterra models, rely on the assumption of a well-mixed system (referred to as mass-action, or mean-field dynamics). This simplification facilitated progress in our most basic understanding of ecological processes, such as competition and predation. Using his new model, for instance, Volterra was able to capture the population cycling dynamics of predator and prey fish populations in the Adriatic Sea after the first World War (Kingsland 1995). Famously, these simple models also neatly captured the dynamics of snowshoe hares and lynx (Gilpin 1973), as well as moose and wolves (Jost et al. 2005).

Over time, ecologists added features to these equations to encompass more of nature’s complexity. By adding a functional response reflecting the behavior of the prey species as it reaches carrying capacity, the Rosenzweig-MacArthur model (Rosenzweig and MacArthur 1963) became a foundational model in ecology, especially in developing of the theory of ecological stability (Holling 1973). Meanwhile, ecologists began to consider what happened when systems were not well-mixed (Andrewartha and Birch 1954, Huffaker 1958). This, in turn, led to more advanced models intended to better capture these dynamics, developing into the fields of metapopulation (Levins 1969) and spatial ecology (Pielou 1959, Levin and Paine 1974). Many methodologies have since emerged to capture spatial patterns in ecology (Dieckmann et al. 2000), and modern coexistence theory (Chesson 2000a) relies on this contemporary understanding to explain how coexistence arises within ecological communities.

Simplifying assumptions are critical to progress in ecological theory because few other systems are as "multi-causal" as ecological ones (Scheiner and Willig 2011). Therefore, understanding when an assumption should be relaxed is as important as knowing when to use one. For example, the inclusion of spatial and temporal heterogeneity was fundamental to defining the stabilizing mechanism—a concept key to modern coexistence theory (Chesson 2000a, b). This initial framework wisely acknowledged heterogeneity’s importance in driving coexistence, but itself had to incorporate simplifications that are being re-examined today. This is because, since these models average competition across all individuals and are mathematically based on invasion analyses, they may not capture a medley of other possible coexistence mechanisms, such as intransitive competition (Grilli et al. 2017, Levine et al. 2017, Soliveres and Allan 2018) or stochastic dilution (Wang et al. 2016). Although the omission of these assumptions facilitated two decades of progress in community ecology, incorporating these nuances will improve our understanding of how species coexist (Jeltsch et al. 2019). The resolution of our ecological understanding has improved over time, as generations of ecologists have re-examined the simplifying assumptions that built the foundation of our current models—and understanding—of ecology.

1.3 Re-examining the concept of the species mean-trait: On intraspecific variation

In functional ecology, the assumption of species' "mean traits" has been the most recently re-evaluated simplification in ecological theory (Vellend 2006, Violle et al. 2012). Since the early 21st century, community ecology has shifted from trying to understand community dynamics through pairwise interactions between species (MacArthur 1968, May 1974) towards "functional ecology," which focuses the traits present in a biological community, rather than the specific species themselves. In 2006, McGill et al. suggested that community ecologists should focus first on describing the fundamental niche of a species in terms of its functional traits and abiotic environment. Then, by comparing this fundamental niche for a given abiotic environment to its realized niche, one can understand the influence of its "biotic interaction milieu." Critical to the effectiveness of this approach is the assumption that, for coexistence to occur, the species' niches cannot overlap past a certain point. This assumption, termed "limiting similarity," has been vital to our understanding of coexistence theory, since its development by MacArthur and Levins (1967), and is itself a generalization of Lokta-Volterra models. However, to functional ecologists, a species' niche mean and width (d and σ, *sensu* MacArthur and Levins [1967]) correlate to its functional traits. Given that trait values within a species vary and are better described by a distribution than a fixed value, it follows that, for limiting similarity to apply, the trait variation—either genetic or plastic—among the individuals within a given species should be smaller than the variation between species. That is, on average, intraspecific trait variation (ITV) must be smaller than interspecific trait variation (McGill et al. 2006, Albert et al. 2011, Violle et al. 2012).

As community ecology shifted towards this new, more functional, paradigm, researchers began to question the assumption of ITV's negligibility (Clark 2010, Messier et al. 2010, Shipley et al. 2016). Understanding how and when ITV changes community assembly has since become a major concern in community ecology (Albert et al. 2010, 2011, de Bello et al. 2011). Initially, in trying to identify when it would be critical to incorporate ITV, researchers focused on its impacts during environmental filtering (De Bello et al. 2010, de Bello et al. 2011, Lepš et al. 2011, Albert et al. 2012, Laughlin et al. 2012, Siefert 2012), as it would likely enable some individuals to persist in inhospitable environments through phenotypic plasticity, where plants shift their traits to match a given environment (Jung et al. 2010, 2014) or through the portfolio effect, where some phenotypes of a species safeguard the species' population during environmental fluctuations (Bolnick et al. 2011). Modeling only species' mean traits may thus stymie any predictions of their relative fitness and fundamental niche (Jung et al. 2010). A global meta-analysis by Siefert et al. (2015) has since found that ITV accounts for 25% of the total trait variation within communities. This reinforces a growing consensus that ITV should be explicitly included in analyses involving small spatial scales (Jung et al. 2010, Albert et al.

2011, Pérez-Ramos et al. 2012), short environmental gradients (de Bello et al. 2011, Lepš et al. 2011, Albert et al. 2012, Laughlin et al. 2012), or species-poor communities (MacArthur 1972, Whitham et al. 2006, Crawford et al. 2019).

Most recently, however, the debate has returned to the assumption of limiting-similarity, investigating whether ITV influences not only environmental filtering but also ecological interactions *per se*, such as competition. The essence of the debate is between the expectations of modern coexistence theory (Chesson 2000b) and "individual variation theory" (*sensu* Violle et al. 2012). Proponents of coexistence theory argue that increased niche overlap will almost always lead to competitive exclusion, while those advocating individual variation theory refer to empirical datasets that suggest the opposite, and argue that these emergent coexistence mechanisms, while difficult to analytically model, are nonetheless present (Clark et al. 2011, Jeltsch et al. 2019). Mechanisms through which ITV could enable species to pass through this "biotic filter" were hypothesized first by Bolnick et al. (2011), but evidence for their influence is rare and often conflicting (Turcotte and Levine 2016). Most recently, a number of mathematical models suggest that ITV will most likely reduce diversity by expanding the overlap between species' trait distributions, and therefore, their niches (Barabás et al. 2016a, Hart et al. 2016). Understanding how ITV changes the "biotic interaction milieu" of the functional framework is a necessary step towards knowing when—and how—to relax the assumption that ITV is marginal in determining species assemblages.

The second chapter of my thesis steps into this debate. By incorporating ITV into a spatially-explicit, individual-based model, I test ITV's efficacy in maintaining diversity in randomly-generated communities. Keeping the environmental parameters—abiotic filters—constant, I determine how ITV shapes diversity over time, isolating its influence on competitive interactions between species. My work furthers our understanding of grassland community assembly by showing that ITV, in a spatially-explicit environment, enables the persistence of rare species. However, its efficacy is highly dependent on the community's initial diversity.

1.4 Belowground herbivores as mediators of the Anthropocene

Multi-causality in grassland systems encompasses far more than the plants' interactions alone. The trophic relationship between plants and their herbivores also drives grassland dynamics. Although the plants' interactions with aboveground herbivores are frequently examined within a grassland context (Borer et al. 2014, Mortensen et al. 2018, Anderson et al. 2018), belowground herbivores remain comparatively underappreciated but are likely as fundamental a determinant of grassland diversity and stability (De Deyn et al. 2003, Stein et al. 2010). Critically, it is increasingly clear that herbivores—both above- and belowground—may be influential mediators of the succession of grassland communities after disturbances (Russell and Connell 2007, Raffaele et al. 2011, Ramirez et al. 2012, Borgström et al. 2017). Therefore, in an era of unprecedented human-mediated change, researchers are now reconsidering their long-held neglect of belowground herbivory.

The problem of belowground herbivory is multifaceted, and likely stems—though myopically—from the difficulty inherent in studying interactions that cannot be readily observed (Hunter 2001). However, as new evidence supports the potential importance of belowground herbivory in affecting diversity (Brown and Gange 1989, De Deyn et al. 2003, Stein et al. 2010), a renewed interest is emerging in the abundance (Parker and Seeney 1997, Jedlička and Frouz 2007, Zvereva and Kozlov 2012) and feeding preferences (Schallhart et al. 2012, Sonnemann et al. 2013, Wallinger et al. 2014) of belowground herbivores. To this end, several recent studies have explored how belowground herbivores affect the ecological interactions of grassland species (Stein et al. 2010, Borgström et al. 2017). Overall, however, we still understand very little about how belowground herbivores shape plant community dynamics. This is especially true after disturbances and during disequilibrium events, when the feeding preferences of belowground herbivores may disproportionately impact the plant community (Wootton 1998), potentially mirroring similar findings for those above ground (Borer et al. 2014, Anderson et al. 2018).

However, before one can investigate how belowground herbivores influence the diversity and stability of grassland communities, it is necessary to better characterize how they choose their meals. Although relatively little research has addressed this key question, some generalizations are possible. In a recent meta-analysis, Kozlov and Zvereva (2017) found that belowground herbivory imposed, on average, a 25% loss of root biomass in grassland communities. Noting that studies of belowground herbivory may tend towards sites with "apparent herbivory," they suggest 10% is a plausible average 'background' (i.e., minimal) herbivory rate. This is roughly the same extent as for foliar herbivores. Notably, a separate meta-analysis by the same authors (Zvereva and Kozlov 2012) determined that generalist belowground herbivores impose considerably greater negative effects on plant biomass and overall fitness than specialists. Given that similar patterns are present aboveground (Zvereva et al. 2010), the authors argue that this may be a general phenomenon that emerges because specialist herbivores exert more selective pressure on their host plants. This, in turn, leads the plants to evolve better defenses against the damage inflicted by these specific herbivores.

Counterintuitively, relatively little is known about how "generalist" belowground herbivores forage. For example, of the generalist herbivores, external chewers are the most damaging, affecting root systems 50% more than either sap feeders or borers (Zvereva and Kozlov 2012). Of this life-history class, species of the genus *Agriotes*, or wireworms, are one the most widespread and abundant in Europe and are often a focal species within studies of belowground herbivory (Parker and Seeney 1997, Jedlička and Frouz 2007). Some studies have suggested that these herbivores have a preference for nutrient-rich species (Hemerik et al. 2003), and several recent analyses found that they tend to prefer plants with greater biomass, higher growth rates, and richer tissue quality (Sonnemann et al. 2012, 2015). Molecular analyses of their diets suggest that they are likely selective in their herbivory, varying their diet throughout the year to favor some species over others (Wallinger et al. 2014), and increasing their preferences towards certain species with increasing plant community diversity (Schallhart et al. 2012).

These feeding preferences will have important impacts on plant communities because, if the herbivores preferentially eat the most dominant species in a grassland, they may maintain biodiversity and potentially offset the negative effects of certain disturbances. This idea has been demonstrated to occur in the aboveground compartment, given that the addition of belowground nutrients increases the fitness of the largest, fastest-growing species (Harpole and Tilman 2007, Hautier et al. 2014, DeMalach et al. 2016, 2017). Aboveground herbivores may counteract the negative effects of eutrophication on biodiversity by reducing competition for light (Borer et al. 2014, Anderson et al. 2018), an effect that may replicate belowground if belowground herbivores predominantly eat the largest, fastest-growing root systems. However, studies investigating this effect should be wary of direct comparisons, as aboveground competition is notably asymmetric (Schwinning and Weiner 1998).

In aboveground competition, taller individuals will overshadow their neighbors, thus intercepting more light in proportion to their photosynthetic biomass. Because of this competitive-asymmetry, herbivory aboveground—when preferential towards the tallest, largest shoots—may reduce the relative fitness differences between the tallest and the shortest plants. However, unlike its aboveground counterpart, belowground competition is often considered symmetric (Weiner et al. 1997, Casper and Jackson 1997, Lamb et al. 2009), and under a symmetric competition regime, herbivory will not have any competitive-asymmetry to reduce. Although if belowground herbivores prefer larger root systems their proximate influence may be to decrease the size of these individuals' root systems, they will not mitigate any underlying asymmetry in the plants' competitive dynamics. Because the herbivores are not reducing any competitive asymmetry, they may be less effective in equalizing competition than their aboveground counterparts.

Clearly, the biodiversity-impacts of belowground herbivores will change based on the extent to which they favor the dominant species. But importantly, given that belowground herbivores are likely ambient determinants of biodiversity, their feeding preferences may be even more important as drivers of ecosystem functioning during disturbances and disequilibrium dynamics. Understanding these patterns will become even more important as human-mediated disturbances continue to impact grasslands worldwide.

Human-mediated stresses are common in contemporary grassland systems. Because they often neighbor agriculture fields or are used as feed, grasslands are frequently victim to exposure to pesticide (De Schampheleire et al. 2007) or herbicide drift (De Snoo and Van Der Poll 1999, Reeg et al. 2017, 2018a), fertilization, and overgrazing (Fischer et al. 2010). In each of these cases, it is likely that the relationship between the producers and their consumers—the plants and their herbivores—may change dramatically. Understanding the consequences for these systems' biodiversity and stability as these relationships shift is thus an important task for ecologists today. Unfortunately, almost no studies investigate belowground herbivores during disequilibrium events (but see Borgström et al. 2017).

To understand how belowground herbivores change grassland assembly during disturbances events, it is necessary not only to consider the herbivores themselves but also how aspects of the disturbance and the grassland itself modulate their impact. For example, the type and intensity of disturbance may differentially influence the proportion of plant biomass to herbivores, while the type of grassland will influence how individual plants compete, and the abundance and feeding preferences of the herbivores may determine which species of plant are most negatively impacted.

The excessive addition of nitrogen and phosphorus to natural systems—especially grasslands (Wesche et al. 2012)—is one of the most pressing concerns of our time (Rockström et al. 2009, Steffen et al. 2015). While this process, eutrophication, may not affect the root herbivores themselves, an increase in belowground resources may primarily benefit the largest, fastest-growing plant species. If belowground herbivory is preferential towards these species, it may be an important buffer against these disturbances. However, if belowground herbivory is non-selective, they may do little to support biodiversity. Further, the symmetry of belowground competition may also undermine the herbivores' impact, limiting any equalizing effects they may have. Indeed, the ultimate magnitude and direction of the belowground herbivores' influence may depend on the relative strength of these different effects. In the fourth chapter of my thesis, I investigate these interactions and observe how belowground herbivores mediate grassland assembly during eutrophication events.

In summary, developing insight into the role of belowground herbivory in grassland communities is likely critical to understanding how they will cope during the coming century. Within this dissertation, therefore, I incorporate belowground herbivory and two different disturbances regimes, modeled as either an increase in belowground resources or the stochastic death of plant-individuals, into an individual-based grassland community model. By varying the preferences of the belowground herbivores from pure generalists, non-selectively feeding on all plants equally, to those highly preferential towards the dominant root systems, I investigate how belowground herbivores change the biodiversity and resilience of these systems to disturbance. Further, by manipulating aspects of the system and the disturbance itself, I can investigate *in silico* how abiotic factors may control this trophic relationship.

1.5 Individual-based modeling as a tool to study community ecology

Individual-based modeling (IBM) has proven a natural medium to explore the consequences of relaxing the assumptions core to our current framework of community assembly. To a large degree, this is ultimately because ecology is a complex system, with ecological communities composed of independent, though interacting, individuals (Grimm and Railsback 2005). While ecologists historically modeled groups of individuals as atomic (their interactions taken to obey the assumption of mass-action), IBMs function inherently on the individual level. With this innovation, these models are a natural step towards understanding how individual interactions lead to emergent dynamics (Huston et al. 1988, Grimm and Berger 2016, Jeltsch et al. 2019). Further, because many IBMs explicitly consider space, individual interactions are fundamentally local. This is especially important for sessile organisms—such as grassland species—because their "neighborhood" is for life.

For each of the ensuing chapters, I employ an individual-based grassland community assembly model that simulates competition between plant-individuals as a spatially explicit process, driven by their biotic parameters (e.g., above- and belowground biomass) and functional traits. For the second chapter of my thesis, using this model affords me the ability to incorporate ITV with few modifications to the underlying simulation. Incrementally changing the model ensures that any new emergent behavior can be easily isolated and identified as a signal of ITV's impact. Further, because previous models of ITV’s influence (Barabás et al. 2016b, Hart et al. 2016) did not include the concept of space, a spatially-explicit IBM enables me to examine how local interactions change with intraspecific variation. This may change the direction or magnitude of ITV's effect through "stochastic dilution" (Wang et al. 2016). Because an individual's neighborhood is stochastic, strong individuals of a weak species could, by good fortune, find themselves in a competitive neighborhood of relatively weak individuals of a dominant species.

For the third and fourth chapters of my thesis, the use of an individual-based model enables me to elegantly track individual-level changes in the plants’ competitive neighborhoods and to then assess how these changes scale to the community level. Connecting these two levels is prohibitive at such a scale empirically, and therefore pressingly needed to build an understanding of how belowground herbivores change grassland assembly and grasslands’ response to various disturbance regimes.

To properly contextualize the results of each of these three chapters, it is necessary to have a broad understanding of how the model I used, IBC-grass, reflects grassland community assembly dynamics. Therefore, in the next section, I briefly describe the model’s history and highlight its central design concepts.

1.6 The model: Individual-based community model of grasslands (IBC-grass)

Throughout this thesis, I use an individual- and trait-based, spatially-explicit grassland assembly model: IBC-grass. Since its introduction (May et al. 2009), IBC-grass has been used to investigate numerous aspects of grassland dynamics, from belowground herbivory (Körner et al. 2014) to recovery after the cessation of aboveground grazing (Weiss and Jeltsch 2015), and species coexistence (Pfestorf et al. 2016, Crawford et al. 2019) to ecotoxicology (Reeg et al. 2018a, b).

Critically, Weiss et al. (2014) parameterized the model with data from trait databases and a survey of plant functional types from German grasslands collected through the Biodiversity Exploratories (Fischer et al. 2010, Pfestorf et al. 2013), and found that the model successfully reproduces, without calibration at the community level, empirically-observed grassland biodiversity and ecosystem-functioning patterns. A pertinent takeaway from this validation is that the diversity (measured through either Shannon diversity or species richness) of grassland plots in the Biodiversity Exploratories is well reflected by IBC-grass across gradients of both land-use intensity and belowground resources.

At its core, IBC-grass simulates local plant community assembly on a two-layer grid space that represents sunlight and soil resources, usually corresponding to roughly 1-2 m^2. During initialization, seeds of each plant functional type (pseudo-species defined by their plant functional traits) are distributed randomly across the grid space. The process of community assembly is then allowed to proceed for some number of years, with weekly time steps in which the plants’ growth and reproduction are calculated.

Plant functional types (PFTs) are defined by their values across four trait axes. These axes define the maximum size of each individual and how far its seeds can disperse, whether it grows in a rosette or erect form, its specific leaf area and palatability, as well as how efficiently it takes sunlight and soil resources from the grid space. These traits, as well as their biotic parameters (such as their above- and belowground biomass), describe each plant-individual and are used to calculate its growth and reproduction.

Within the simulation, plants gather resources based on zone-of-influence (ZOI) competition modeling (Weiner et al. 2001). While a plant without neighbors grows sigmoidally to its maximum size, when neighbors exist competition occurs where the plants' ZOIs (determined by their biomasses and trait values) overlap, reducing the two plants' biomasses in proportion to how much competition reduces their effective photosynthetic area. Aboveground, competition is asymmetric, with taller plants extracting more resources in proportion to their biomass than their smaller, shorter, neighbors. This process simulates the overshadowing that occurs in real grassland communities (Schwinning and Weiner 1998). Belowground, competition is symmetric, and plants share resources when their ZOIs overlap, in proportion to their belowground biomass (Weiner et al. 1997).

A more complete overview of the IBC-grass model is contained within each chapter of my thesis, which detail the modifications I made to the model to support that chapter's simulation scenarios.

1.7 Outline of this thesis

In the second chapter of my thesis, I relax one of the most fundamental assumptions in functional ecology, that intraspecific trait variation (ITV) can safely be omitted from community-level analyses. By incorporating ITV into the IBC-grass model, I examine how it changes the plant community's biotic interactions (i.e., competition) and thus mediates grassland diversity. Chapters 3 and 4 of my thesis shift the focus to interactions between the biotic and abiotic forces that drive grassland diversity. Chapter 3 begins by exploring how belowground herbivores shape the resilience of grassland diversity to a very simple disturbance—the stochastic death of plants—by investigating how the belowground herbivores and aspects of the grassland itself modulate the disturbance's impact. Chapter 4 continues this line of inquiry by centering on a specific disturbance that threatens contemporary grassland ecosystems: eutrophication. By conducting a factorially-designed experiment, crossing the removal of above- and belowground herbivory with eutrophication, I isolate the impact of each on diversity. Finally, in the fifth chapter of my thesis, I synthesize the data, show how my results relate to the current research on grassland community assembly, and suggest promising directions for further research.

1.8 References

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2. Intraspecific trait variation increases species diversity in a trait-based grassland model

Abstract

Intraspecific trait variation (ITV) is thought to play a significant role in community assembly, but the magnitude and direction of its influence are not well understood. Although it may be critical to better explain population persistence, species interactions, and therefore biodiversity patterns, manipulating ITV in experiments is challenging. We therefore incorporated ITV into a trait- and individual-based model of grassland community assembly by adding variation to the plants' functional traits, which then drive life-history trade-offs. Varying the amount of ITV in the simulation, we examine its influence on pairwise-coexistence and then on the species diversity in communities of different initial sizes. We find that ITV increases the ability of the weakest species to invade most, but that this effect does not scale to the community level, where the primary effect of ITV is to increase the persistence and abundance of the competitively-average species. Diversity of the initial community is also of critical importance in determining ITV's efficacy; above a threshold of interspecific diversity, ITV does not increase diversity further. For communities below this threshold, ITV mainly helps to increase diversity in those communities that would otherwise be low-diversity. These findings suggest that ITV actively maintains diversity by helping the species on the margins of persistence, but mostly in habitats of relatively low alpha and beta diversity.

Crawford, M. et al. 2019. Intraspecific trait variation increases species diversity in a trait-based grassland model. - Oikos 128: 441–455.

2.1 Introduction

Intraspecific trait variation (ITV) is thought to be a significant source of the diversity in natural communities (Siefert et al. 2015). It is increasingly acknowledged that this variation can be important in understanding the dynamics governing diversity in these systems (Violle et al. 2007; Clark 2010; Bolnick et al. 2011, Albert et al. 2015). However, a deeper understanding of the magnitude and direction of ITV's influence on diversity remains elusive, and the mechanisms underlying it are nuanced and difficult to isolate (Turcotte and Levine 2016).

While modern coexistence theory has shown that environmental and competitive effects interact in shaping community composition, the historical idea of separating them into two “filters” (Violle et al. 2012) can provide a suitable perspective through which to analyze the impacts of ITV on community assembly. In the first filter, it has been shown that ITV is a critical factor in "external filtering," which is composed of all filtering processes external to the species community itself, most notably environmental filtering (Albert et al. 2010, 2012; de Bello et al. 2010; Siefert 2012). Studies have shown that inclusion of ITV into gradient analyses increases the predictive capacity of functional ecology, by better approximating species' ability to pass through these environmental filters (Lepš et al. 2011, de Bello et al. 2011, Laughlin et al. 2012). In essence, ITV may enable the persistence of species that are on average ill-suited to a local abiotic condition because a few well-adapted individuals can maintain a population (Jung et al. 2010).

The second, "inner filter," considers how ITV impacts community assembly through biotic interactions, e.g. competition or facilitation. This filter encompasses the community-level processes that determine the ability of a species to persist. Bolnick et al. (2011) suggests a number of different mechanisms through which ITV can mediate community assembly and species diversity, but the degree to which these mechanisms are present and the direction of their effects has been a topic of significant debate, reinforced by often contradictory empirical evidence (Turcotte and Levine 2016). Central to this discussion is the expectation of modern coexistence theory (Chesson 2000) that an increased amount of niche overlap, driven by variation in the populations’ functional traits, will only exacerbate the dominance of the better competitor unless stringent assumptions—e.g. a mean-variance trade off (Lichstein et al. 2007)—are met. On the other hand, proponents of individual variation theory (Violle et al. 2012) argue that coexistence mechanisms emergent from ITV may be difficult to analytically model but nonetheless are critical to the maintenance of diversity (Clark 2011).

Most recently, several theoretical studies have introduced ITV into mathematical models of pairwise competition to isolate its impact on coexistence. First, Hart et al. (2016) used a two-species plant competition model and added ITV into the species' demographic parameters. They found that ITV will only reinforce the competitive dominance of the superior species, primarily because the benefit to the inferior species due to improved demographic rates—in their case, higher seed production—is more than outweighed by the corresponding increase in the superior species' fitness. Only under very constrained circumstances will ITV promote coexistence. In a second study, Barabás and D'Andrea (2016) added ITV to a two-species Lokta-Volterra model, where the species differ along a one-dimensional trait axis. The fitness of a species within their model was a function of its location on the trait axis and how much its niche overlapped with the other species, as defined by the distance between their two trait kernels. They observed that the impact of ITV was generally negative, again except for very specific mean-variance values. In an important additional step, they then modified their model and tested ITV's impact on community assembly with a saturated species pool, again finding that ITV hurts coexistence and lowers species richness. Interestingly, when they added heritable ITV, they found that while richness still declined, the resulting community was much more resilient to environmental perturbations.

These studies provide an important starting point for analyzing the impact of ITV on community assembly and biodiversity patterns. Their overall conclusion is that ITV does not increase diversity. However, the mathematical models used are based on simplifying assumptions that might not capture all aspects of how ITV can affect community assembly and dynamics. Thus, to complement them by relaxing some of their key assumptions, we use an established individual- and trait-based grassland simulation model to increase our understanding of the magnitude and direction of ITV's influence. Although more difficult to interpret than mathematical models, individual-based models lend themselves especially well to studying ITV for two reasons.

First, ITV is ultimately a process that works on individuals' traits. It is intuitive that if ITV acts on a demographic parameter and there is no extant trade-off (i.e. higher fecundity leads to less fit offspring) it will improve the superior competitor as much as it helps the inferior competitor. However, it is rarely the case in ecology that demographic parameters do not have underlying trade-offs which limit their potential returns (Herben et al. 2012, Laughlin and Messier 2015, Dwyer and Laughlin 2017), otherwise Darwinian demons would suppress diversity (e.g., Kneitel and Chase 2004). We expect that ITV's influence may change if it is introduced at the level of the functional trait, and if these traits drive life-history trade-offs. Because the most fit species may already have the most optimal combination of traits—minimizing all underlying trade-offs—introducing ITV into its traits would not further increase its fitness but may increase the fitness of its less optimally-located inferior competitor.

Second, ITV hasn't to our knowledge been tested in a spatially-explicit context, and so we have very little understanding of how ITV influences assembly when the assumption of a well-mixed system is removed. The ability to model local interactions is a key benefit of IBM, and could, through stochastic sampling, alter ITV's effect on competition. This process was recently termed the "stochastic dilution hypothesis," and operates on the notion that, although competition is deterministic, dispersal and recruitment mechanisms may enable some individuals to be surrounded by a favorable neighborhood (Wang et al. 2016). It is possible that—through stochastic dilution—the stronger individuals of the weak species could, by good fortune, find themselves in a neighborhood of relatively weak individuals of the dominant species. Using a spatially-explicit IBM could enable these effects to emerge.

A third assumption of previous studies that should be examined—though not remedied by IBM *per se*—is the influence of the size of the species pool. As the number of interspecific competitors on a given trait axis increases, the proportional importance of ITV will decline (Kraft et al. 2015). By gradually increasing the number of species initially introduced to the communities, we can assess the impact of ITV as the trait axes become more packed with interspecific competitors. Therefore, we will scale up from pairwise invasion experiments to communities of different sizes. This will show us if ITV's impact changes as the amount of interspecific diversity increases, as focusing only on saturated communities (Barabás and D'Andrea 2016) may give only a single perspective of how ITV works on community assembly.

In this study, we address these assumptions by incorporating the effects of ITV into an empirically validated (Weiss et al. 2014), spatially-explicit, trait- and individual-based grassland model, IBC-grass (Individual-based community model of grasslands), which includes local interactions, trade-offs, and stochastic dilution. Since its introduction (May et al. 2009), IBC-grass has been used to investigate different aspects of grassland community dynamics (Körner et al. 2014, Weiss and Jeltsch 2015, Pfestorf et al. 2016, Reeg et al. 2017, Reeg et al. 2018). Importantly, Weiss et al. (2014) parameterized the model with data from trait databases and a survey of plant functional types from German grasslands collected through the Biodiversity Exploratories (Fischer et al. 2010, Pfestorf et al. 2013). The model successfully reproduced, without calibration at the community level, empirically-observed grassland biodiversity patterns.

In previous studies IBC-grass used the same value for each of the plant functional types' (PFT) traits. We added non-heritable ITV and varied it, observing the resulting changes in biodiversity. We began our analysis by breaking competition down to its simplest case—pairwise invasion experiments of all 81 PFTs in our hypothetical regional pool. By testing the PFTs' ability to coexist in pairs, we can better compare our model to that of the other contemporary attempts at modelling ITV. We can observe the magnitude and direction of ITV's influence, as well as investigate the underlying traits that drive this influence.

We then shifted our perspective to that of the community, testing for ITV's impact on communities of varying initial richness, and then more thoroughly investigating its influence on two-hundred and fifty 16-PFT communities. Initially, we scaled our initial community richness from small, perhaps dispersal-limited, species pools to larger communities with many more PFTs than can coexist in our spatial extent at one time. We can therefore see how ITV's importance changes as the degree of interspecific competition increases. Then, by focusing on the community richness in which ITV had most effect, we thoroughly examine the lower-level dynamics that drive its behavior. In this analysis, we looked at how different initial species pools lead to different outcomes and how the traits most important for persistence and abundance in communities change with increasing levels of ITV.

2.2 Methods

We used the individual-based and trait-based, spatially-explicit grassland assembly model, IBC-grass (May et al. 2009), and added variation to individuals' functional traits. While in the original model each plant of a given plant functional type (PFT) was parameterized with the PFT's trait means, we added variation to the plants' trait syndromes and thereby made each individual functionally unique. However, within this approach we maintained all trait correlations included in the trait syndromes that were defined in the original model version based on empirical knowledge on trait correlations (May et al. 2009).

A full description of the original model and our modifications can be found in the ODD (Overview, Design concepts, Details) protocol (Grimm et al. 2010, 2006; Supplemental Material A). The following is a brief summary of the model as well as an explanation of our modifications to it.

2.2.1 Overview of the IBC-grass model

IBC-grass simulates local community dynamics on a 100 x 100 cell grid, where each cell corresponds to 1 cm^2 and can hold one plant's stem. Its time step corresponds to one week, and there are 30 weeks per year representing the vegetation period. A plant is characterized by its functional traits and the biomass of its three distinct compartments: aboveground mass, belowground mass, and reproductive mass. A plant's competitive area is defined by an aboveground and a belowground “zone of influence” (ZOI). The two ZOIs are both circular areas around the plant’s stem, from which it acquires either above- or belowground resources (Schwinning and Weiner, 1998; Weiner et al. 2001). While the plant’s stem is contained within one grid cell, its ZOI can cover many.

When two plants' ZOIs overlap they compete for resources. A cell's aboveground resources correspond to light while its belowground resources correspond to water and nutrients. The proportion of a cell's resources a plant obtains during competition depends on its competitive abilities and how many other ZOIs overlap the cell. Aboveground competition is size-asymmetric, i.e. the larger plant takes up resources from each contested cell not only in proportion to its competitive ability, but also in proportion to its aboveground mass and height advantage over the smaller plants (Supplemental Material A). In other words, aboveground competition disproportionately favors the larger competitor. Belowground competition, however, is size-symmetric, i.e. only their competitive abilities are considered, and their relative sizes are considered proportionally. Intraspecific competition is also included in the form of negative-density dependent competition, reflecting species-specific predators or pathogens (May et al. 2009). This density-dependent competition was modeled by decreasing the resource uptake of an individual in proportion to the square-root of the number of conspecifics in its neighborhood ZOI. This modelling decision is further explored in Supplemental Material D, removing the intraspecific negative density dependence and observing the impact of ITV without it. All grid cells' total resources are kept constant through space and time; only a plant’s biotic neighborhood influences the amount of resources available to it at any given time step.

When a plant is unable to gather enough resources, it changes its resource allocation between above- and belowground parts, depending on which compartment is more limited (i.e. shoot or root). If resource uptake in any of the two compartments it below a certain threshold, the plant is considered as stressed. Each consecutive week a plant is stressed increases its chance of mortality linearly, in addition to a background, stochastic, annual mortality of 20%.

Aboveground grazing events occur in each time step and reduce the aboveground biomass of plants by 50% and remove all of its reproductive mass. Plants are subject to grazing based on a weighted lottery, with the tallest and most palatable individuals being the most prone to being grazed (Díaz et al. 2001).

Plants are characterized by four sets, or syndromes, of functional traits, a subset of those proposed as the “common core list of plant traits” by Weiher et al. (1999). The first set of traits defines the plant's maximum size (m_{max}), which positively correlates with seed size and negatively correlates with dispersal distance (Eriksson and Jakobsson 1998; Jongejans and Schippers 1999). The second defines the plant's growth form, or leaf to mass ratio (LMR), which describes the plant as either a rosette, erect, or intermediate growth form type. The third set defines its competitive ability, or maximum resource utilization per time step (g_{max}), and negatively correlates with its stress tolerance (Grime 2001). The fourth trait set describes the plant's grazing response, positively correlating its palatability with its specific leaf area (SLA) (Westoby et al. 2002). An exploration of how these traits—and the trade-offs they are component in—determine the life-history of a plant is contained in the ODD supplement (Supplemental Material A8.1.8: *trade-offs*). The original model (May et al. 2009) was parameterized with three settings for each functional trait, leading to a pool of 81 possible plant function types (PFT) from which communities did assemble. We maintained these trait means but added individual variation.

2.2.2 Model extension: Intraspecific trait variation

Intraspecific trait variation (ITV) was modeled by varying each new individual’s functional trait values. This was accomplished through adding to each trait value a random variate, drawn from a Gaussian distribution with a mean of 0 and standard deviation of *ITVsd*, and normalized to the trait’s mean value. This distribution was truncated at -1 and 1 before normalization to ensure that no trait garners a negative value. After drawing the variate from this distribution, it is multiplied by the trait's mean and then added to the mean trait value. This results in a normal distribution with the mean being the PFT’s mean trait value, and the coefficient of variation (σ/μ) being *ITVsd*.

Within each trait set, correlations have to be considered. For example, a plant’s maximum size is correlated with the size of its seeds and those seeds’ dispersal kernel. When varying these sub-traits intraspecifically, they must vary together. Positively tied traits are modified by the same variate while negatively tied traits are varied inversely by negating the variate for one of the traits. Furthermore, because the original magnitude of these traits can be quite different—a large plant can have a maximum size of 5,000 mg and a seed size of 1 mg—they vary together proportional to their original value. Table 1 illustrates the process of varying these traits for one individual plant.

Seedling establishment is the only trait for which ITV is not considered in the model. Instead, it uses a weighted lottery to simulate the seedling’s competition. The probability of a given PFT establishing on a cell, therefore, is the sum of its reproductive mass proportional to the total reproductive mass present on that cell. For pragmatic runtime considerations, we did not introduce ITV into this algorithm. However, after an arbitrary seed of the winning PFT is chosen to establish, its mass after germination is varied according to the ITVsd of the current simulation.

Table 1. Adding intraspecific variation to an individual plant's traits with an ITVsd of 0.5. Each plant has four sets of traits: "Growth form," determining whether the plant grows as a rosette or erect pattern; "Max plant size," describing its maximum biomass, but also its seed size and dispersal kernel; "Resource response," determining how the plant responds to resource stress, which is inversely correlated to how well it competes with other plants; and "grazing response," which documents how palatable the plant is to grazers. Each trait set is composed of multiple correlated sub-traits. To derive an individual plant's new, varied trait value, a random number is drawn from a Gaussian distribution with a standard deviation of ITVsd and normalized to the PFT's mean trait value. This normalized modifier is then added to the PFT's mean trait value. Each correlated sub-trait uses the same modifier, though the direction of the correlation is maintained.

Set	**Trait**	**Description**	**Sample mean trait value**	**Sample variate (*ITVsd* = 0.5)**	**Tied variation direction**	**Varied trait value**
Growth form	LMR	e.g. rosette or erect	0.75	-0.4922944	NA	0.3807792
Max plant size	m_{max}	Max plant size	5000 mg	-0.1805448	+	4097.276
	m_{seed}	Seed mass	1 mg	-0.1805448	+	0.8194552
	$mean_{disp}$	Mean dispersal distance	0.1 m	-0.1805448	-	1.180545
	sd_{disp}	Standard deviation of dispersal distance	0.1 m	-0.1805448	-	0.1180545
Resource response	g_{max}	Maximal resource utilizations per time step and ZOI area	20 resource units/cm^2/week	0.5275132	+	30.55026
	$surv_{max}$	Maximum survival time under resource stress exposure. Whole number.	6 weeks	0.5275132	-	2.8349208
Grazing response	$palat$	Palatability – susceptibility to grazing	0.5	0.1906902	+	0.5953451
	SLA	Above-ground ZOI area per leaf mass.	0.75	0.1906902	+	0.8930177

2.2.3 Simulation experiments

We ran three batches of simulations (Table 2). We first ran a batch that models pairwise invasion experiments for all PFTs, followed by a batch that simulates small-scale community assembly, initially on a gradient of initial species richness and then targeting an initial species richness of 16 PFTs. The PFTs used in these models were derived by using three positive values—low, medium, and high—for each of the four traits (May et al. 2009). This resulted in $3^4 (= 81)$ possible PFTs, each composed of some permutation of template trait values.

For each batch of simulations, the probability of a grazing event was preset at a moderate probability of 0.20 per week. We did not explore resource gradients but used a resource level that, in the original model, lead to the highest species richness for a moderate level of grazing.

Table 2. Parameterizations of the four sets of simulations run on IBC-grass. The first dataset, "Pairwise invasion criterion," is a mutual invasion experiment where 81 PFTs invade each other PFT in the set. This is used to understand how the ability of two PFTs to coexist changes with ITV and their traits. The second set, "Community data," includes a large array of ITVsd levels. The third set of simulations varies the size of the input community, to understand how the effectiveness of ITV changes with the community's saturation.

	Set 1 – Pairwise invasion criterion	**Set 2 – Community**	**Set 3 – Community size**
Communities	-	250	150
Replicates	20	50	10
PFTs / community	-	16	8, 16, 32, 64
***ITVsd* values**	0, 0.05, 0.10, …, 0.5	0, 0.05, 0.10, …, 0.5	0, 0.1, 0.2, …, 0.5
Stabilizing mechanism	Present	Present	Present
Duration (years)	10 year warm up, 50 year test	100	100
Recorded variables	Terminal population counts and biomass for each PFT, extinction times.	Shannon diversity, Total terminal biomass per PFT, extinction times	Shannon diversity, Total terminal biomass per PFT, extinction times
Record frequency	Yearly	Yearly	Yearly

Pairwise invasion

Our first batch of simulations focuses on simplifying the competitive dynamics between PFTs, to explore how differences in trait-sets affect the coexistence of pairs along an ITV gradient. We designed these simulations as pairwise invasion experiments, allowing us to generalize whether two PFTs can coexist with a greater theoretical grounding and more directly compare our results to that of Hart et al. (2016) and Barabás and D'Andrea (2016). We generated pairs of each PFT invading every other PFT, excluding itself, resulting in $81 \cdot 80\ (= 6480)$ total pairs. We ran 10 replicates each of these pairwise invasions across eleven different levels of ITV ranging from an ITVsd of 0–0.5.

To run a single pairwise invasion, we grew the resident species for 10 simulation-years—generating a monoculture—and then introduced 100 seeds of the invading species. If the invading species was present for the simulation's entire duration—50 years—we counted it as successful. If an invasion fails, in the overwhelming majority of cases it does so well before this point, most often within the first ten years.

We calculate three metrics with these simulations: First, average invasion success, which corresponds to the number of successful invasions divided by the total number of replicates. In each pair, we designate whichever PFT successfully invades more frequently as the "superior" PFT, and the other as the "inferior." For example, if PFT A invades PFT B 80% percent of the time, and B invades A 20% of the time, A is the superior PFT.

Second, we take a more granular approach towards understanding these differences in invasive ability between the PFTs and define each PFT's competitive ability as the difference between its own and its resident's invasion success rate. We term this their invasion disparity. Returning to our earlier example, PFT A would have a disparity of 0.60, while PFT B would have a disparity of -0.60.

The third metric, abundance disparity, is similar to the invasion disparity, however using PFT abundances rather than the rate of invasion success. For example, PFT A may have an average final abundance of 500 plants after invading PFT B, and in turn PFT B may have an average abundance of only 50 plants post-invasion. Therefore, the abundance disparity of PFT A invading PFT B would be 450, while PFT B invading PFT A -450.

The use of these last two metrics better estimates the competitive difference between PFT-pairs. It is difficult to quantify the competitive differences between two PFTs by only looking at each PFT's invasion success rate in isolation, because any single invasion success rate will mean something different in context. For example, if PFT A never invades PFT B, our understanding of the competitive hierarchy then depends on whether—and by how much—PFT B invades A. If PFT B never invades A, they are both mutually uninvasible and therefore more likely to be similar in competitive ability. However, if PFT B always invades A, PFT B is significantly more fit than A. We also lack sufficient context by only classifying them into "superior" and "inferior" PFTs, because while an invading PFT with a rate of 0.5 would be inferior to a mutually-invading PFT with an invasion rate of 1.0, it would also be inferior to a mutually-invading PFT with an invasion rate of 0.51. By classifying each pair with a continuous value, we can discern more easily these nuances across pairs.

Small-scale community assembly

The second and third batches model small-scale community assembly. We first ran simulations testing the sensitivity of our model to the species richness of the input community. While maintaining the 1 m^2 spatial scale, we generated communities on a gradient of starting diversity, from 8 to 64 species out of the total 81. We then used this community saturation gradient to understand whether the influence of ITV depends on how tightly packed the species are along the four trait-axes. It may be the case that, with only a few species, a significant amount of the trait space may be "unoccupied" and therefore exploitable through ITV. However, with many species initially added, ITV might not help coexistence because the traits axes are already occupied. Simulations were ended after 100 years and we recorded the Shannon diversity for six different levels of ITVsd.

We then shifted our focus by concentrating on the initial community richness in which ITV has the most impact. We generated 250 communities, each consisting of 16 PFTs, and ran each with 11 different levels of ITVsd, replicating each level 50 times. These communities were derived by randomly drawing subsets of 16 PFTs from the original 81. Sampling communities out of the species pool more accurately models what a typical 1 m^2 of grassland would look like if dispersal limited the number of input species. Although we ultimately decided to focus on Shannon diversity, we also decomposed diversity into richness and evenness, measured as the probability of interspecific encounter (Hulbert

1971; Chase and Knight 2013). These data as well as their corresponding statistical models—mirroring those presented below—are contained in Supplemental Material C. The results of the following statistical analyses are consistent for all three metrics. We focus on Shannon diversity because it incorporates both richness and evenness.

For both of these simulations batches, the model was initialized by randomly distributing 10 seeds of each PFT onto the grid space. Their germination probability was forced to 1 for the first year, to begin the simulation with an equal population of each PFT. Simulations ended after 100 years, long after most communities generally reach an equilibrium, and we then recorded the community's Shannon diversity as well as each PFT's total biomass and, if applicable, time of extinction.

To understand the more aggregated patterns associated with these communities, we used a linear mixed-model (R Package lme4, Bates et al. 2015) to estimate the relationship between Shannon diversity and ITV with the community's identity—its unique input set of species—as a random effect. This allows us to understand how these different species sets, stochastically selected from a species pool, will inherently assemble to different communities, and how this fact may mediate how that community's successional pathway changes with ITV. A linear model is then used to examine how a community's Shannon diversity without any ITV (its intercept) predicts its response to increasing levels of intraspecific trait variation (its coefficient).

2.2.4 Variable importance through Random Forests

Because the only difference between PFTs' are their traits, these traits will be the primary factor that decides whether two PFTs can coexist or whether a PFT can persist within a community. Thus, we can trace which traits are the most important in determining a PFT's performance in both a pairwise and community context, and then we can test how this importance changes with the addition of ITV. We therefore used random forests (Breiman 1999, Liaw and Wiener 2002) to predict the invasion success rates and final abundance of a given PFT based on both its traits and the resident's traits in a pairwise context, and to predict the presence-absence and final abundance at the end of the simulation in the community context. Random forest is a supervised machine learning algorithm, in which an ensemble of decision trees is created with random subsets of the training dataset and the predicted response value is calculated by averaging the trees' predictions. This technique will allow us to account for the nonlinear relationships within and between the PFTs' trait sets, as well as their complex interactions with ITV. We stratified each dataset by ITVsd and generated an independent random forest for each level, resulting in eleven different forests for both the pairwise dataset and the community dataset. By calculating the variable importance of each predictor, we visualized the relative predominance of each trait's predictive power over a gradient of increasing ITVsd, and therefore observed how changing levels of intraspecific variation influence the balance of which traits hold sway over a PFT's fate. For all forests, we withheld 30% of the dataset for validation. Summary statistics on the robustness of the forests are reported in Supplemental Material B.

In a separate analysis, contained in Supplemental Material E, we use partial dependence plots—a technique frequently used to explore random forests—to investigate how the random forests' predictions of the PFTs' abundance, persistence, and invasion rate change for each trait across the gradient of ITV. In other words, through this technique we are able to understand how ITV mediates increases or decreases in the fitness of the PFTs by visualizing how it changes the behavior of the underlying traits.

2.3 Results

2.3.1 Pairwise invasion success

On average, higher ITVsd increased the probability of successful invasion in pairwise invasion experiments. Categorizing the two PFTs in a pair based on which is more likely to successfully invade without ITV, we observed that the "inferior" PFTs were the main beneficiaries of intraspecific variation (Fig. 1). While the superior PFTs stayed generally constant in their invasion rates, the inferior PFTs saw a larger increase: From no ITV to an ITVsd of 0.5, the difference in invasion rate and abundance between the superior and inferior PFTs fell by 59%, and 45% respectively.

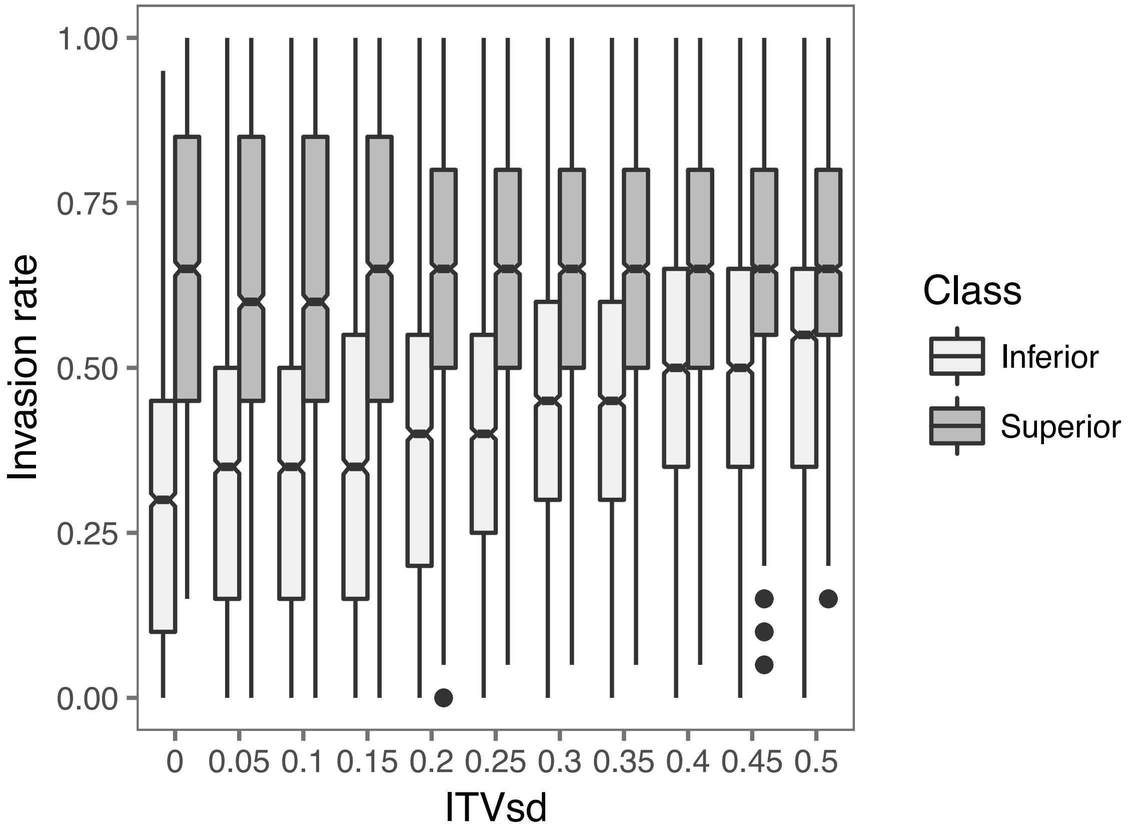

Figure 1. Pairwise invasion success rates. For each pair, the PFT with the lower invasion rate is classified as "inferior," and the higher as "superior." Notches represent 95% confidence intervals around the median.

Our more detailed approach based on invasion disparity reinforces the observation that, despite a great deal of variation being present among different pairs, there was a consistent pattern of the comparatively weaker PFTs becoming more likely to invade (Fig.

2A). However, while—consistent with the coarser metric—the superior PFTs (those with an invasion disparity greater than 0) did not change in their invasion probabilities on average, the more detailed metric indicates that a significant number of superior PFTs actually decrease in their invasion rate, especially those with the largest disparities without ITV. In other words, the PFTs that are the strongest without ITV are those that suffer the most with ITV (Fig. 2A). By contrast, inferior PFTs—those with an invasion disparity less than 0—invaded 22% more often with an ITVsd of 0.5 than no ITV at all.

When we consider abundance disparity, we find that PFT pairs who are relatively evenly matched usually both benefit as invaders, increasing in their post-invasion abundance (Fig. 2B). PFTs that are disproportionately strong without ITV, however, decrease substantially in post-invasion abundance with added ITV. On average, the positive impact of ITV on very low-abundance PFTs is relatively weak, with most of the benefit of added abundance being accrued to the PFTs who are somewhat evenly matched.

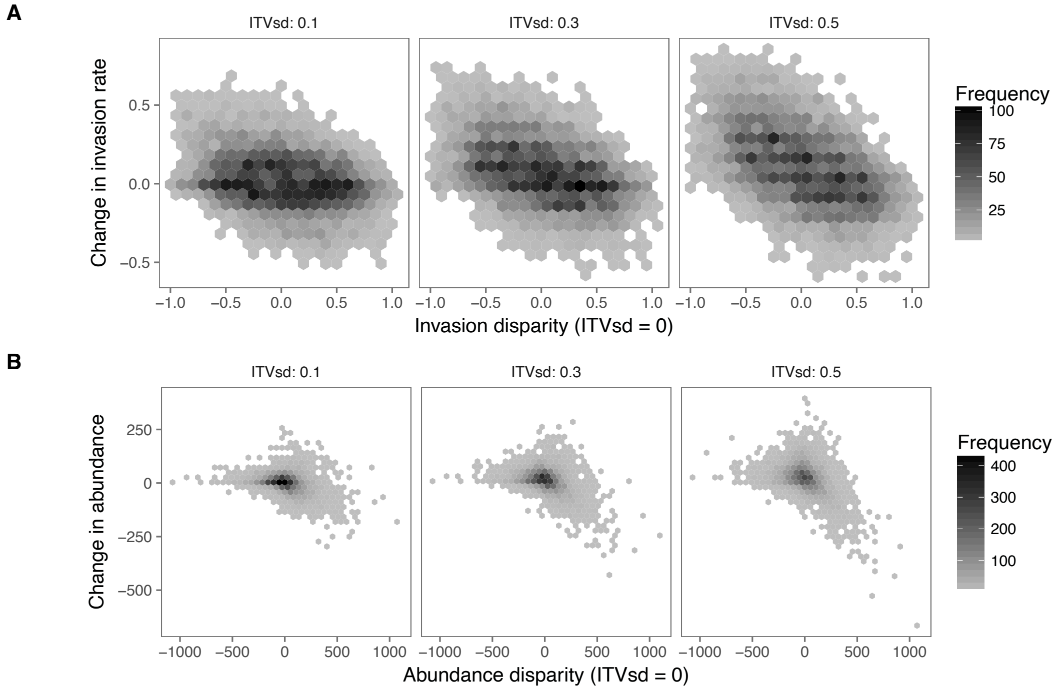

Figure 2. The more continuous measurements, for persistence and abundance disparities, changing with increasing ITV. For the persistence disparity (A), each point represents the average change in invasion rate from no ITV for one invasion (i.e. PFT A invading PFT B is a different point from PFT B invading PFT A). The abundance disparity (B) is the same process except using the species' abundances rather than their invasion rates.

2.3.2 Small-scale community assembly

The initial batch of simulations, varying the initial species richness of the initial input community, found that below a certain input community richness ITV increases Shannon diversity. However, with larger communities—initialized with either 32 or 64 PFTs—we found that ITV completely lost its ability to increase Shannon diversity over the long term. In fact, in these saturated communities, low levels of ITV decreased the amount of coexistence in the communities, compared to no ITV, albeit slightly (Fig. 3). From here, we focused on a moderate level of initial diversity (16 PFTs) to better understand how ITV impacts unsaturated communities.

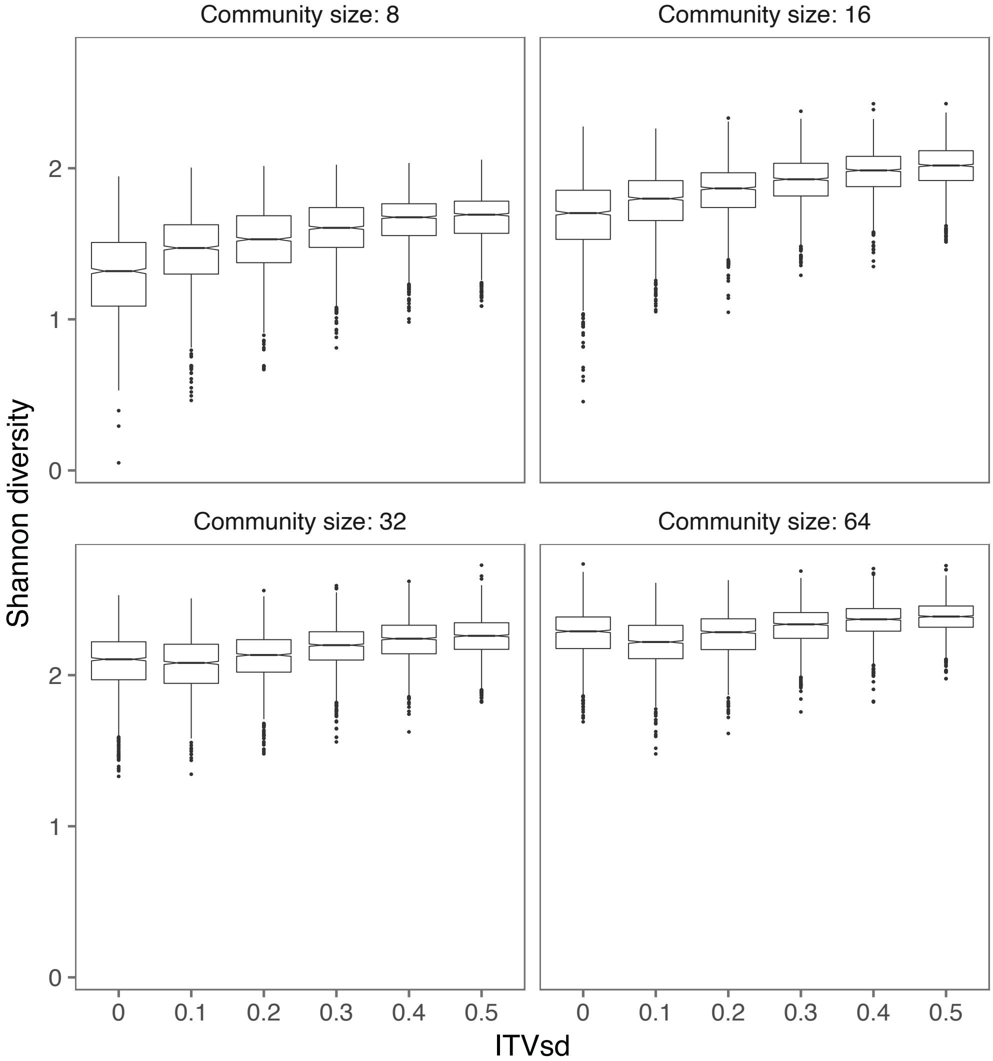

Figure 3. Effect of input community size on ITV's ability to increase diversity. With small input community sizes, ITV is able to increase the Shannon diversity of the final community. However, with larger initial species pools, the efficacy of ITV degrades and it does very little, apart from slightly decrease diversity with moderate values.

The 16-PFT communities show a gradual increase in Shannon diversity with ITVsd (Fig. 3B, Supplemental Material C Fig. 1). The amount of variation between communities and replicates also decreases substantially; without ITV, there are a number of communities that frequently fall to a richness of only two or three PFTs. The number of these outliers decreases with ITV, and the variation in Shannon diversity drops by half between no ITV and an ITVsd of 0.5.

Focusing on the differences between communities, there is a great deal of variation between how each community responds to an increase in additional trait variation (Fig. 4). We derived a linear mixed-effect model predicting the response of Shannon diversity to increasing ITV with a random effect of both intercept and slope for the community identity (marginal $R^2 = 0.27$, conditional $R^2 = 0.56$; Nakagawa and Schielzeth 2013; Lefcheck 2016). This statistical model shows that each community—initialized with a random sample of PFTs—will have a unique emergent structure and therefore, without ITV, has a different Shannon diversity (random intercept SD = 0.17). More importantly, we find that each community will respond to ITV differently because of these inherent compositional differences (random slope SD = 0.29). However, there is a consistent pattern which communities improve most with the inclusion of intraspecific variation. The linear model correlating the response of a community to ITV (i.e. the slope of the coefficients in the previous model) to the intercept of those communities without ITV shows a strong negative relationship (estimate = -1.22, R^2 = 0.50), meaning that ITV most positively increases the Shannon diversity of those communities that, without ITV, have the lowest Shannon diversity (Fig. 5). In other words, increasing ITV disproportionately helps those communities that are dominated by a few species.

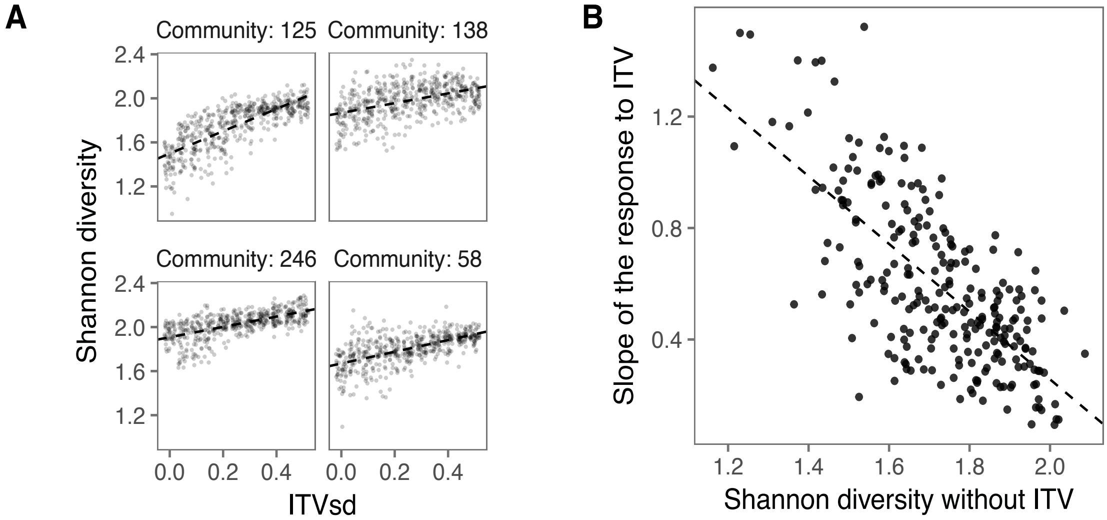

Figure 4. (A) Four randomly selected communities shift in their emergent Shannon diversity with increasing values of ITVsd. The intercept of each community represents the average Shannon diversity without intraspecific variation, which naturally varies based on the species introduced during model initialization. The slope of each fit represents how each community's composition influences its response to ITV. (B) Communities that start with lower Shannon diversity values without ITV generally increase more in their diversity relative to their already-high diversity counterparts. This linear model is derived with the intercept—the Shannon diversity without ITVsd—and slope—the response of Shannon diversity to ITVsd—of each community.

2.3.3 Relating the influence of ITV on invasion and community assembly

We next viewed changes in the community, i.e. changes in PFTs' persistence and abundance, through the lens of the changes within the pairwise invasions, either through their invasion or abundance disparities. We found that the PFTs which increase most in their persistence in the community context are those that have intermediate invasion disparity in pairwise experiments (Fig. 5A). In other words, it is not the "most inferior" PFTs that benefit from increased ITV at the community scale, it is those in the middle range of fitness. Interestingly, the abundance disparity shows a subtly different pattern (Fig. 5B). With low levels of ITV, it is the moderate PFTs that increase both in their average persistence as well as their abundance. However, as the amount of ITV in the system increases, we found that some highly ranked PFTs begin to decrease in both their persistence as well as abundance, and that other highly ranked PFTs seem to take their place, increasing substantially in their abundance as well as persistence.

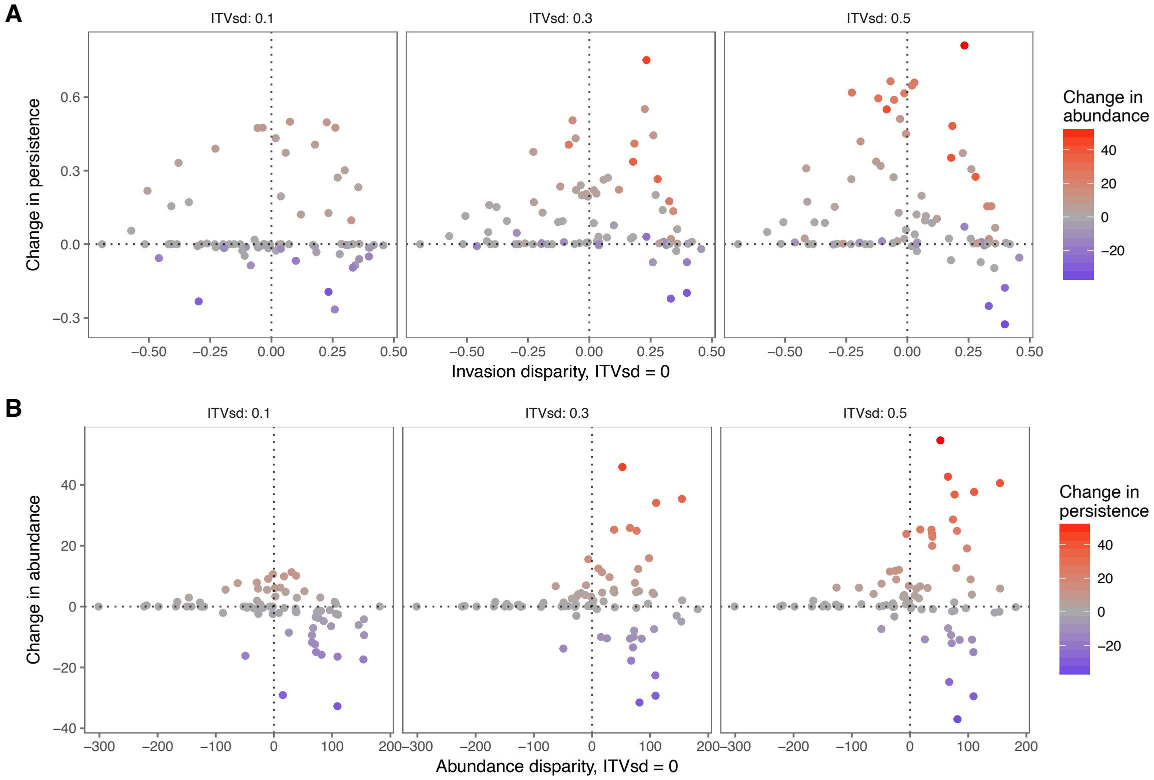

Figure 5. (A) Each PFT's change in persistence, averaged across all communities it is present in, in relation to that PFT's invasion disparity value without ITVsd. Color represents the corresponding average change in abundance for that PFT. PFTs in the middle of the invasion disparity spectrum—those that are usually evenly-matched against the other PFTs—increase the most in their persistence at the community level. (B) represents this same process except averaging the PFTs' change in abundance against their abundance disparity. With low levels of ITV, several of the stronger PFTs decrease in their abundance, while many PFTs in the middle of the disparity—those that are often evenly matched in their abundance with the resident species—increase in their abundance. With higher ITVsd values, this effect changes, showing an increasing amount of relatively strong PFTs—those that outcompete more, but not all of their competitors—become the strongest, while other PFTs at the high end of the spectrum become weaker and persist less frequently.

Further, as the level of ITV increases, there are fewer unaffected PFTs; with the lowest level of ITVsd (0.05), 50 out of 81 PFTs are on average left unaffected in their communities. With the highest level of ITVsd (0.5), 35 are unaffected in their communities in their persistence and 42 in their abundance. Not all of the PFTs benefit positively from the inclusion of more ITV into the simulation. Several, almost entirely at the higher end of the abundance disparity spectrum, decrease in both their community-level persistence and abundance with the inclusion of more ITV. Interestingly, this effect is felt almost immediately, even with very low levels of ITV.

For the most part, while many PFTs increase in their persistence, sometimes quite significantly, most are relatively unchanged in their average abundance (Fig. 5A). This indicates that most species are more reliably "hanging on" to persistence as rare species—not becoming significantly more abundant. Those that increase the most in their abundance seem to be PFTs that already do quite well, but only when they actually are present in the community.

2.3.4 Using random forests to understand which traits drive invasion and assembly

Pairwise invasion experiments

Random forests for the pairwise experiments reveal that the traits governing the ability of a PFT to invade, i.e. to persist even if only just, are different from those governing its a population (Fig. 6A). We find that the most important predictor of invasion success is consistently the resident's SLA, remaining static in its importance across ITV relative to the other traits. Partial dependence plots (Supplemental Material E Fig. 1) reveal that low SLA residents are significantly easier to invade than medium and high SLA species. The relative importance of the invader's g_{max} changes the most, linearly increasing with ITV, but this is the only important trait from the invader's set. With the residents' traits, each varies with ITV: resident g_{max} and LMR become slightly less important, while m_{max} becomes slightly more. However, none of these effects are pronounced.

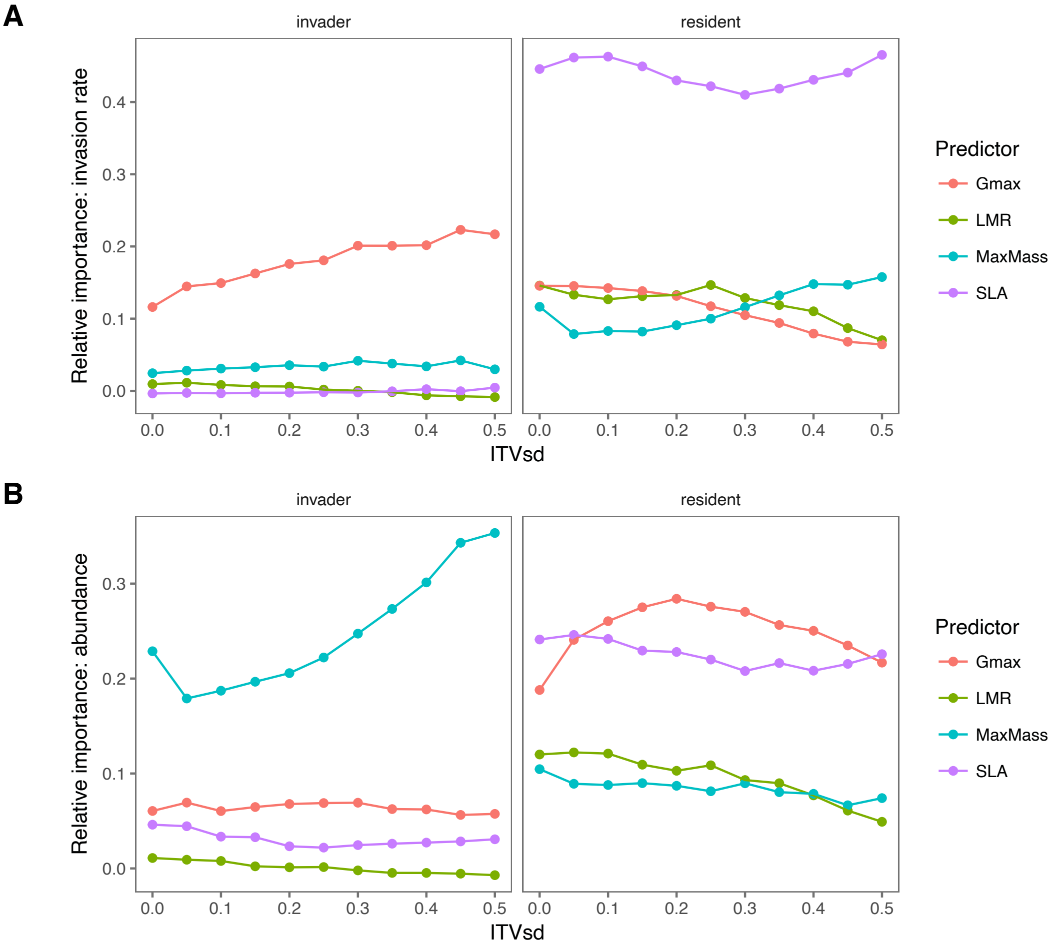

Figure 6. (A) Random forest relative importance of each functional trade-off in predicting a PFT's invasion success rate across an ITVsd gradient. Resident traits far overwhelm invader traits in importance. While most invader traits do not change in their importance over ITVsd, invader g_{max} does increase in importance. Resident SLA is the most important functional trait and maintains its importance regardless of ITVsd. While the other resident traits do vary with ITVsd, none do to a great extent. (B) Random forest relative importance of each functional trade-off in predicting the invading PFT's final population size across a gradient of ITV. The invading PFT's m_{max} is the most responsive trade-off to increasing ITV, but all other invading PFT's traits are unresponsive. The resident's traits are generally more important than the invading PFT's traits in determining its final population size.

Switching to predicting invader abundance (Fig. 6B), the two most prominent shifts are, first, that the invader's m_{max}, rather than g_{max}, is most predictive in describing final population size and becomes steadily more important in proportion to the other traits. The partial dependence plots (Supplemental Material E Fig. 2) show that low m_{max} invaders reliably acquire high population sizes, while high m_{max} invaders have significantly lower population levels. Moderate sized PFTs fall somewhere in the middle. Second, the residents' g_{max} is also now a significant trait. The partial dependence plots show that it is much easier for an invader to obtain a high abundance if invading a low g_{max} resident than medium or high g_{max} residents.

These random forests, focusing on invasion rate and abundance, explain 80% and 90% of the variance ($R^2 = 0.80$; $R^2 = 0.90$), and correlate to the testing dataset with coefficients of 0.87 and 0.94 respectively.

Community assembly

The first set of random forests, trained to predict persistence of the PFTs in the final community (Fig. 7A), shows that g_{max} and m_{max} are by far the most important traits in predicting performance. LMR and SLA are largely uninfluential. While g_{max} and m_{max} start as equally important without ITV, with low a low ITVsd g_{max} becomes critically important, before being gradually overtaken by m_{max} with the highest levels of ITV. Partial dependency plots (Supplemental Material E Fig. 3) indicate that PFTs with a low g_{max} rarely persist until relatively high levels of ITV, when their persistence rate gradually increases by 50%. This reduces the difference between the predicted persistence of PFTs with different g_{max} values, which therefore reduces the amount of sway—importance—the trait has in determining the persistence rate of a given PFT. The partial plots further indicate that a very low level of ITVsd (0.05) significantly increases the persistence rate of the largest sized PFTs, which otherwise persist rarely. This initial bump in persistence rate also

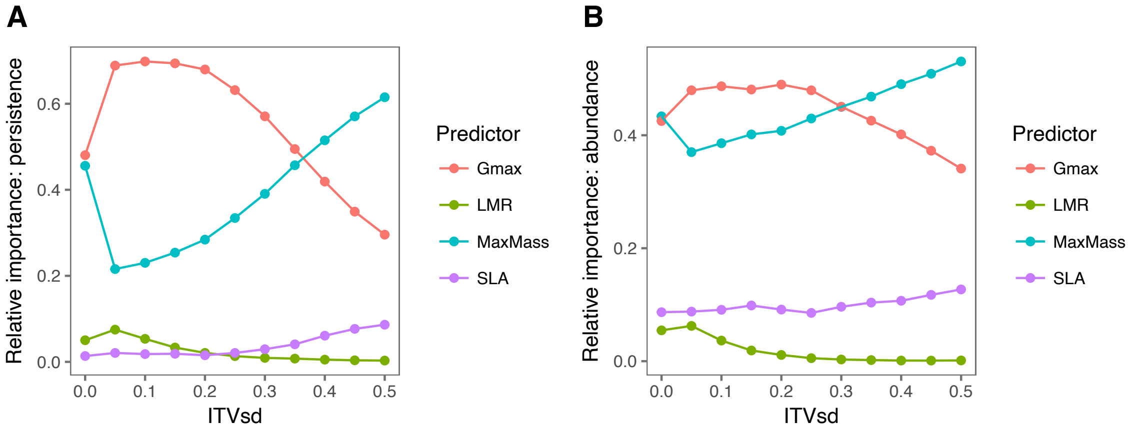

Figure 7. Random forest relative importance of each functional trade-off as predictors of persistence probably (A) and final population size (B) in the community assembly simulations. Measuring how often a PFT is present in a community is not substantially different from measuring how abundant it is within the community g_{max} *is regardless the most important trait, with* m_{max} *close behind for both metrics.*

decreases the distance between the predicted persistence rates of different levels of m_{max}, which perhaps explains the immediate and significant fall in the traits relative importance.

The second set of random forests, trained on the final abundances of the PFTs (Fig. 7B), conveys a very similar pattern to the persistence dataset: g_{max} and m_{max} are the most important, while SLA and LMR remain unimportant. This set of forests, however, is less extreme than the first. While LMR again loses its importance entirely with more ITV, SLA actually explains slightly more variance than it did before. Further, while their pattern remains consistence, the trade-off between g_{max} and m_{max} are significantly less peaked. Partial dependence plots (Supplemental Material E Fig. 4) are largely consistent with those of the persistence dataset.

Both sets of random forests explain roughly 75% of the total variance ($R^2 = 0.75$) and correlated with the testing data with a coefficient of 0.92.

2.4 Discussion

Bolnick et al. (2011) argue that theoreticians must seek to understand not just to what extent traits vary intraspecifically, but also what ecological implications this variation has. Our methodology enables us to watch, in silico, the consequences of trait variation scale from pairs to communities. This provides insight into how ITV affects biodiversity in an environment with multiple competing species and multidimensional trade-off axes.

2.4.1 Pairwise invasion experiments

In pairwise invasion experiments, we found that ITV significantly promotes the ability of the weakest PFTs to successfully invade, but perhaps more importantly it increases the abundance of PFTs in the middle of the competitive hierarchy and decreases the abundance of the dominant PFTs. While the weakest PFTs may see the largest percent change in persistence or invasion success, they are still disadvantaged in their fitness compared to the other PFTs. Because ITV works on all of our trade-offs, a PFT that is well positioned on most trade-off axes for the given environment—and need only improve on one axis—will be the PFT that sees beneficial impact on their population size. And, since our traits are components in underlying trade-offs rather than demographic rates, already having the optimal position for all traits will mean that variation only hurts a PFT's abundance. An interesting observation lies in that the traits critical to invasion are not necessarily the same as those conveying abundance for the pairs (Supplemental Material E). For example, the invader's m_{max} is unimportant in predicting persistence, yet crucial for conveying abundance. This behavior demonstrates an inherent difference between these two processes: given the model is spatially explicit, only so many plants can fit into 1 m^2. Larger plants take up more space, therefore decreasing the predicted population abundance (Supplemental Material E) and making the mass of the invader important. However, this relationship is inconsequential for persistence, because any abundance counts as persistence.

2.4.2 Community assembly

Shifting to the perspective of community assembly, we find that the impact of ITV is significantly dependent on the richness of the species pool and even the specific PFTs initially present. With many species introduced to our relatively small spatial scale, we observe that ITV does little to improve diversity. Our "species" are simply permutations of traits evenly spaced along all four trade-off axes. When these axes are packed with interspecific competitors, there will be little room for ITV to improve the fitness of sub-optimal PFTs; for every inch gained by a very weak PFT, a slightly less-weak PFT will get even closer to the optimal trait set. This finding is in concurrence with previous empirical literature, which has found that ITV is more likely to promote coexistence when alpha-diversity is low and therefore inter-specific diversity relatively limited (Albert et al. 2011, Kraft et al. 2015). In agreement with Barabás et al. 2016, if the trade-off axes are "saturated," ITV will not improve diversity. Contrary to their results, however, apart from an initial—albeit slight—drop in diversity with a moderate *ITVsd*, ITV *per se* does not decrease the number of coexisting species in the saturated case.

This result may be consistent with the importance of space in differentiating our approach from those previous. Although it is well appreciated in the study of coexistence, to our knowledge no theoretical work has incorporated spatially-explicit dynamics into their model of ITV. Considering ITV without paying attention to the target individual's neighborhood may be similar to disregarding the impact of alpha diversity; just as an area's local diversity will determine a species' ability to persist, an individual's neighborhood will determine its relative fitness. Of course, over larger scales both of these influences' importance degrade, but the study of ITV is normally considered important only at the small spatial scale (Albert 2011).

Lastly, the observation that low alpha-diversity communities are those most benefitted by ITV is further reinforced in that one of the most striking differences between low and high ITV scenarios is not necessarily the moderate change in median diversity, but the drastic change in its variation. Even a moderate level of ITV leads to a large decrease in prevalence of extremely low-diversity communities. These communities, which without ITV would be only two or three species, are the main beneficiaries of moderate ITV scenarios, when most communities only see a marginal change in their overall diversity.

One caveat regarding our community results and their interpretation is that we assumed immigrant PFT's were a random sample from the species pool, despite there being differences between PFTs—perhaps even more so with ITV—that would mediate which species make it into the initial community. We decided to ignore this possible effect because it would demand the inclusion of arbitrary assumptions and further complexity. Future studies should investigate this initial sorting from the species pool in more detail to understand its influence.

It should also be noted that the initial number of individuals in the simulations varied with the size of the species pool because each PFT started with 10 individuals. Initial communities from species-rich pools thus had much higher initial densities. We considered this assumption more realistic than assuming a certain fixed initial number of individuals, but from a theoretical point of view it might be interesting to explore the effects of initial density, in particular in terms of the saturation effect that we assumed regarding the effects of ITV.

It is lastly also necessary to reflect on the importance of the models' intraspecific negative density dependence (INDD), modelled phenomenologically based on species identity rather than the species'—or individuals'—traits. This presents a confounding variable that is explored in Supplemental Material D, and should be considered for full context when considering our model's results. INDD is critical to the long-term persistence of the community; without it, regardless of ITV, diversity gradually declines over 50 simulation years to one or two species. Although without INDD ITV continues to increases diversity, its impact is likewise short-lived; even with ITV diversity will eventually decline. Future work with the IBC-grass model should replace the mechanism on which INDD works—the species—with either some additional trait or the relative similarity of two individuals within trait space. Even with this limitation, however, the species' traits are the only factor responsible for their relative fitness (i.e. the impact of INDD is constant across species), and therefore it is valuable to consider ITV's impact on their traits and consequently their fitness.

2.4.3 Scaling from pairs to communities

When we look more closely at how ITV influences coexistence, we see parallels between how it behaves in pairs and communities, as well as striking differences. While the traits most important in driving abundance are similar for both pairs and communities, those driving invasion success are very different. For pairs, the most important traits in determining invasion success—defined as a population greater than zero at the end of the simulation run, i.e. presence/absence—were overwhelmingly the resident's SLA and then the invader's g_{max}, with ITV mostly interacting with the invader's g_{max}. Extrapolating this finding to the community scale, one would expect to find that SLA and g_{max} are the driving traits behind persistence in the community as well. However, this is not the case; SLA is one of the least important traits in determining a PFT's ability to persist in a community. Further analysis (see partial dependence plots, Supplemental Material E) reveals that the ability of a species to invade is heavily influenced by the SLA of the resident species; low SLA residents are much more accepting on invaders. One potential explanation for this phenomenon is that SLA is a dominant trait in the derivation of a plant's ZOI. Given that germination is prohibited when a cell is covered by a plant, large SLA plants may cover more area and therefore better resist invasion than their low SLA counterparts. While this behavior is important to resist invasion, it is relatively unimportant in predicting abundance. This is an important observation, because it undermines the idea that behavior level of pairwise interactions can be extrapolated to the community scale (Roxburgh and Wilson 2000). Indeed, recent literature has called into question this frequent assumption, arguing that high-order interactions (e.g. interactions chains and intransitive competition) can and often will drive local assembly dynamics, and baffle the predictions made through observations of pairwise coexistence (Soliveres et al. 2015, Gallien et al. 2017, Grilli et al. 2017, Levine et al. 2017). Our results therefore reinforce the idea that communities are more than the sum of their pairs.

Interestingly, however, we do find similarities in the random forest variable importance of abundances in the pairwise and community contexts. Although not completely comparable, the hierarchy of the traits' importance and shape of their interaction with ITV suggests that the processes governing abundance are much more similar between pairs and communities than are the processes that govern invasion and persistence. In other words, the processes that increase a species' growth rate at low density may not be important at high densities.

Overall, our trait analyses indicate that the role specific traits play in determining ITV's effects on the community level is complex and that simple lessons are hard to extract. One reason is that for both invasions (from the resident's and invader's perspective) and long-term coexistence, different demographic processes are often important (e.g. reproduction, establishment, competition, growth and mortality). All of these processes are driven by different traits—and combinations of traits—and the relative importance of each process can depend on the relative density of the species (e.g., as an invader or a resident species in invasion experiments) or the trait syndromes of the other species in the community. Given potential idiosyncrasies of our model, we do not claim that our results will mirror the relative importance of traits in nature. However, our simulated results highlight the critical issue that the effects of any trait-based study might be strongly determined by the choice of specific traits, possible trade-offs, and the specific demographic processes that are included. Further simulation experiments with our and other models in combination with well-designed experiments on how traits and trait combinations modify ITV impacts on biodiversity are likely the best option for further insights.

Lastly, within both the pairwise invasion experiments and the community assembly experiments, it is not the weakest, but the average, species that benefit most from the inclusion of ITV. While the most common species often decline in their abundance, the average species tend to increase in both their persistence and abundance. Rare species, on the other hand, tend to only increase in their persistence. This suggests that although weakest species benefit from ITV, this benefit is not strong enough to confer a population size large enough to ensure persistence over the long term. It is probable that although these species are able to persist at low density, environmental perturbations or demographic stochasticity could easily extirpate them from the system. While ITV may not be influential enough to enable the weakest species to consistently survive, it is strong enough to enable an average species to increase in abundance substantially. Those species in the middle of the abundance disparity were the first species to increase in their abundance. Interestingly, as more ITVsd is included to the simulation, we see that those species that are not necessarily always present but are competitive when they do, that benefit the most in their abundances. These species have a high value in the abundance disparity, often outperforming their counterparts in terms of population size, but are mediocre in their invasion disparity, i.e. often in the middle. It is perhaps the case that variation in some trait weakens the competitive advantage of the most fit species and releases these from their suppressing influence. This could be accomplished by either helping the newly fit species or hurting the previously dominant one.

2.5 Conclusions

Theoretical models of ITV have made good progress in outlining the possible impacts of ITV on community assembly. Our computational approach adds to this growing body of knowledge, as it fills in gaps left by the assumptions of the existing mathematical approaches. However, until empirical research begins to encounter these results with data, we must consider that ITV could—and probably does—influence communities in widely different ways depending on the scale and species present. This complication, coupled with the difficulty of extrapolating pairwise invasion experiments to the community level, will inevitably slow our understanding of ITV's impact on coexistence and biotic interactions, especially given the difficult task that is its empirical study (Turcotte and Levine 2016). Future research into ITV's community-level impact should be careful to quantify the alpha- and beta- diversity components of their study sites, as these relationships may determine whether ITV is helpful or harmful for coexistence.

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3. Root herbivores interact with belowground resources to mediate plant community resilience and succession after disturbance in a grassland model

Abstract

A disturbance that disproportionately impacts one of multiple trophic levels may trigger new interactions between them. These effects could be important in understanding primary succession in grassland ecosystems, which are frequently subject to disturbance driven by agricultural practices such as eutrophication, mowing, and exposure to herbicides or pesticides. While literature has investigated the influence of aboveground herbivores on primary succession, few studies have researched that of root herbivory, even though current meta-analyses indicate it may be as or even more important in shaping the plant community than its aboveground counterpart. Outlining the ways root herbivores impact these systems, and describing how other aspects intrinsic to disturbances (such as their timing and intensity) interact with their effect, is thus important to guide future work. We therefore incorporate root herbivory into a grassland community model and then introduce a pulse disturbance—replicated along a gradient of intensity—that kills a given percentage of the plant community. After the disturbance, we examine the differences between the resistance and recovery of the communities with and without root herbivores. We find that high resource, low diversity, communities are significantly more impacted by the presence of root herbivory than low resource, high diversity, communities. In high resource communities, root herbivores lower the resistance and increase the time to recover. In low resource communities, by contrast, root herbivory only slightly lowers the resistance of the community, and actually decreases the time it takes for it to recover to its previous state. This suggests that the level of belowground resources mediates the influence of a common trophic interaction on this system's stability. We finally considered how some memory of the pre-disturbance community impacts the system's resilience, by either incorporating a long-term seed bank or by shifting the disturbance until after the plants' seeds have already dispersed. We find that both measures diminish the disturbance's impact. Taken together, our results suggest that root herbivores may be of critical importance in understanding grassland resilience and stability.

Crawford, M. et al. 2019. Root herbivores interact with belowground resources to mediate plant community resilience and succession after disturbance in a grassland model. *Rejected with invitation to resubmit at OIKOS.*

3.1 Introduction

It is essential to understand how communities respond to disturbance as human-mediated environmental change stresses many ecological systems. A system's resilience—its tendency to remain in, or return to, its original state after being disturbed (Holling, 1973; Grimm and Wissel, 1997; Hodgson et al. 2015)—is determined by the disturbance's properties as well as those of the system itself. When a community undergoes a disturbance that disproportionately impacts only one of its trophic levels, new interactions may alter that community's successional path, with resulting changes in biodiversity and ecosystem functions (Wootton 1998).

Understanding these processes is particularly important in grasslands, which are frequently subject to human disturbance such as mowing, eutrophication, and exposure to pesticides or herbicides (Fischer et al. 2010). Within this system, understanding how the trophic interactions between plants and their consumers—their herbivores—change with disturbance has driven a significant body of literature (Davidson 1993; Coffin et al. 1998; Carson and Root 1999). However, despite over 40-70% of net primary productivity being belowground (Vogt et al. 1996) and root herbivores likely removing as much or more biomass than foliar herbivores (Zvereva and Kozlov 2012, 2017), only a few studies have been conducted on how root herbivores mediate succession after disturbance (but see Brown and Gange 1989; De Deyn et al. 2003; Schädler et al 2004). We hypothesize that, when they are present in a grassland, the feeding preferences of these herbivores will shape the successional dynamics of the plant community after disturbance. However, it should also be considered that aspects of the disturbance (e.g. its timing and intensity) as well as parameters of the grassland itself (e.g. resource levels, or whether a seed bank in present) may also shape this effect.

Broadly, it is known that the concentration and feeding preferences of root herbivores may guide the process of community assembly in favor of specific species or plant functional types (PFTs; Maron 1998; Sonnemann et al. 2012, 2013; Borgström et al. 2016; Pfestorf et al. 2016), potentially promoting herbs at the expense of grasses, though no single functional attribute is sufficient to predict a species' response (Stein et al. 2010). In principle, if root herbivores tend to prefer the dominant species in a grassland (as found in Sonnemann et al. 2012, 2015), they may reduce the fitness difference between strong and the weak species. This effect may be especially pronounced after disturbances, when the amount of edible belowground biomass in a plot is suddenly reduced. Because the previous vegetation supported a higher density of herbivores, if the herbivores remain they will exhibit an intense selective pressure on the emerging plant community, potentially leading to the emergence of nonlinear—and difficult to predict—succession dynamics.

Importantly, aspects of the disturbance, such as when it occurs during the growing cycle, may also be important in determining the root herbivores' impact on succession. Empirical studies have shown that disturbances can change species composition (Smith 2006) and even drive some species to local extinction based on when in the plants' life-cycle they occur (Crawley 2004). Using a mathematical model, Miller et al. (2011) demonstrated that succession after disturbances early in the growing season—before seed production and dispersal—is mediated by the storage effect, because the plant species will rely on their seed banks from the previous vegetative period to reestablish their populations. Biodiversity maintenance after late disturbances, by contrast, will depend on competition between the species. We suggest that root herbivores may influence these relationships by differentially impacting the endogenous grassland species.

The herbivores will also interact with other aspects of a grassland, such as its level of resources (e.g. nutrients and water), or whether a seed bank is present, in shaping the plant community after a disturbance. For example, Borer et al. (2014) found that aboveground vertebrate herbivory "rescued" diversity at sites that would be otherwise driven to low richness by eutrophication. However, few studies have investigated how root herbivores affect assembly during initial community assembly (but see Schädler et al. 2004, Borgström et al. 2017). It remains unclear, however, how the combination of these effects would together mediate succession after disturbance.

In this study, we use a model of grassland community assembly to investigate how the feeding preferences of root herbivores mitigate or amplify the impact of disturbance on grasslands under variable abiotic conditions. In the model, after an initial phase in which the plant community settles into quasi-equilibrium, we disturb it along an intensity gradient by destroying a variable percentage of the plants. We then observe, for different types of herbivory, nutrient levels, seed banks, and disturbance timings, how intensely Shannon diversity responds immediately after the disturbance (resistance), how long it takes for the initial plant community to return to its pre-disturbance Shannon diversity (return time, a measure of recovery), and how the size structure of the community changes through time. Our results indicate that root herbivores shape the plant community multidimensionally, with their impacts tightly tied to the amount of belowground resources present in the grassland. We discuss the repercussions of these patterns on the emergent grassland community as well as the dimensionality of its stability (Donohue et al. 2013).

3.2 Methods

We used the individual-based and trait-based, spatially-explicit grassland assembly model, IBC-grass (May et al. 2009), and added root herbivory and disturbances. Since its introduction (May et al. 2009), IBC-grass has been used to investigate different aspects of grassland community dynamics (Körner et al. 2014; Weiss and Jeltsch 2015; Pfestorf et al. 2016; Reeg et al. 2017; Reeg et al. 2018). Importantly, Weiss et al. (2014) parameterized the model with data from trait databases and a survey of plant functional types (PFTs) from German grasslands collected through the Biodiversity Exploratories (Fischer et al. 2010; Pfestorf et al. 2013). The model successfully reproduces, without calibration at the community level, empirically-observed grassland biodiversity patterns.

A full description of the original model and our modifications can be found in the ODD (Overview, Design concepts, Details) protocol (Grimm et al. 2010, 2006; Supplement A). The following is a brief summary of the model as well as an explanation of our modifications to it.

3.2.1 Overview of the IBC-grass model

IBC-grass simulates local community dynamics on a 141 x 141 cell grid, where each cell corresponds to 1 cm^2 (i.e., a roughly 2 m^2 grid space) and can hold one plant's stem. Its time step corresponds to one week, and there are 30 weeks per year representing the vegetation period. A plant is characterized by its functional traits and the biomass of its three distinct compartments: aboveground mass, belowground mass, and reproductive mass. A plant's competitive area is defined by an aboveground and a belowground “zone of influence” (ZOI). The two ZOIs are both circular areas around the plant’s stem, from which it acquires either above- or belowground resources (Schwinning and Weiner 1998; Weiner et al. 2001). While the plant’s stem is contained within one grid cell, its ZOI can cover many.

When two plants' ZOIs overlap they compete for resources. A cell's aboveground resources correspond to light while its belowground resources correspond to water and nutrients. The proportion of a cell's resources a plant obtains during competition depends on its competitive abilities and how many other ZOIs overlap the cell. Aboveground competition is size-asymmetric, i.e. the larger plant takes up resources from each contested cell not only in proportion to its competitive ability, but also in proportion to its aboveground mass and height advantage over the smaller plants (Supplement A). In other words, aboveground competition disproportionately favors the larger competitor. Belowground competition, however, is size-symmetric, i.e. only their competitive abilities are taken into account. Intraspecific competition is also included in the form of negative-density dependent competition, reflecting species-specific predators or pathogens (May et al. 2009). This density-dependent competition was modeled by decreasing the resource uptake of an individual in proportion to the square-root of the number of conspecifics in its neighborhood ZOI. All grid cells' total resources are kept constant through space and time; only a plant’s biotic neighborhood influences the amount of resources available to it at any given time step.

When a plant is unable to gather enough resources, it changes its resource allocation between above- and belowground parts, depending on which compartment is more limited (i.e. shoot or root). If resource uptake in either of the two compartments is below a certain threshold, the plant is considered stressed. Each consecutive week a plant is stressed increases its chance of mortality linearly, in addition to a background, stochastic, annual mortality of 20%.

Aboveground grazing events occur with a probability of 0.2 per time step and reduce the aboveground biomass of grazed plant individuals by 50% and remove all of its reproductive mass. Plants are subject to grazing based on a weighted lottery, with the tallest and most palatable individuals being the most prone to being grazed (Díaz et al. 2001).

Plants are characterized by four sets, or syndromes, of functional traits, a subset of those proposed as the “common core list of plant traits” by Weiher et al. (1999). The first set of traits defines the plant's maximum size (m_{max}), which positively correlates with seed size and negatively correlates with dispersal distance (Eriksson and Jakobsson 1998; Jongejans and Schippers 1999). The second defines the plant's growth form, or leaf to mass ratio (LMR), which describes the plant as either a rosette, erect, or intermediate growth form type. The third set defines its competitive ability, or maximum resource utilization per time step (g_{max}), and negatively correlates with its stress tolerance (Grime 2001). The fourth trait set describes the plant's grazing response, positively correlating its palatability with its specific leaf area (SLA) (Westoby et al. 2002).

3.2.2 Root herbivory

Root herbivory was implemented such that each time step some percentage of the extant biomass is removed from each of the plants, with a gradient of preference in root size ranging from generalist to preferential (i.e. disproportionally eating larger root systems).

The feeding need at week t, n_t, is calculated as a defined percent (feeding rate, f) of that week's expected root mass, which is estimated by averaging each previous week's total realized root biomass R_i for the previous w weeks,

$$n_t = f \cdot \frac{\sum_{i=t-w}^{t-1} R_i}{w} \qquad \text{eq. 1}$$

For this analysis, the feeding rate (f) is 0.2 per week, an approximation of a typical root herbivory pressure (Zvereva and Kozlov 2012), and the number of weeks used to estimate the expected root mass, w, is 10. This value ensures that the herbivores have normalized by the beginning of the next vegetative season. Both these parameters are tested for their sensitivity in Supplement B but held constant in the following analysis.

The biomass to be removed from each individual's root mass $(g_{i,t})$ is calculated each week as:

$$g_{i,t} = \left(\frac{r_{i,t}}{R_t}\right)^{\alpha} \cdot n_t \qquad \text{eq. 2}$$

where $r_{i,t}$ is the expected root mass of individual i in week t and R_t is the week's realized total root mass, which may differ from the expected root mass especially after disturbance (Supplement A, Fig. A3). R_t differs from R_i in eq. 1 in that R_i refers for the total realized root biomass on week i, whereas R_t refers to the total realized root biomass on the current week. The parameter α represents the generality of the herbivory; set at $\alpha = 1$, $g_{i,t}$ will equal the plant's root mass $(r_{i,t})$ in proportion to the total root mass (R_t) at time t. Above 1, α will increase the preference of the herbivores to disproportionally favor large root systems (Sonnemann et al. 2013). This parameter is measured for sensitivity in Supplement B but here set at either 1 (generalist) or 1.25 (preferential). If the biomass to be removed from a plant is larger than its total root mass (which may occur, based on the distribution of plant biomasses and α), the plant is killed and the overshoot biomass remains in the feeding need (n_t), to be removed from other plants.

The amount of edible biomass will be significantly reduced immediately after the disturbance (see Supplement A, Fig. A3), but a large number of herbivores will remain in the system. During these initial few weeks, when there is less root biomass available to the herbivores than their feeding need, we leave a small amount of the total root biomass ungrazed to mimic a feeding response wherein the herbivores would have to spend more time searching for the remaining biomass. This percentage is set at 5% of the total root biomass for the following analysis but is tied—positively correlated—to the feeding rate (f) and inspected in the sensitivity analysis (Supplement B).

3.2.3 Disturbance

Disturbance was modelled parsimoniously, as a pulse causing the death of some percentage of the plant individuals, chosen randomly. When a plant is killed, its above- and belowground biomass is left to degrade normally (see Supplement A: Plant growth and mortality). Using this simple model enables us to focus on the influence of root herbivores on succession by simplifying the high-dimensional impacts of the disturbance itself. The disturbance occurs once during the simulation after a "burn-in" period of 100 simulation years, either directly before or directly after seed dispersal, and does not impact any dispersed seeds or the root herbivores. With only a transient seed bank, a complete disturbance of the community before seed dispersal will therefore result in the community being "reset" entirely through immigration (see Supplement C), while a complete disturbance after seed dispersal will mean that the "memory" of the community's previous species abundance distribution is also present, potentially decreasing the time it takes for the community to recover. The seed bank is parameterized into two types: transient and long-term. Transient seed banks exist for only one year, so that the seeds dropped during the last year have a chance to establish in the current year. In long-term seed banks, the seeds are able to persist for three years, barring germination or overwintering mortality (with a probability of 0.5 per year). This is also tested for its sensitivity in Supplement B.

3.2.4 Simulation design and experiments

The plant community was composed initially of 10 seeds of each of the 86 PFTs parameterized by Weiss et al., 2014, who fit data from the Biodiversity Exploratories (Fischer et al., 2010) into the trait framework of IBC-grass. Initial germination probability was preset to 1.0 to insure equal initial population sizes for all PFTs. A constant number of seeds of each PFT (10 seeds/PFT/m^2; Weiss et al., 2014) were added into the grid per year to mimic seed addition from the meta-community. Aboveground herbivory by livestock reflects a moderate level of land-use (May et al., 2009), with a 20% chance per week of a grazing event (i.e. the stochastic removal of 50% of aboveground biomass, see Supplement A).

Simulations were run on a disturbance gradient with 26 levels, killing from 0% (the control) to 100% of the plants, and coupled with two different disturbance timings (either before or after seed dispersal). The root herbivory was either generalist ($\alpha = 1$) or preferential ($\alpha = 1.25$), and the percentage of biomass being removed weekly was held constant at 20%. There were two seed bank scenarios; one in which dropped seeds could survive in the seed bank for one year, and the other for three. All seeds were subject to normal winter mortality (50%) each year (May et al. 2009). The interaction of root herbivory and disturbance was tested on two levels of belowground resources, either limiting (60 belowground resource units; Weiss et al. 2014) or rich (90) soil resources. Aboveground resources—light—were held constant and high (100 aboveground resource units). Each simulation lasted 300 years, with the disturbance occurring on year 100 (after the community settles into a quasi-equilibrium), and each parameterization was replicated 100 times.

To understand how belowground grazing interacts with disturbance to guide succession, we primarily focused on Hodgson et al.'s (2015) two resilience metrics: resistance and recovery. Resistance was measured as the absolute change in a community's Shannon diversity one growing season after the disturbance (i.e. year 101), and recovery was measured as the number of years it takes for a community's Shannon diversity to return to its pre-disturbance levels (return time). Return time was defined as the number of years it took for a given simulation's Shannon diversity to pass within $\pm 1\ \sigma$ of the controls'—no disturbance—mean Shannon diversity. This methodology is visualized in Fig. 1, and Supplement D1 contains a visualization of example communities, tracing each PFTs' abundance through time with the different herbivory, seed bank, and belowground resource scenarios.

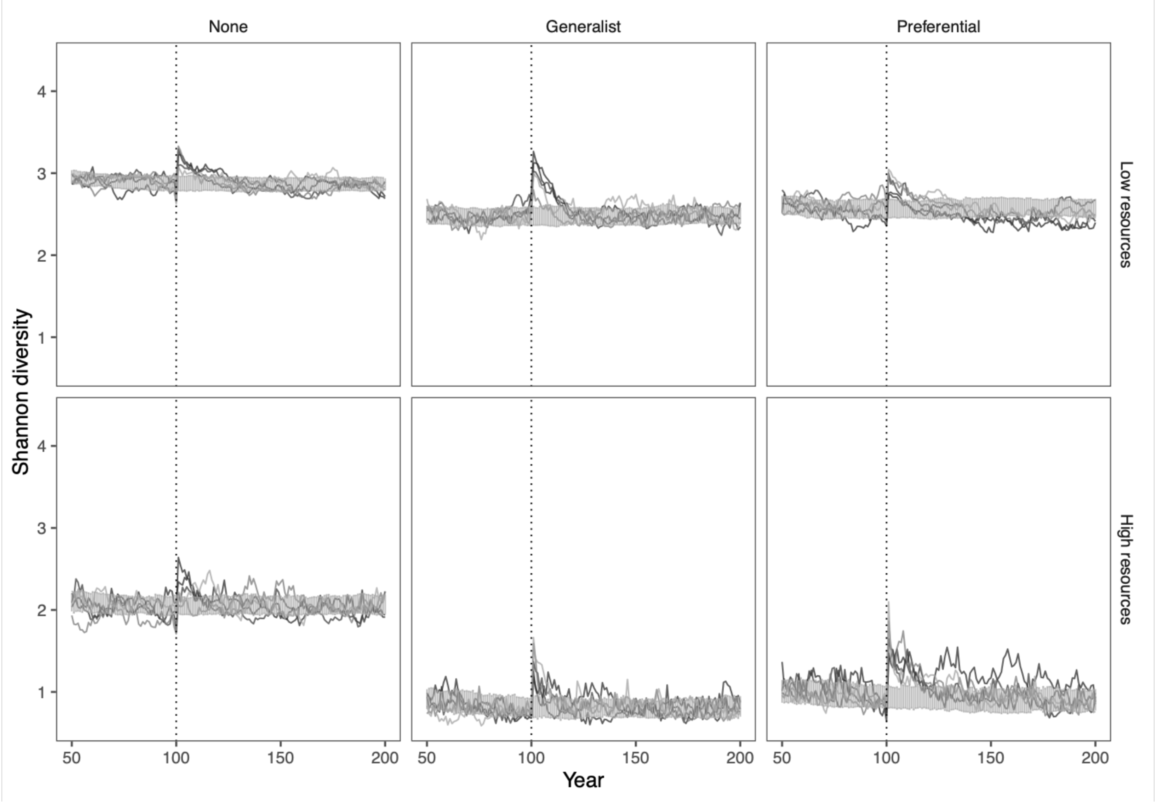

Figure 1. Shannon diversity of the plant community over time for five replicates (each a shade of gray) per parameterization. The grey envelope indicates ±1 σ of the control diversity (no disturbance) for that parameter set.

3.3 Results

3.3.1 Resistance

Immediately after the disturbance there is significantly less change in the plant communities' Shannon diversity within low resource grasslands than high resource grasslands (Fig. 2). With seed addition from the metacommunity (but see Supplement C for results without seed addition) disturbance on average increases Shannon diversity (but see Supplement C). A general pattern emerges with preferential herbivory increasing Shannon diversity more than generalist, which in turn increases diversity more than no herbivory at all. However, in low resource grasslands root herbivory only marginally amplifies the change in Shannon diversity compared to the control. Without herbivory or disturbance, low resource grasslands have a richness of about 35 species, while high resource grasslands have about 20 species (Supplement D2). Together, these two effects suggest that low resource, high richness, grasslands are more resistant (*sensu* Hodgson et al. 2015) to disturbances than high resource, low diversity, grasslands.

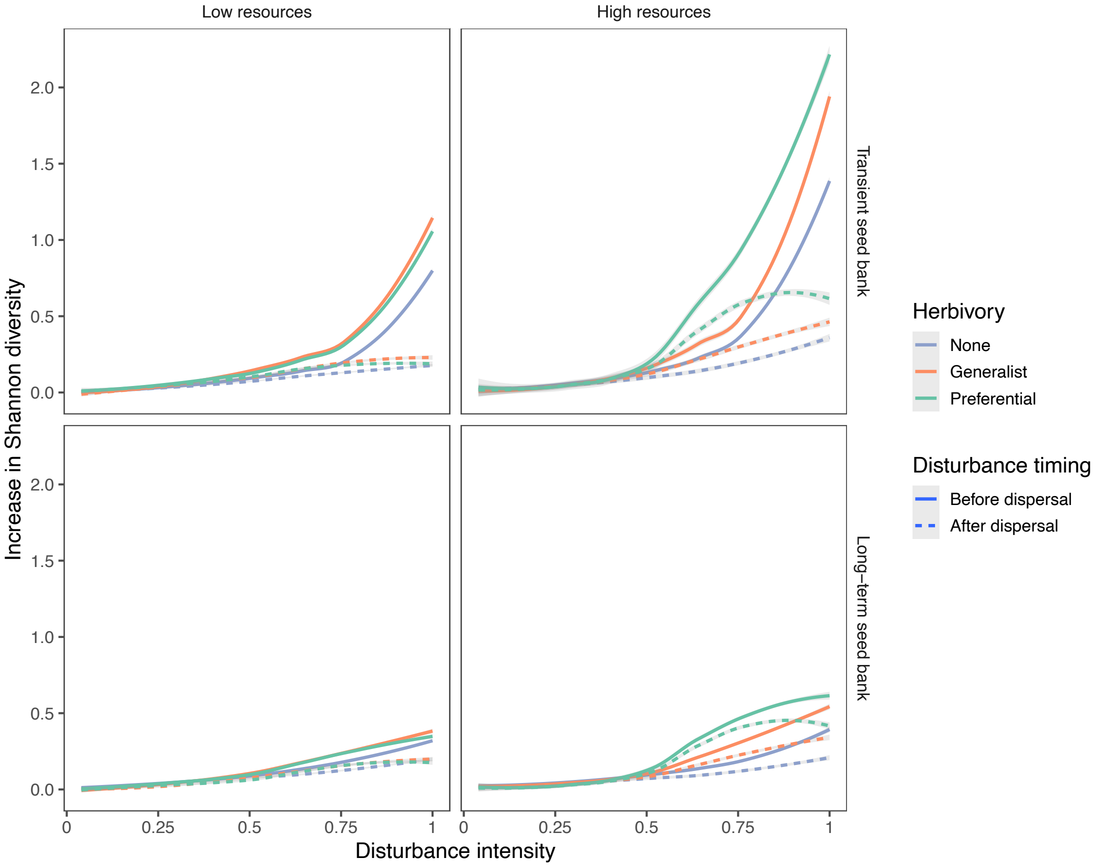

Figure 2. Absolute increase in the plant communities' Shannon diversity from pre-disturbance to one growing year after. Curves are derived from a local regression (LOESS) of all replicates along the disturbance gradient, with 100 replicates per intensity. Supplement D5 contains all raw data.

Disturbing the community after seed dispersal—thus ensuring that the community is "restarted" from a representative seed bank—greatly reduces the potential of root herbivores to lower the resistance of the grassland to disturbance (Fig. 2). This is even more clear when a longer-term seed bank is incorporated into the model, as low resource grasslands see little average impact on their Shannon diversity of any disturbance intensity, regardless of the presence of root herbivory. In Supplement D5, examining the raw resistance data indicates that the Shannon diversity of many low resource grasslands are actually negatively impacted by the disturbance in reference to the no-herbivory control, but that the average effect is very mildly positive. In high resource scenarios, the presence of a seed bank significantly blunts the impact of pre-dispersal disturbances, limiting the increase in Shannon diversity from over 2 to merely 0.5. In disturbances before dispersal, but with seed bank from previous years, preferential herbivory exhibits a slight hump-shaped curve wherein the most severe disturbances have a slightly lower effect on Shannon diversity than disturbances that leave some number of surviving plants.

3.3.2 Recovery

With increasing disturbance intensity, the number of years required to return to the plant communities' pre-disturbance Shannon diversity—a measurement of recovery—increases (Fig. 3). Until a threshold of around 50% disturbance mortality, both resource regimes and all herbivory regimes behave similarly, and return to their previous diversity levels within approximately 10 years. After the 50% threshold, the type and timing of disturbance as well as the type of seed bank becomes crucial in shaping the time it takes to return.

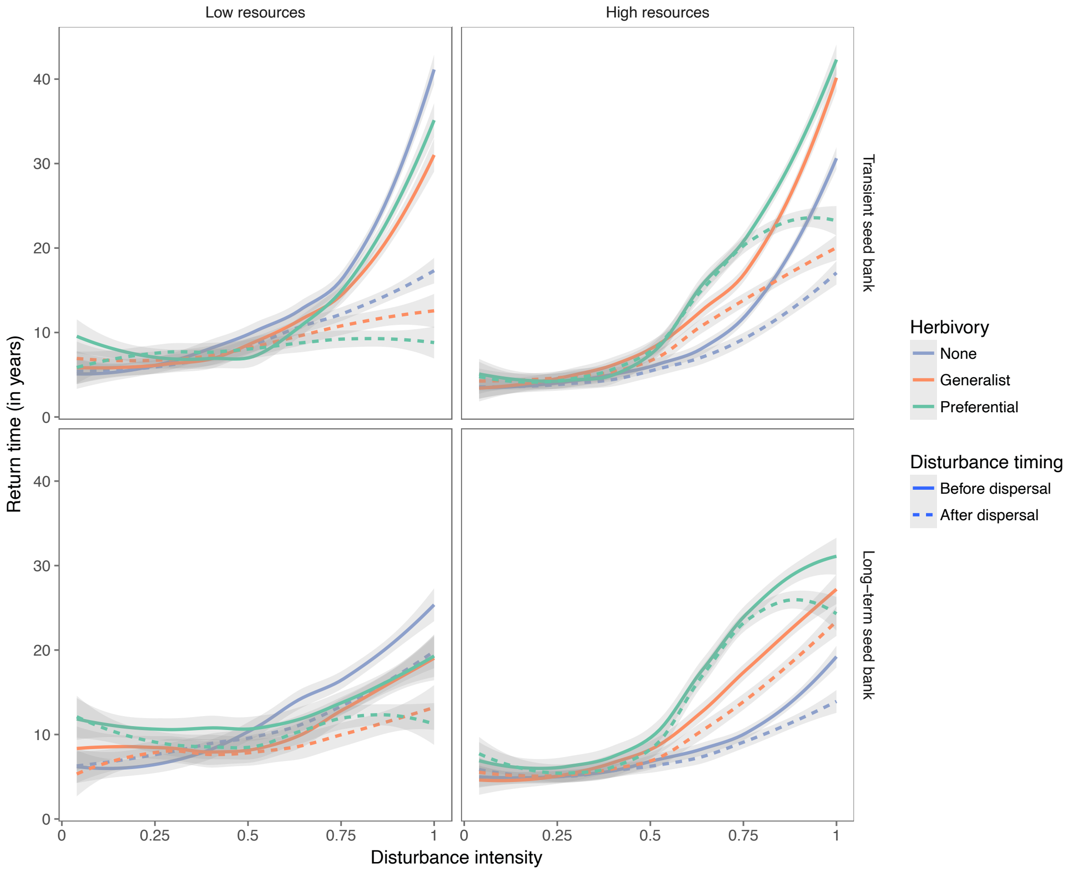

Figure 3. Number of years required to return within ±1 σ of the control (no disturbance) plant community's Shannon diversity. Curves are derived from a local regression (LOESS) of all replicates along the disturbance intensity gradient, with 100 replicates per intensity level (see Supplement D6 for raw data).

For high resource scenarios, preferential herbivory is the most impactful, and especially if a memory of the previous community is present. In these cases, i.e. either if the disturbance occurs after dispersal or if a longer-term seed bank exists, the return time of preferential herbivory scenarios plateau or even peak at disturbance intensities above 0.80. The generalist and no-herbivory control scenarios, by contrast, return faster than preferential herbivory but increase more steadily and peak at disturbance intensities of 1.0. At the highest disturbance intensity, generalist and preferential herbivory scenarios tend to take nearly the same time to recover. Without a long-term see bank, disturbances before dispersal will take as much as 40 years to return to the previous Shannon diversity. In effect, without a seed bank and with a disturbance before dispersal, the plant community will be "restarted" from the seed rain except with an abnormally high herbivory pressure.

Notably, with low resources, herbivory hastened the recovery of the system to its previous Shannon diversity, with preferential herbivory being more effective than generalist herbivory. This pattern is further contextualized in Supplement D3, which also shows how the resistance and recovery rate (measured in Shannon units per year) covary during intense disturbances. Any "memory" of the previous community—either through a long-term seed bank or a post-dispersal disturbance—largely mitigated the impact of even the most intense disturbances. Specifically, even without a long-term seed bank, disturbing the system after dispersal almost completely dissipated the impact of even the most intense disturbances. In scenarios with a long-term seed bank, there was little pattern between the different herbivory and disturbance treatments; while harsher disturbances did in general take longer to recover, and the no-herbivory control returned more slowly than those simulations with herbivory, the preference of the herbivores, as well as the timing of the disturbance, played no clear role in the recovery.

3.3.3 Shift in plant community size composition

Disturbance, regardless of the presence of herbivory, changes the distribution of plant sizes. By comparing the treatment communities' size compositions five years after the disturbance to those of the control community—no disturbance but the same herbivory and resource parameters—we observed that disturbance will decrease the proportional representation of the largest size-class of plants and increase the number of smaller individuals (Fig. 4). However, herbivory accentuated these changes, increasing the disturbance's impact and duration. The size-class distribution of communities without disturbances are shown in Supplement D4.

The type of herbivory, as well as the timing of disturbance, type of seed bank, and resource level of the plot, will mediate this effect. Disturbing the community before seed dispersal leads to, in the case of a low resource community, a substantial decrease in the total biomass of the largest plants and in turn a resurgence of the smaller and more moderately sized plants compared to the control scenario (Fig. 4). With preferential rather than generalist herbivory the pattern is similar but more extreme. In high resource communities, it is interestingly not the smaller plants that come to prominence after disturbance, but the above-average competitors. These plants are still comparatively large but are able to flourish under an herbivory regime that suppresses their slightly-larger competitors. This effect is also present when a long-term seed bank exists in the simulation.

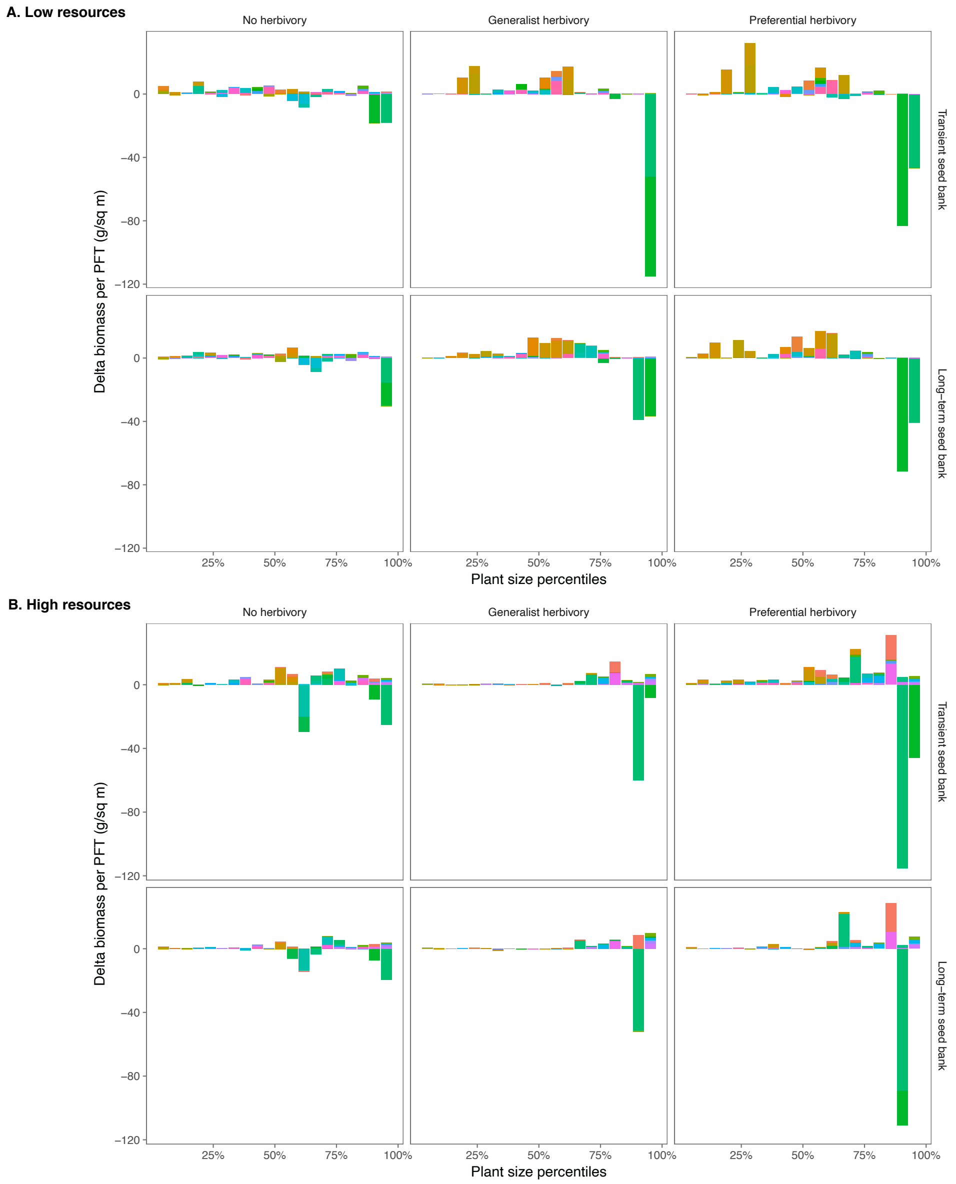

Figure 4. Change in total biomass per PFT ($g \cdot m^{-2}$) from no-disturbance control community along the distribution of plant biomass (i.e. the largest plants are represented in the 100th percentile). Each color represents a different PFT. Size distributions are derived from the control dataset. For simplification, only the disturbance before dispersal plots are shown, though they are qualitatively similar to the disturbance after dispersal parameterizations (contained in Supplement D7).

Disturbing the community after dispersal leads to much the same pattern (Supplement D7), especially for low resource scenarios. However, for high resource scenarios the added seeds enable the second-to-largest (upper-middle-class) size classes to overwhelm the community even more, increasing both their population size and total biomass compared to their smaller-sized competitors.

3.3.4 External seed addition

We turn off seed addition from the metacommunity and explored this design decision in Supplement C, finding that without seed addition disturbances to low resource communities were generally negative in their impacts on diversity (i.e. decreasing Shannon diversity), while disturbances to high resource communities were still positive (i.e.

increasing Shannon diversity). Without external seed addition, a pre-dispersal disturbance on a community with only a transient seed bank will completely eliminate that community. With external seed addition, however, the recovery process is similar to that of the beginning of the simulation except with a disproportionately high root feeding pressure.

3.4 Discussion

In this study, we found that root herbivory can dramatically change the resilience (resistance and recovery; Hodgson 2015) and successional dynamics of a model grassland. The effect, however, varied considerably based on the parameters of a given simulation (i.e. disturbance intensity, presence of a long-term seed bank, timing of disturbance, and resource level). This suggests that the magnitude and direction of herbivory's effect may vary considerably in the real world, based on the characteristics of the given system. Although root herbivory's interaction with disturbance is multidimensional, there were several consistent patterns that we observed.

We found that our simulated grasslands were resilient to disturbances below a 50% threshold. Above this threshold, for intermediate disturbances preferential herbivory was the most impactful, but with very intense disturbances there was little difference between generalist and preferential herbivory. In general, herbivory decreases the resistance of our simulated grassland plots, but has contrasting effects on recovery based on the amount of belowground resources accessible to the plant community. Some "memory" of the previous community, either because the disturbance occurred after seed dispersal or because a long-term seed bank is present, mitigates the impacts of the disturbance and stunts the impact of the root herbivores.

However, aside from the intensity of the disturbance, by far the most important parameter modifying the direction of the herbivores' impact was the level of belowground resources present. All other parameters strongly interacted with belowground resources, making generalization of herbivory's impact on resilience difficult without it as context. Indeed, the magnitude and direction of the herbivores' influence on resilience was tightly intertwined with the level of resources in the grassland plots, and when and when coupled with the dispersal timing and the type of seed bank, could completely eliminate the impact of the herbivores, a striking result that has not been explored in the empirical literature.

3.4.1 Effects of root herbivory depend on resource level

The relative importance of the different mechanisms that confer resilience to ecological communities changes across environmental gradients (Hallett et al. 2014). As a factor impacting resilience, our results suggest that root herbivory does as well. In our simulation, root herbivory reduces the resistance of the grasslands to a pulse disturbance, and this effect is especially pronounced in grasslands with high belowground resources. While herbivory increases the number of years it takes for a high resource grassland to return to its pre-disturbance diversity, it actually decreases this time to return for low resource grasslands. Although there is some indication that the addition of nitrogen to a semi-arid grassland can decrease its resistance to intense drought (Xu et al. 2014) while leaving recovery relatively unaffected, and root herbivores may have a larger impact on community dynamics at elevated than ambient nitrogen levels (Borgström et al. 2017), to our knowledge no research other than ours has been conducted on the role of root herbivores after disturbance. Our results emphasize the need to fill this gap, because grasslands are increasingly subject to changes in precipitation (IPCC 2014) and eutrophication (Tilman et al. 2002; Dentener et al. 2006), becoming more similar to our high resource scenarios.

One possible mechanism for our finding that high resource, low diversity, grasslands are more destabilized (less resistant) by root herbivory is that in general, low diversity ecosystems are more susceptible to disturbance. It has been frequently found that diverse systems are more resilient to disturbance than their low diversity counterparts (Tilman and Downing 1994; Naeem et al. 2000; Isbell et al. 2015). A number of mechanisms have been proposed that could generate this pattern, such as species asynchrony (Tilman 1999; Isbell et al. 2009), compensatory effects (Loreau and de Mazancourt 2008), or the portfolio effect (Hallett et al. 2014). One possibility is that since eutrophication weakens the stabilizing effects of diversity in grasslands (Hautier et al. 2014), it would lower their resistance to herbivory-mediated succession. Low resource grasslands, therefore, would be more resistant to disturbance. Caution, however, is necessary when considering this explanation, because it is difficult to disentangle whether the higher resistance we see in our low-resource plots is a secondary effect of their diversity, or an effect of the resource level itself.

A surprising finding within our analysis is that root herbivores speed up the recovery of low resource communities, while they slow down the recovery of high resource communities. Considering these dynamics within the context of the pre-disturbance community provides more clarity. In their "equilibrium" state, low resource communities are composed of slow growing, stress tolerant species. Within IBC-grass, adding root herbivores to these communities tends to increase the proportion of large, competitive species (Supplement D4), able to quickly regrow biomass lost to herbivory. After the disturbance, communities without herbivores will recover slowly, cycling through early succession wherein an abundance of unutilized resources enables competitive, fast growing PFTs to temporarily proliferate. Low resource communities with root herbivores recover more quickly than their counterparts without herbivores because their community composition tends to resemble these competitive, early successional communities more closely.

It is initially counterintuitive, therefore, that root herbivores do not hasten the recovery of high resource communities as well. Indeed, while one can observe an increase in the rate of recovery within low resource communities, there is very little change in recovery rate of high resource communities with the addition of root herbivores (Supplement D3). Comparing these communities without disturbance provides a clue: The species found within high resource grasslands are already highly competitive. Because both the presence of root herbivores and high levels of resources belowground select for competitive plant species, there are diminishing returns. Therefore, in high resource communities, the time to recovery is not controlled by the rate of succession after the disturbance, but instead on the impact of the disturbance itself. Supplement D3 further shows that the magnitude of disturbance's impact increases significantly with the inclusion of belowground herbivores into high resource grasslands. While their rate of return remains relatively constant, they must undergo a significant amount of succession to return to their pre-disturbance equilibrium.

3.4.2 Belowground resources mediate root herbivory’s impact on the "dimensionality of stability"

A second generality from our results is that the correlation of our model’s stability properties—resistance and recovery—changes across a resource gradient. In other words, after a disturbance in high resource (low diversity) grasslands, resistance and recovery are correlated in their response to the presence of root herbivores. However, in low resource (high diversity) grasslands, resistance and recovery after a disturbance are negatively correlated in their response to the same herbivory. This punctuates an interesting challenge in quantifying stability (of which resilience is a key component; Donohue et al. 2016); correlation between the properties of stability (e.g. resistance and recovery) may change based on the system and disturbance in question. This "dimensionality of stability" (Donohue et al. 2013) refers to the correlative structure of different stability properties. If these properties are correlated, the dimensionality is low. This concept has recently generated significant interest within the resilience literature (Donohue et al. 2013; Hillebrand et al. 2018; Radchuk et al. 2019). Within our simulated grassland system, while resistance and recovery are positively correlated for high resource communities, they are negatively correlated in low resource communities. In other words, the correlation of our simulation’s stability properties shift across an environmental gradient, reflecting a change in our system’s dimensionality of stability.

If a system's dimensionality is low, managers are able to monitor few of its stability properties without sacrificing accuracy in predicting a system's response to disturbance. In our grassland model, root herbivores interact with the belowground resources of the system to change correlative structure of our two stability properties, thus changing the dimensionality of stability. This means that gradual changes in environmental conditions, such as an increase in average precipitation or eutrophication, could alter how a given community reacts to a pulse disturbance in the presence of herbivores. Therefore, the level of herbivory present in the system at any given time will influence the trajectory of succession differently based on the resources present in the grassland. Without an awareness of this relationship, managers could incorrectly gauge their system’s stability. This result reinforces the importance of incorporating multiple stability metrics into monitoring natural systems, because the influence trophic interactions on the dimensionality of stability will change based on the abiotic environment.

3.4.3 Herbivore preference shapes the distribution of plant biomasses

The level of belowground resources (i.e. nutrient and water) not only modifies the impact of root herbivores on resilience, but also the size distribution of the plants during the community’s recovery. We observe that there is a large difference between the size distributions emergent from communities with and without herbivory. However, preferential herbivory does not greatly change the size distribution versus generalist herbivory; far greater is the difference between herbivory’s impact on low and on high resource grasslands. In low resource grasslands, herbivory mainly advantages the broad middle, while in high resource scenarios the size-class of plants just below the largest benefits the most. This suggests contrasting pressures driving succession. On one hand, in scenarios with high belowground resources, size-asymmetry in competition for aboveground resources is critically important in determining the winners of competition (Weiner 1990; DeMalach et al. 2016, 2017). In our simulation, a few highly competitive species will dominate these grasslands. However, these same winners will be overwhelmingly predated because of this size advantage, leaving a significant amount of aboveground resources to the next highest size class. On the other hand, in low resource grasslands asymmetric aboveground competition is less important in determining the species composition, as belowground resources are more limiting (Weiner 2004; May et al. 2009). In this scenario, since belowground resources are not size asymmetric, the fitness of a species after disturbance won't be as strongly tied to its size. Since larger size does not necessarily endue higher fitness, the beneficiaries of this period after disturbance will be more evenly distributed across the size-spectrum.

3.4.4 Resources interact with seed banks and seed addition to shape the post-disturbance impact of root herbivores on diversity

Root herbivores will increase the probability that a less competitive species can invade a disturbed plot, as long as that species is present in the seed bank, or otherwise not dispersal limited. It is worth exploring both these effects to better estimate their generality.

The presence of a long-term seed bank blunts the amplifying effect of root herbivory, increasing the community's resilience. However, the occurrence of such seed banks may be the exception rather than the norm. For example, in European calcareous grasslands it has been found that roughly 60% of seeds cannot remain viable for more than one year (Stöcklin and Fischer 1999). While there is some indication that species with longer-lived seeds have lower extinction rates (Stöcklin and Fischer 1999), grassland seed banks may be too short-lived to successfully enable the recovery of a grassland (Bossuyt and Honnay 2007). Further, land-use intensity (e.g. the timing and intensity of mowing or tilling, or fertilization) is also known to decrease the species richness of seed banks, and therefore these factors may further decrease the ability of a seed bank to support the recovery of a community after disturbance (Bekker et al. 1997; Klaus et al. 2017). Lastly, it has been found that long-term nitrogen deposition depletes grassland seed banks (Basto et al. 2014), which suggests that with time, root herbivory-mediated disturbances may become more intense, more greatly reflecting those scenarios without a long-term seed bank.

In our simulation without seed addition, a species' extinction is permanent since no metacommunity exists from which it can recolonize. Because we are interested in root herbivory's potential ability to reduce the fitness of the strongest species after a disturbance—and therefore potentially aid in the recolonization of the plots—we decided to have a continuous, low level of seed addition each year (Weiss et al. 2014). Since our seed addition contains all PFTs evenly, our simulation will overestimate the positive effect of disturbance on Shannon diversity, as dispersal limitation will not keep rare species from recolonization. We turn off seed addition and thoroughly explore this design decision in

Supplement C, finding that without seed addition disturbances to low resource communities will generally decrease their Shannon diversity, while disturbances to high resource communities continued to increase it. A likely explanation for this is purely mathematical. Grasslands with high belowground resources tend to be less diverse, dominated by only a few highly competitive species. If these species are eliminated by the disturbance, ruderal species will temporarily flourish and substantially increase diversity, before once more becoming rare. In grasslands with low belowground resources, by contrast, diversity is the norm. Therefore, while the disturbance may change the species composition, their Shannon diversity may not reflect the change. In principle, the effect of the disturbance on diversity will depend on the diversity of the surrounding landscape; if a species is not dispersal limited, it will establish in the newly-disturbed plot.

3.5 Conclusions

Understanding what factors shape the recovery of an ecosystem after an intense disturbance is of critical importance in a world increasingly shaped by human influence, such as land-use intensification and climate change. Root herbivory and belowground resources will interact to mediate a community's resilience to these disturbances. In this paper, we have presented a basic understanding of how these processes may occur, using parsimonious herbivory and disturbance regimes. Our results suggest that a typical level of root herbivory (Zvereva and Kozlov 2012) can play an important role in these communities after such disturbances, and therefore need further investigation. In real systems, pulse disturbances will be frequent, diverse, and complex in their behavior, and therefore may lead to different emergent community-level patterns. Future work must seek to develop an understanding of these patterns, emergent from a panoply of disturbances in systems with and without root herbivory. Importantly, our results suggest that the belowground resources will be critically important in predicting the impacts of root herbivores on grassland succession dynamics after disturbance and should be considered in subsequent investigations.

3.6 References

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4. While shoot herbivory mitigates, root herbivory exacerbates eutrophication's impact on diversity in a grassland model

Abstract

Eutrophication is widespread throughout grassland systems and expected to increase during the Anthropocene. Trophic interactions, like aboveground herbivory, have been shown to mitigate its effect on plant diversity. Belowground herbivory may also impact these habitats' response to eutrophication, but the direction of its influence is much less understood, and likely to depend on factors such as the herbivores' preference for dominant species and the symmetry of belowground competition. If preferential towards the dominant, fastest growing species, root herbivores may reduce these species' relative fitness and support diversity during eutrophication. However, as plant competition belowground is commonly considered to be symmetric, root herbivores may be less impactful than shoot herbivores because they do not reduce any competitive asymmetry between the dominant and subordinate plants.

To better understand this system, we used an established, two-layer, grassland community model to run a full-factorially designed simulation experiment, crossing the complete removal of aboveground herbivores and belowground herbivores with eutrophication. After 100 years of simulation, we analyzed communities' diversity, competition on the individual-level, as well as their resistance and recovery. The model reproduced both observed general effects of eutrophication in grasslands and the short-term trends of specific experiments. We found that belowground herbivores exacerbate the negative influence of eutrophication on Shannon diversity within our model grasslands, while aboveground herbivores mitigate its effect. Indeed, data on individuals' above- and belowground resource uptake reveals that root herbivory reduces resource limitation belowground. As with eutrophication, this shifts competition aboveground. Since shoot competition is asymmetric—with larger, taller individuals gathering disproportionate resources compared to their smaller, shorter counterparts—this shift promotes the exclusion of the smallest species. While increasing the root herbivores' preferences towards dominant species lessens their negative impact, at best they are only mildly advantageous, and they do very little reduce the negative consequences of eutrophication. Because our model's belowground competition is symmetric, we hypothesize that root herbivores may be beneficial when root competition is asymmetric. Future research into belowground herbivory should account for the nature of competition belowground to better understand the herbivores' true influence.

Crawford, M. et al. 2019. While shoot herbivory mitigates, root herbivory exacerbates eutrophication's impact on diversity in a grassland model. Rejected with invitation to resubmit at Ecology.

4.1 Introduction

Eutrophication, i.e. excessive nutrient (e.g. N and P) deposition into ecosystems, reduces diversity worldwide and may likely worsen as globalization drives land-use intensification (Vitousek et al. 1997; Lambin et al. 2001; Steffen et al. 2015). In terrestrial ecosystems, grasslands are heavily impacted by eutrophication (Stevens et al. 2004; Dupré et al. 2009; Bobbink et al. 2010; Hautier et al. 2014). Those in central Europe, for example, have seen reductions in plant diversity of 50% over the last 50 years, mostly attributable to local nutrient input and land use intensification (Wesche et al 2012).

These negative impacts emerge as competitive plant functional types (PFTs) begin to dominate the community (Harpole and Tilman 2007; Hautier et al. 2009). No longer resource-limited, these species—well adapted to quickly converting nutrients into biomass—rapidly grow to overshadow their smaller neighbors. Their initial superiority is further compounded by the asymmetry inherent in aboveground competition, with taller plants obtaining disproportionately more light than their shorter counterparts (Weiner et al. 1986; DeMalach et al. 2016, 2017; Hautier et al. 2018). This asymmetry is the primary reason trophic interactions are recognized as an important mechanism through which grassland diversity can resist and potentially recover from eutrophication.

Aboveground herbivory tends to inhibit competitive exclusion by reducing the competitive asymmetry between the largest and smallest plants. By disproportionately affecting the largest, fastest growing functional types, aboveground herbivory increases the light available to smaller individuals (Borer et al. 2014). Thus, aboveground herbivory presents a countervailing force that may constrain the species loss due to eutrophication, safeguarding diversity by decreasing the performance of the strongest species (Olff and Ritchie 1998; Anderson et al. 2018; Mortensen et al. 2018; but see Borgström et al. 2016). Further, several recent studies have also indicated that trophic interactions such as herbivory can increase the resilience of grasslands to stress through trophic compensation (Thébault and Fontaine 2010; Eisenhauer et al. 2011; Giulia et al. 2015), though not eutrophication *per se*.

While the role of aboveground herbivory in mitigating the impact of eutrophication on diversity has been established, the impact of its counterpart belowground is poorly understood (Blossey and Hunt-Joshi 2003). Despite 40–70% of annual net primary production being belowground (Vogt et al. 1995) and root herbivores likely removing as much, or more, biomass than their foliar cousins (Zvereva and Kozlov 2012; Kozlov and Zvereva 2017), practical obstacles in its research have left belowground herbivory historically “out of sight, out of mind,” (Hunter 2001). The two studies that have investigated root herbivory's role in the response of grassland systems to eutrophication have shown that herbivores compound its effect, further decreasing biodiversity (La Pierre et al. 2014; Borgström et al. 2017).

Most recently, Borgström et al. (2017) designed a factorial experiment, crossing the presence of aboveground herbivores, belowground herbivores, and eutrophication. They found that while aboveground herbivory decreased the relative biomass of grasses and thus counteracted the impact of eutrophication, root herbivores consistently decreased diversity, regardless of the other treatments. These results are striking: Above- and belowground herbivory are not equivalent. This highlights the need to investigate the underlying mechanisms behind this difference more deeply. By further developing this understanding, we will improve our ability to predict biodiversity in grassland ecosystems, as well as their response to eutrophication.

Some evidence shows belowground herbivores are preferential towards larger root systems, rather than generalist, and that they may reduce these plants' dominance and support diversity (Sonnemann et al. 2012, 2015). Indeed, several studies have shown that belowground herbivores increase diversity, albeit in non-eutrophic systems (De Deyn et al. 2001; Stein et al. 2010). However, the mechanisms underlying above- and belowground herbivory may be more complicated than comparing their feeding preferences alone. This is because contrary to plant competition aboveground, belowground resources are most often symmetrically allocated based on plant size (Schwinning and Weiner 1998). Without a competitive asymmetry to equalize, root herbivores are unlikely to foster diversity maintenance (Chesson 2000). By way of analogy, if aboveground competition were not size-asymmetric, size asymmetric herbivory would be less effective in increasing the community’s diversity.

To summarize, the literature suggests that belowground herbivores do not necessarily mitigate eutrophication, but their effects may hinge on their preference towards competitive species as well as the symmetry of belowground competition. To break down how root herbivory influences the diversity and resilience of grassland systems—and their reaction to eutrophication—it would be helpful to test in isolation not just the effect of herbivory (above- and belowground) and eutrophication, but also of the belowground herbivores’ preferences towards dominant PFTs. These nuances are ripe to be investigated with ecological modeling, which enables researchers to continuously monitor high-resolution variables describing not only the plants’ state but also their above- and belowground competitive environment. Further, given that the full extent of eutrophication’s influence may only emerge over the long-term (Kidd et al. 2017), modeling may provide additional useful insights.

In this paper, we extend on the empirical short-term results of Borgström et al. (2017) by implementing their factorial design inside of an established grassland community model. We then parameterize the feeding preferences of the belowground herbivores to reflect a gradient from generalist to preferential. While “generalists” will consume all species equally, proportional to their biomass, “preferential” herbivores will disproportionately focus on the dominant species within the grassland, asymmetrically consuming those species that have larger root systems.

We also expand on their work by examining herbivores’ impact on the resilience of grasslands to eutrophication. Despite some studies predicting that trophic interactions will increase the stability of ecological systems (Thébault and Fontaine 2010; Eisenhauer et al. 2011; Giulia et al. 2015), no studies have examined how belowground herbivores mediate the response of grasslands to stresses like eutrophication. Therefore, in addition to examining the impact of herbivores on grasslands diversity *per se*, we also investigate how the removal of herbivores (above- and belowground) impact the resistance and recovery (sensu Hodgson et al. 2015) of these grasslands to eutrophication.

4.2 Methods

We used the individual-based and trait-based, spatially-explicit grassland assembly model, IBC-grass (May et al. 2009), that incorporates above- and belowground herbivory. Since its introduction (May et al. 2009), IBC-grass has been used to investigate numerous aspects of grassland dynamics, from resilience (Weiss and Jeltsch 2015; Radchuck et al. 2019), to species coexistence (Pfestorf et al. 2016; Crawford et al. 2018), and ecotoxicology (Reeg et al. 2017; Reeg et al. 2018). Importantly, Weiss et al. (2014) parameterized the model with data from trait databases and a survey of plant functional types from German grasslands collected through the Biodiversity Exploratories (Fischer et al. 2010; Pfestorf et al. 2013). With this empirical parameterization the model successfully reproduces, without calibration at the community level, empirically-observed grassland biodiversity patterns (Weiss et al. 2014).

A full description of the model can be found in the ODD (Overview, Design concepts, Details) protocol (Grimm et al. 2010, 2006; Supplemental Material A). The following is a summary of the model as well as an explanation of our modifications to it.

4.2.1 Overview of the IBC-grass model

IBC-grass simulates local community dynamics on a 141 x 141 cell grid, where each cell corresponds to 1 cm^2 (resulting in a roughly 2 m^2 grid space) and can hold one plant's stem. Its time step corresponds to one week, and there are 30 weeks per year representing the vegetation period. A plant is characterized by its functional traits and the biomass of its three distinct compartments: aboveground mass, belowground mass, and reproductive mass.

A plant's competitive area is defined by an aboveground and a belowground “zone of influence” (ZOI). The two ZOIs are both circular areas around the plant’s stem, from which it acquires either above- or belowground resources (Schwinning and Weiner 1998; Weiner et al. 2001). While the plant’s stem is contained within one grid cell, its ZOI can cover many. Belowground, the area of a plant’s ZOI is related directly to its root biomass (Supplemental Material A: Eq. A3a). Aboveground, the area is the product of its aboveground biomass as well as two functional traits, leaf-mass ratio (LMR) and specific leaf area (SLA) (Supplemental Material A: Eq. A1). The plant’s LMR describes its proportion of photosynthetically active (leaf) tissue to the total shoot tissue and its SLA is a constant ratio between leaf mass and ZOI area. In IBC-grass, a plant with a low LMR will generally have a small shoot area, but overshadow its shorter neighbors; a high SLA corresponds to a leaf that is larger and therefore able to gather more aboveground resources, but also less well defended from aboveground herbivory than its lower-SLA counterparts.

When two plants' ZOIs overlap they compete for resources. A cell's aboveground resources correspond to light while its belowground resources—likewise unidimensional—therefore correspond to water and nutrients. The proportion of a cell's resources a plant obtains during competition depends on its competitive abilities and how many other ZOIs overlap the cell. Aboveground competition is size-asymmetric, i.e. the larger plant takes up resources from each contested cell not only in proportion to its competitive ability (measured as the maximum units it can acquire per week, termed its g_{max}), but also in proportion to its aboveground mass and LMR^{-1}, reflecting its height advantage over the smaller plants (Supplemental Material A: Eq. A3b). In other words, aboveground competition disproportionately favors the larger, taller competitor. Belowground competition, however, is size-symmetric, i.e. only their competitive abilities (their g_{max}) are considered (Supplemental Material A: Eq. A3a).

Intraspecific competition is also included in the form of negative-density dependent competition, reflecting species-specific predators or pathogens (May et al. 2009). This density-dependent competition was modeled by decreasing the resource uptake of an individual in proportion to the square-root of the number of conspecifics in its neighborhood ZOI (Supplemental Material A: Eq. A3c).

All grid cells' total resources are kept constant through space and time; only a plant's biotic neighborhood influences the amount of resources available to it at any given time step. When a plant is unable to gather enough resources, it changes its resource allocation between above- and belowground parts, depending on which compartment is more limited (i.e. shoot or root). If resource uptake in either of the two compartments is below a certain threshold, the plant is considered stressed. Each consecutive week a plant is stressed increases its chance of mortality linearly, in addition to a background, stochastic, annual mortality of 20%.

The plants are characterized by four sets, or syndromes, of functional traits, a subset of those proposed as the "common core list of plant traits" by Weiher et al. (1999). The first set of traits defines the plant's maximum size (m_{max}), which positively correlates with seed size and negatively correlates with dispersal distance (Eriksson and Jakobsson 1998; Jongejans and Schippers 1999). The second defines the plant's growth form, or leaf to mass ratio (LMR), which describes the plant as either a rosette, erect, or intermediate growth form type. The third set defines its competitive ability, or maximum resource utilization per time step (g_{max}), and negatively correlates with its stress tolerance (Grime 2001). The fourth trait set describes the plant's grazing response, positively correlating its palatability with its specific leaf area (SLA) (Westoby et al. 2002).

4.2.2 Aboveground herbivory

Aboveground grazing events, modelling the herbivory of large mammals, reflect the partial removal of a plant's aboveground biomass. The frequency of grazing is specified by a constant weekly probability (p_{graz}) of a grazing event. The grazers tend to act selectively towards certain traits, with a preference for larger, taller individuals exhibiting high SLAs, which corresponds to relatively palatable leaves (Díaz et al. 2001).

$$s_{graz} = m_{shoot} \cdot LMR^{-1} \cdot SLA \qquad \text{eq. 1}$$

The probability for a given individual to be grazed within one week is derived as its grazing susceptibility (s_{graz}) in proportion to the current maximum individual susceptibility of all the plants (in other words, the susceptibility of the most-susceptible plant). All plants are checked to be grazed in a random order. If a plant is grazed, 50% of its shoot mass and all of its reproductive mass are removed. The random choice of plants is repeated without replacement until 50% of the total aboveground biomass on the grid has been removed or the residual biomass is reduced to less than (15 g/m², Schwinning and Parsons 1999) what is considered ungrazable. After a pass through the entire plant community, if either of these two end conditions are unmet the process is repeated. This allows a plant individual to be grazed never or several times during one week with a grazing event.

In this study, we use a grazing probability of 0.2 per time step, consistent with previous studies using this submodel.

4.2.3 Belowground herbivory

Belowground herbivory was implemented such that each time step some percentage of the extant biomass is removed from each of the plants, with a gradient of preference in root size ranging from generalist to preferential (i.e. disproportionally eating larger root systems). This herbivory algorithm is intended to reflect the influence of belowground, invertebrate herbivores, such as those belonging to the genus *Agriotes*, one of the most abundant root herbivores in Europe. As this genus generally tends to eat plants with high biomass and growth rates (Sonnemann et al. 2012, 2015), we refrain from explicitly modelling the plants' roots palatability.

The feeding need at week t, n_t, is calculated as a defined percent (feeding rate, f) of that week's expected root mass, which is estimated by averaging each previous week's total realized root biomass R_i for the previous w weeks,

$$n_t = f \cdot \frac{\sum_{i=t-w}^{t-1} R_i}{w} \qquad \text{eq. 2}$$

For this analysis, the feeding rate (f) is 0.1 per week, potentially lower than the typical belowground herbivory pressure (Zvereva and Kozlov 2012), but equal to the aboveground herbivory pressure commonly used in IBC-grass. The number of weeks used to estimate the expected root mass, w, is 10. Both parameters are held constant in the following analysis.

The biomass to be removed from each individual's root mass ($g_{i,t}$) is calculated each week as:

$$g_{i,t} = \left(\frac{r_{i,t}}{R_t}\right)^{\alpha} \cdot n_t \qquad \text{eq. 3}$$

where $r_{i,t}$ is the expected root mass of individual i in week t and R_t is the week's realized total root mass, which may differ from the expected root mass (Supplemental Material A: Fig. A3). R_t differs from R_i in eq. 2 in that R_i refers to the total realized root biomass on week i (and ranging backwards by w weeks), whereas R_t refers to the total realized root biomass on the current week. The parameter α represents the generality of the herbivory; set at $\alpha = 1$, $g_{i,t}$ will equal the plant's root mass ($r_{i,t}$) in proportion to the total root mass (R_t) at time t. Above 1, α will increase the preference of the herbivores to disproportionally prefer large root systems (Sonnemann et al. 2013). This parameter is varied from 1 (generalist) to 2 (extremely preferential). If the biomass to be removed from a plant is larger than its total root mass (which may occur, based on the distribution of plant biomasses and α), the plant is killed and the overshoot biomass remains in the feeding need (n_t), to be removed from other plants.

4.2.4 Eutrophication

Eutrophication was simulated as an increase in belowground resources (BRes) from the baseline resource rate. Therefore, in IBC-grass a eutrophication intensity of 10 would translate to an increase in belowground resources of 10 BRes for the duration of the experiment. Immediately after the experimental period, the belowground resources return to their pre-eutrophication level for 100 simulation years, for the analysis of the plots' recovery. Although abiotic modifications to natural communities (e.g. nutrient, herbicide, or pesticide addition) will degrade more slowly than is modelled in our present work, we argue that as a first approximation, this simplifying assumption will demonstrate—in principle—how the biotic community will respond to the cessation of these human-caused disturbances. For this analysis we increased the amount of belowground resources by 50% over their baseline levels (Weiss et al. 2014), increasing from 60 to 90 BRes during the experimental period.

4.2.5 Simulation design and experiments

We implement a full-factorial design mirroring Borgström et al. (2017) inside of IBC-grass. After a burn-in period of 100 simulation-years wherein the communities settle into quasi-equilibrium, they are experimentally manipulated through the application of aboveground herbivore exclusion, belowground herbivore exclusion, and eutrophication, fully crossed. Before the experimental treatments begin, all simulations have a moderately-low level of baseline belowground resources (60 resource units) and both above- and belowground herbivory. The belowground herbivory is parameterized along a gradient of preferentiality, such that each community has one of five levels from 1 (generalist) to 2 (very preferential, see *Methods: Belowground Herbivory*). During the experimental period, aboveground and belowground herbivore exclusion is modelled as the complete elimination of these two submodels. This period lasts for 100 simulation years, long enough for all communities to reach a quasi-equilibrium once again. After the experimental window ends, the presence of above- and belowground herbivores, as well as the level of belowground resources returns to their pre-experiment values and the simulation is left to run for another 100 years, so that the communities' recovery can likewise be examined. Each parameterization is replicated 50 times.

To understand how these three factors (above- and belowground herbivory, and eutrophication) influence the diversity of our model grasslands, we examine the simulated communities' Shannon diversity—which combines the effects of richness and evenness—shortly after the experiment begins and immediately before it concludes. We then investigate the corresponding shifts in the individuals' resource uptake levels (a proxy for competition). To understand the grasslands' resilience dynamics, we also inspect two key resilience metrics (*sensu* Hodgson et al. 2015), resistance and recovery. Resistance is the magnitude of change some metric (e.g. diversity) undergoes directly after a disturbance. In our case, we were exploring the effects of eutrophication on diversity with and without above- and belowground herbivory. Experimentally removing the herbivores was thus a diagnostic—or proximate disturbance—meant to reveal the stabilizing effects of herbivory, while the ultimate disturbance of interest was eutrophication. Recovery is the amount of time needed for a system to reach its original state (measured as time to recovery, TTR). Here we explored recovery, with and without eutrophication, after herbivory was reinstated. Recovery necessitates some external seed input, so for the duration of the recovery period we add a modicum of seeds—$10\ seeds\ m^{-2}\ PFT^{-1}\ year^{-1}$ (Weiss et al. 2014, Reeg et al. 2018)—to reintroduce any species extirpated during the experimental phase. A community is considered to have recovered once its diversity returns to within two standard deviations of the control communities'—no herbivory removal or eutrophication—diversity.

4.3 Results

After 100 years, both eutrophication and the presence of generalist belowground herbivory decrease Shannon diversity, while aboveground herbivory increases it (Fig. 1). A linear model predicting Shannon diversity through the three-way interaction of these variables (Table 1) revealed significant interactions between eutrophication and both above- and belowground herbivory. While aboveground herbivory can partly mitigate the negative impacts of eutrophication on diversity, belowground herbivory exacerbates it. Interestingly, while there was no interaction between above- and belowground herbivory at ambient levels of belowground resources, a significant three-way interaction with eutrophication indicates that—in grasslands with eutrophication—combined above- and belowground herbivory result in a significantly lower Shannon diversity than if there was no interaction present (i.e. their effects were additive). This interaction was larger than the negative effect of belowground alone.

Comparing our results to Borgström et al. (2017), the patterns of Pielou's evenness (E) shortly after the experimental period begins (3 years, mirroring Borgström et al. 2017) are broadly concordant (Supplemental Material B: Fig. 1).

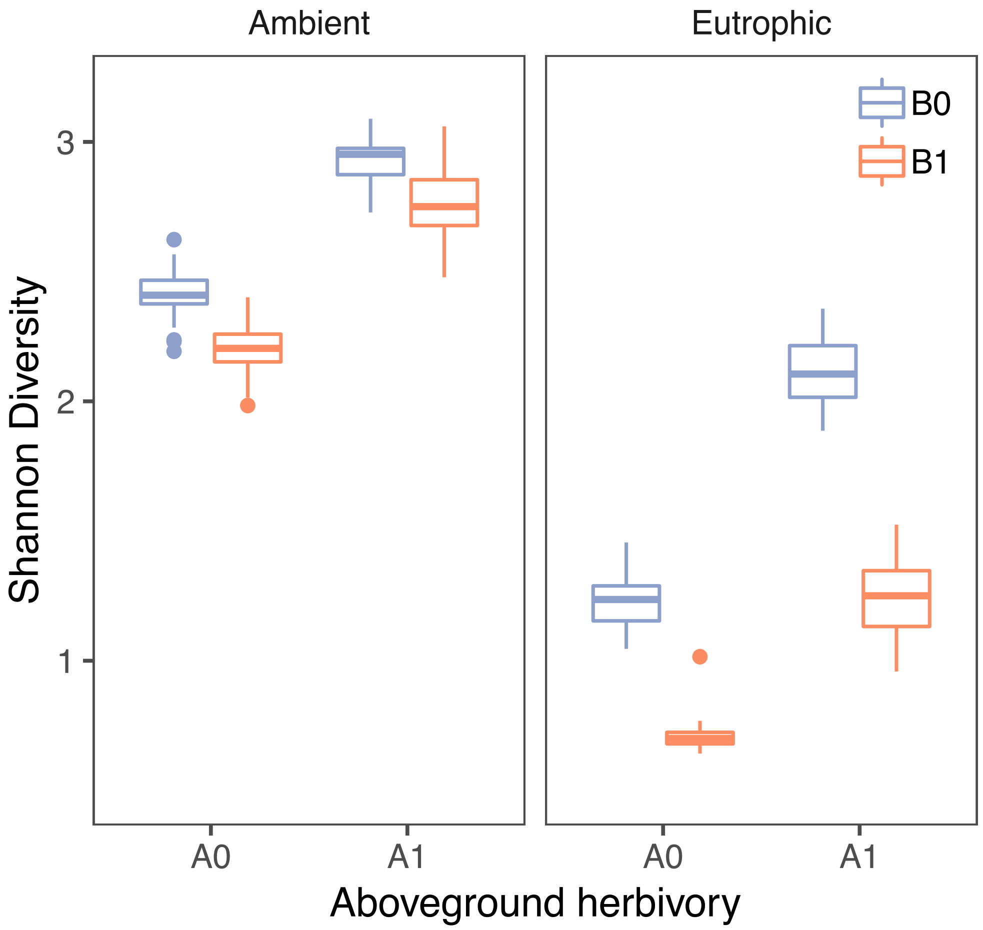

Figure 1. Shannon diversity after 100 years of experimental treatment. Control treatment retains above- and belowground herbivory with ambient resource levels. A0 – Aboveground herbivory removed, A1 – Aboveground herbivory present; B0 – Belowground herbivory removed, B1 – Belowground herbivory present. While aboveground herbivory increases diversity, belowground herbivory has a negative effect on diversity, exacerbating the negative effect of eutrophication.

Table 1. Impact of above- and belowground herbivory on the diversity response of simulated grassland plots to eutrophication.

Variable	Estimate	Std. Error	t-value	p-value
Intercept	2.413	0.015	164.669	< **0.001**
Eutrophication	-1.177	0.021	-56.783	< **0.001**
A1	0.522	0.021	25.188	< **0.001**
B1	-0.212	0.021	-10.240	< **0.001**
Eutrophication:A1	0.357	0.029	12.197	< **0.001**
Eutrophication:B1	-0.319	0.029	-10.879	< **0.001**
A1:B1	0.024	0.029	0.831	0.407
Eutrophication:A1:B1	-0.36	0.041	-8.894	< **0.001**
Adjusted R-squared: 0.981; F-statistic: 2976 on 7 and 392 DF				

4.3.1 Variation with root herbivore preference

We next shift our attention from generalist belowground herbivores to those with increasing preference towards dominant species, by testing a gradient from generalist herbivores ($\alpha = 1$) to those extremely preferential towards large root systems ($\alpha = 2$). We found that increasing the herbivore's preference towards dominant plants increased diversity relative to purely generalist herbivores, but that this effect was insufficient to mitigate the negative effects of eutrophication (Fig. 2). Although in grasslands with ambient resources, very preferential herbivores had no impact on diversity (especially compared to generalist herbivores, which significantly reduced it), eutrophication reduced diversity by threefold the positive impact of preferential herbivores, overshadowing any positive influence of preferential herbivory. Therefore, preferential herbivores, at most, neutrally impact diversity.

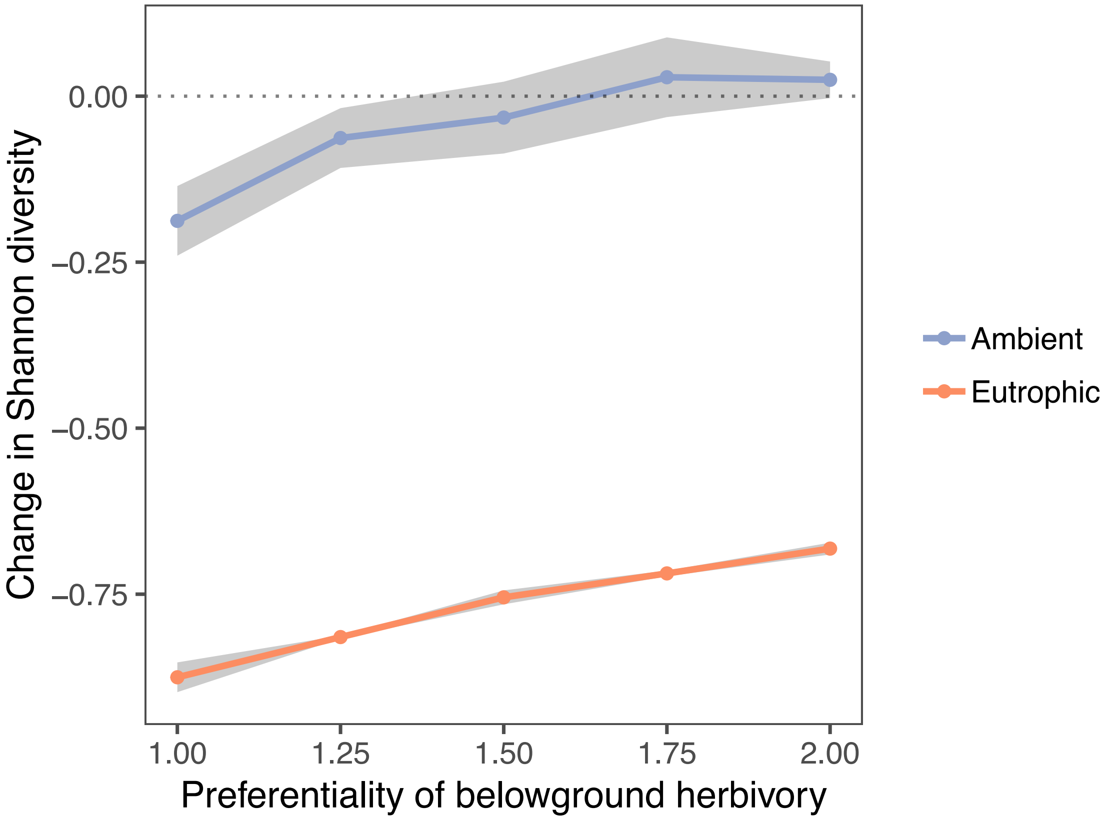

Figure 2. Change in Shannon diversity (relative to the diversity with belowground herbivores excluded) with increasing degree of belowground herbivore preference towards the largest plant functional types. Aboveground herbivory is held constant and present. Ribbons indicate one standard deviation around the mean. Preferentiality of root herbivores only slightly lessens the negative effect of root herbivory on diversity. However, this is not sufficient to mitigate the negative influence of eutrophication.

To understand how preferential herbivory differentially impacted species fitness more deeply, we isolated the dominant PFT from each community with generalist herbivores, defining it to be the PFT with the largest summed root biomass. We then plotted its total root biomass under the gradient of herbivore selectivity, and found that only under ambient belowground resource levels do higher levels of selectivity decrease the total root biomass of the most dominant PFTs in the community (Supplemental Material B: Fig. 2).

Under eutrophication, there is no interaction between that PFT's root biomass and the herbivores' preference for larger root systems.

4.3.2 Competition on the individuals' level

We also measured the shoot- and root- resource uptake per individual after the experimental period. This measure, the ratio of resource uptake to biomass above- or belowground, is a proxy for competition in each compartment; a high ratio reflects less competition, because the plant is receiving more resources per unit biomass. Lower values, therefore, reflect higher competition wherein few resources are available for the individual to take up. The average ratio between an individual's aboveground resources uptake to it shoot biomass ($ARes : m_{shoot}$) increased in the presence of aboveground herbivores (Fig. 3A). This reflects a decrease in aboveground competition, as the removal of aboveground biomass reduces the number of plants competing for each cells' resources. The introduction of belowground herbivory mitigated this impact, in effect reducing aboveground herbivory's ability to decrease aboveground competition. Eutrophication was even more disruptive to the efficacy of aboveground herbivory, drastically reducing the aboveground resource uptake ratio. This suggests a large increase in aboveground competition, with plants in eutrophic conditions needing significantly more aboveground biomass to their requisite aboveground resources.

A complementary pattern emerged when inspecting the average root uptake ratio of each community ($BRes : m_{root}$, Fig. 3B). A high root uptake ratio corresponds to a plant taking up many resources per gram root biomass per time step, reflecting low competitive intensity; plants receive much of the resources they can take up. By contrast, a low uptake ratio means that plants only take up few resources for each gram of their root biomass, reflecting an intense competitive environment. Eutrophic conditions dramatically increased the amount of belowground resources taken up per gram biomass, reflecting a decrease in

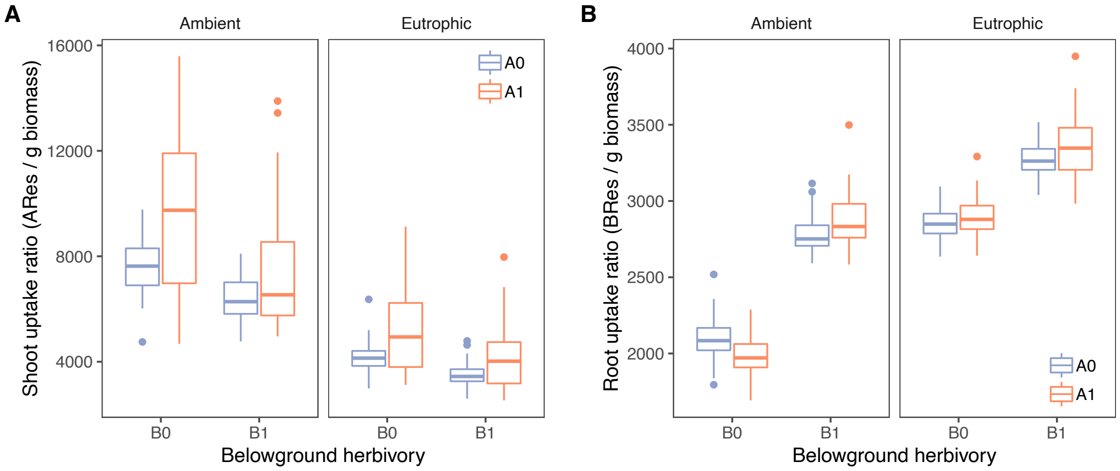

Figure 3. (A) Shoot uptake ratio and (B) root uptake ratio with experimental treatment. Each ratio reflects the resources acquired per unit biomass. An increasing ratio indicates decreasing competition for the respective resource. Boxplots are derived by averaging all plant-individuals' per replicate, one simulation year before the experimental treatment terminates. A0 – Aboveground herbivory removed, A1 – Aboveground herbivory present; B0 – Belowground herbivory removed, B1 – Belowground herbivory present. While shoot herbivory decreases the amount of competition aboveground, belowground herbivory mimics the influence of eutrophication in shifting competition aboveground.

belowground competition. Likewise, introducing belowground herbivores also decreased belowground competition, as removal of root biomass increased the amount of remaining uncontested resources. Introducing aboveground herbivory had a split effect: Without belowground herbivores, it increased the amount of belowground competition, as the reduction in competition aboveground reverberated into the belowground compartment. With belowground herbivory, however, the two effects cancelled out.

4.3.3 Resilience dynamics during eutrophication

We next investigated the two metrics central to resilience: resistance and recovery (Hodgson et al. 2015) with respect to simulated Shannon-diversity. The diagnostic resistance of our model grasslands, i.e. the response of diversity one year after herbivory was removed, was significantly lower when eutrophication was part of the treatment (Fig. 4). Without eutrophication, there was very little immediate change when belowground herbivores were removed, though aboveground herbivore removal was mildly impactful (Table 2). In other words, eutrophication has a very large immediate effect on how herbivory affected diversity, suggesting that herbivory, and its characteristics, are important modulators of diversity in eutrophic grasslands. The only other strongly significant interaction was between eutrophication and the removal of belowground herbivores, with the removal of root herbivores somewhat mitigating the immediate impact of eutrophication.

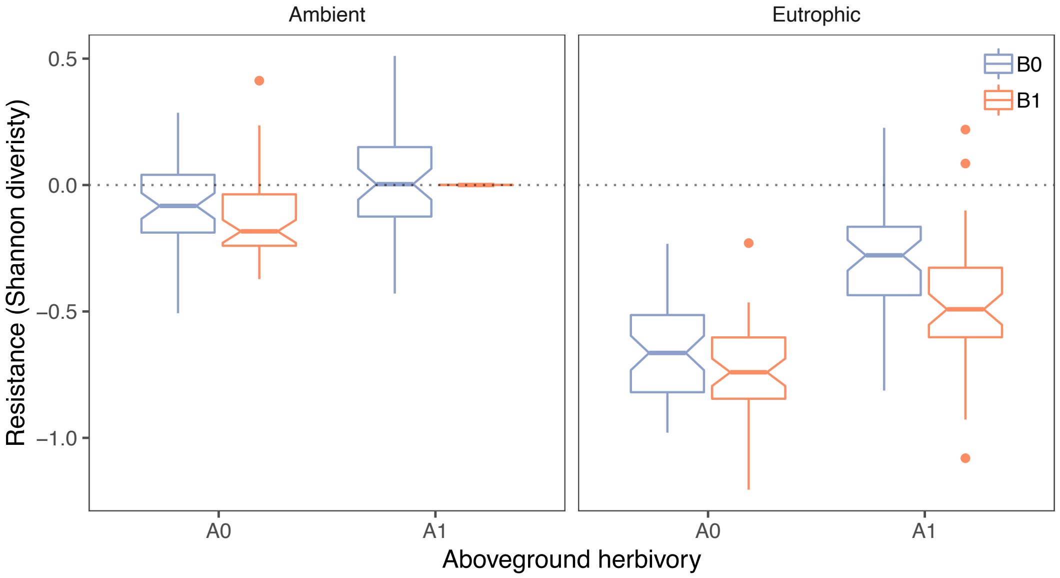

Figure 4. Resistance of Shannon diversity to the experimental treatment. Resistance is measured as the change in Shannon diversity from the control diversity one year after the treatment begins. The control diversity is defined as the treatment maintaining ambient belowground resources and both above- and belowground herbivory. A0 – Aboveground herbivory removed, A1 – Aboveground herbivory present; B0 – Belowground herbivory removed, B1 – Belowground herbivory present. Notches indicate 95% confidence intervals of the medians. While aboveground competition increases the resistance of grasslands to eutrophication, belowground herbivory decreases its effect.

Table 2. Impact of above- and belowground herbivory removal on the resistance response of simulated grassland plots to eutrophication.

Variable	Estimate	Std. Error	t-value	p-value
Intercept	1.199e-15	0.026	0.000	1.000
Eutrophication	-0.467	0.037	-12.729	**< 0.001**
A0	-0.131	0.037	-3.578	**< 0.001**
B0	0.012	0.037	0.322	0.748
Eutrophication:A0	-0.134	0.052	-2.588	**< 0.05**
Eutrophication:B0	0.171	0.052	-2.588	**< 0.01**
A0:B0	0.040	0.052	0.768	0.443
Eutrophication:A0:B0	-0.149	0.073	-2.035	**< 0.05**
Adjusted R-squared: 0.692; F-statistic: 129.1 on 7 and 392 DF				

Recovery was measured as the number of years it takes the community to return to its starting Shannon diversity. As expected, the control scenario—with ambient belowground resources and retaining both compartments' herbivores—was the fastest to recover (Fig. 5), taking on average two years to fall within two standard deviations of its sample mean for ten years (see *Methods: Simulation design and experiments*), in line with a normally distributed test of the algorithm (see Supplemental Material B: Fig. 3). The removal of belowground herbivores increased the TTR compared to the control, but the most damaging experimental configuration—in terms of TTR—was removing aboveground herbivores yet leaving those belowground. In scenarios with eutrophication, the community is quicker to recover if it had a history of belowground herbivory removal, agnostic of aboveground herbivory.

Analyzing the impact of the belowground herbivore's preferentiality (α) on the TTR of Shannon diversity, we found that there is little difference between the different herbivory regimes aside from one effect: with ambient belowground resources, the presence of generalist herbivores slightly reduced the time to return compared to the various levels of preferential herbivory, though its median stayed the same (Supplemental Material B: Fig. 4).

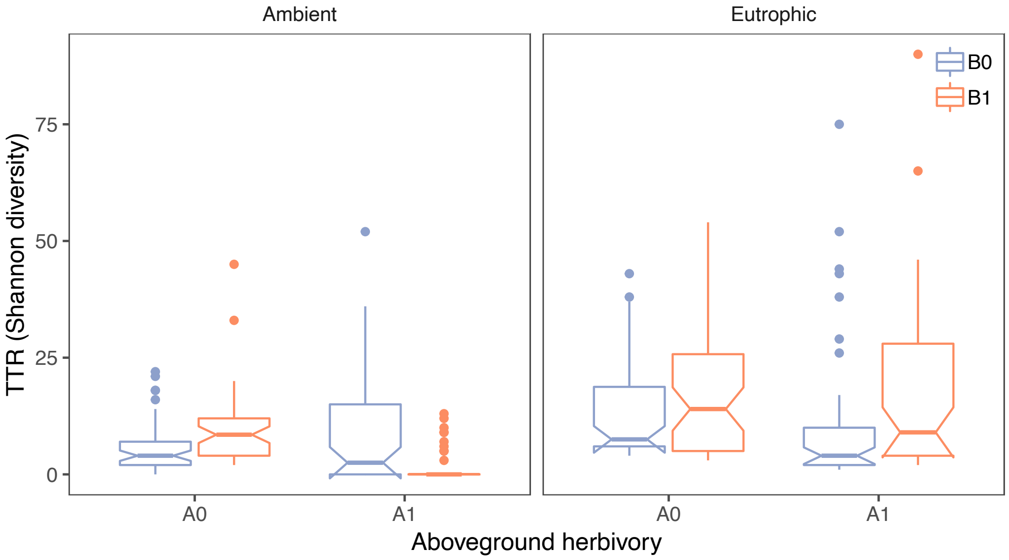

Figure 5. Recovery of Shannon diversity after the experimental treatment. Recovery is measured as the number of years required for Shannon diversity to return to and stay within 2σ of its pre-disturbance level for ten simulation years (time to return, TTR). The control is defined as the treatment maintaining ambient belowground resources and both above- and belowground herbivory. A0 – Aboveground herbivory removed, A1 – Aboveground herbivory present; B0 – Belowground herbivory removed, B1 – Belowground herbivory present. Notches indicate 95% confidence intervals of the medians.

4.4 Discussion

Although the interaction between grassland eutrophication and aboveground herbivory has driven significant interest (Borer et al. 2014, Anderson et al. 2018), the relationship between eutrophication and belowground herbivory has remained largely unexplored. Eutrophication tends to decrease species richness by shifting competition from the belowground compartment to the aboveground compartment, giving a disproportionate advantage to fast growing, tall, species (Bobbink et al. 1998; Hautier 2009; Farrer et al. 2016).

In our analysis, using a simulation model we factorially removed above- and belowground herbivores and introduced eutrophication. We found that belowground herbivory compounds the impact of eutrophication on diversity, because like eutrophication it increases the relative proportion of belowground resources to root biomass, resulting in more resources available to the plants' remaining roots. This shifts competition to the aboveground compartment, exacerbating the advantage of largest, fastest growing plants.

The clearest evidence of this dynamic within IBC-grass is the relative change in the plants' uptake ratios (Fig. 3). Disregarding above- and belowground herbivory, eutrophication *per se* increases the amount of belowground resources available to the plants, increasing the resources available per gram of remaining root biomass. This new resource abundance shifts competition aboveground, leading to the competitive exclusion of short and slow-growing species. These dynamics are consistent with the most contemporary understandings of eutrophication in grasslands (DeMalach et al. 2016, 2017). As these dynamics were not imposed within the model's design (May et al. 2009; Weiss et al. 2014), they can be considered an independent, successful prediction—a strong indicator of structural realism of IBC-grass, defined as its potential to realistically capture the key elements of a grassland's internal organization (Wiegand et al. 2003; Grimm and Berger 2016).

Our analysis of belowground herbivory suggests that its main effect is to also increase the amount of resources available to the plants' roots; rather than increasing the amount of nutrients in the soil, root herbivores decrease the amount of biomass present to compete for it. This synthesis of the theory behind eutrophication and the potential impacts of belowground herbivores is new, and has very little footprint within the literature, with only two empirical studies previously examining it.

In the first, La Pierre et al. (2014), found that removing belowground herbivores increased plant species evenness after eutrophication events, finding that they behaved as a top-down control on the sub-dominant species within the grassland. Once the herbivores were removed, these species were also able to utilize the new resources and diversity increased. In the second, the relationships between above- and belowground herbivory and eutrophication were also examined empirically by Borgström et al. (2017)—the template for our study's design. They found that both belowground herbivores and eutrophication depress diversity, while aboveground herbivory increases it. Although these general effects are consistent across both our studies, the smaller interactions are not fully consistent. While Borgström et al. (2017) also found that root herbivory generally decreased species evenness, they found that the herbivores' effects were more pronounced with ambient resource levels. As these two experiments represent very different study systems, some discrepancies between them are not surprising. As a simulation model, IBC-grass enables us to observe the diversity patterns of a simplified grassland, emergent from basic ecological assumptions. Since Borgström and colleagues used grassland mesocosms, their results will incorporate nuances endemic to their grassland system. This degree of detail, however, may obscure the larger picture; while models' simplifications inevitably omit some of the more complex interactions embedded in real grasslands, simplification enables us to examine the processes likely general to most grassland ecosystems.

Several secondary factors confound the direct comparison of the two studies. IBC-grass uses a larger spatial extent and much larger species pool, and its aboveground herbivory is modeled after ungulates rather than invertebrates. Further, while Borgström et al. (2017) could precisely measure the amount of nitrogen added to the soil, in IBC-grass belowground resources are phenomenological and correspond simply to the "resources taken up belowground," and therefore could be water or nutrients. Therefore, it is not surprising that these systems react somewhat differently to our experimental treatments. However, the main effects found in the empirical study could be replicated without finetuning the model's parameters: Belowground herbivory and eutrophication generally negatively impact diversity while aboveground herbivory increases it.

4.4.1 Root herbivory's influence on symmetric competition for belowground resources

Setting aside eutrophication *per se*, given root herbivores' prevalence in grasslands (Kozlov and Zvereva 2017), building a theoretical understanding of their impact is critical to understanding these systems' diversity. There is little consensus on how herbivory belowground could change a grassland's diversity, with studies finding its influence anywhere from negative (Brown and Gange 1989A, 1989B; Fraser and Grime 2001; Körner et al. 2014) to positive (De Deyn 2003; Stein et al. 2010; Borgström et al. 2017), to neutral (Wurst and Rillig 2011). We argue that this variation in root herbivory's effect stems from two processes: The preferentiality of the root herbivores as well as the (a)symmetry of belowground competition itself. Our results suggest that for root herbivores to positively impact grassland diversity, belowground competition must be asymmetric. When it is not, even very preferential herbivores will, at best, neutrally impact diversity.

For a resource like light, herbivores reduce the competitive asymmetry between the largest and smallest plants by generating space in the upper canopy, feeding the plants lower to the ground (Borer 2014; Anderson 2018). However, as belowground competition is often symmetric, our results suggest that herbivores will reduce the plants' biomasses without equalizing their competitive fitness. Any decrease in root biomass will only result in an excess of belowground resources per remaining root biomass, thus reducing root competition. As the belowground compartment is no longer limiting, aboveground competition will increase, and because aboveground competition is asymmetric, its increase will consequently lead to the exclusion of shorter, slower growing species.

To contextualize this result, it helps to compare the mechanisms behind belowground herbivory to those aboveground. Compared to root herbivory, the impact of shoot herbivory is composed of two asymmetries: The largest plants are eaten asymmetrically, but crucially this reduction in the plants' sizes minimizes a competitive asymmetry between large and short individuals. With symmetric belowground competition, by contrast, no such competitive asymmetry exists. Therefore, root herbivores will generally not be as effective in maintaining biodiversity as their aboveground cousins.

If belowground competition is symmetric, our results further indicated that even extremely preferential root herbivory may be unable to increase diversity compared to scenarios without root herbivores. This reflects a balance between the positive influence of disproportionately reducing the largest plants' root biomasses and the corresponding increase in aboveground competition. Of course, relative to purely generalist herbivores, even a low degree of feeding preference will increase diversity (Fig. 2). This suggests that when belowground competition is asymmetric, it is likely that any preference of the root herbivores towards dominant plant functional types could prove to be a strong mechanism maintaining a grassland's diversity. Given that other empirical analyses of root herbivory suggest that it may stabilize diversity (De Deyn 2003; Stein et al. 2010; Borgström et al.

2017), future research should investigate the possibility of underlying asymmetries in belowground competition within these study systems.

That belowground resources are symmetrically allocated has been an important assumption in grassland and forest modeling (Schwinning and Weiner 1998). Although numerous empirical tests have found this to be the case (Casper and Jackson 1997; Weiner 1997; Berntson and Wayne 2000; Blair 2001; Wettberg and Weiner 2003; Cahill and Casper 2003; Lamb 2008), under certain conditions it is likely to be asymmetric as well (Weiner 1990; Rajaniemi 2002, 2003; Rajaniemi et al. 2003, Weiss et al. 2019). Understanding when belowground herbivory is likely to be asymmetric is therefore necessary to fitting our model's results into a broader context.

The empirical literature has found that asymmetry in belowground competition is increased when nutrients are patchy in the soil, giving a competitive advantage to larger root systems that can disproportionately access them (Fransen et al. 2001; Facelli and Facelli 2003; Rajaniemi 2002; Rajaniemi et al. 2003). A model of belowground competition (Raynaud and Leadley 2005) furthered this hypothesis, finding that the symmetry of belowground competition should also depend on how nutrients diffuse in the soil. In wet soils, nutrients will be more diffuse and therefore plant competition will become more dependent on the plants' uptake kinetics, shifting competition towards asymmetry. This hypothesis has been supported by at least one empirical test (Rewald and Leuschner 2009). Belowground competition could also become asymmetric through its vertical dimension (Schenk 2006), with root systems higher to the surface receiving a larger proportion of water and nutrients (van Wijk and Bouten 2001).

To summarize, although belowground competition is often more symmetric than aboveground competition, this balance should not be taken for granted. When belowground competition is symmetric, our model indicates that root herbivory will not support diversity and may even substantially decrease it as it shifts competition aboveground, leading less competitive species towards exclusion. Given that even an extreme asymmetry in the feeding preferences of the herbivores did not shift the direction of their influence on coexistence, our results indicate that variation in the empirical literature on root herbivores likely results not from their feeding preferences in isolation, but also from asymmetries in belowground competition.

4.4.2 Resilience of grassland systems to eutrophication

Trophic interactions, such as herbivory, are acknowledged as important contributors to the stability of ecological systems through their compensatory effects (Hillebrand et al. 2007; Gruner et al. 2008; Ghedini et al. 2015). To supplement our investigation into the mechanisms through which herbivory influences grasslands' responses to eutrophication, we also measured how above- and belowground herbivory change the resistance and recovery of our model grasslands to eutrophication. Our main findings indicate that the removal of herbivores is relatively mild in its immediate effect on diversity (Fig. 4), and that once the herbivores return diversity follows relatively quickly (Fig. 5).

With eutrophication, however, the magnitude of change is much larger. For resistance, as predicted by ecological theory (Hillebrand et al. 2007; Gruner et al. 2008;

Kohli et al. 2019) and empirical evidence (Eisenhauer et al. 2011; Post 2013; Ghedini et al. 2015; McSkimming et al. 2015), the presence of aboveground herbivory compensates—albeit weakly—for the immediate effects of a strong eutrophication event (Fig. 4), and over the course of the 100-year treatment, its impact becomes much more influential (Fig. 1). This suggests that a long experimental duration is necessary to understand the full array of interactions forming a grassland's response to eutrophication (Kidd et al. 2017). Further, simulations retaining aboveground herbivores returned to their pre-disturbance state more quickly than those without it (Fig. 5).

Belowground herbivory, however, does not neatly dovetail with ecological theory: Indeed, the presence of root herbivory coincides with a reduction in resistance to eutrophication (Fig. 4), as well as a longer time to return (Fig. 5). This is unsurprising, however, given our finding that belowground herbivores tend to exacerbate the dominance of the strongest competitors, unlike their counterparts aboveground. Once established, these plant species will retain their dominance for a long period of time after nutrient addition is halted.

4.5 Conclusions

As anthropogenic changes such as eutrophication increasingly stress grassland ecosystems, understanding what aspects of these communities mediate their ability to resist degradation is becoming increasingly important. Trophic interactions between the plant community and their herbivores are one such aspect. Our results suggest that rather than strengthening a plant community's resilience to a eutrophication event, belowground herbivores compound its negative influence on plant diversity and resilience. These results are tightly interlinked with the symmetry of belowground competition and preferences of the herbivores themselves. Future research must investigate how prevalent competitive asymmetries are within the belowground compartment, as they may be a necessary condition for root herbivores to positively influence diversity.

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5. General Discussion

In this thesis, I investigated how fundamental aspects of grassland systems—intraspecific trait variation, trophic interactions, and eutrophication—mediate plant communities' diversity and resilience.

In the second chapter of my thesis, I focused on a focal question in contemporary functional ecology: What are the ecological effects of intraspecific trait variation (ITV), and how and when should we incorporate it into our community analyses? I found that ITV may increase diversity, but this benefit is largely limited to communities of low alpha diversity. I also note that the effects of ITV—both at the level of the species and the functional trait—will differ based on whether the analysis in question considers species pairs or communities, and persistence or abundance.

In the third and fourth chapters, I focused on an underappreciated trophic interaction, investigating how belowground herbivores change the diversity of grassland communities as well as mediate their resilience to a null disturbance – the stochastic death of plant individuals – and one of the most pervasive disturbances in grasslands today, eutrophication. In particular, I found that belowground herbivores may be critical players in the maintenance of biodiversity during these disequilibrium events, but that their exact influence will likely depend on aspects of the plant community, such as the degree of asymmetry in belowground competition and the type and timing of the disturbance itself.

5.1 Intraspecific trait variation shapes the assembly and diversity of grassland ecosystems

Fundamental aspects of functional-community ecology are being reconsidered in light of ITV. Although a growing body of evidence suggests that trait variation enables species to pass through abiotic filters (Jung et al. 2010, Lepš et al. 2011, Siefert 2012), how it influences biotic filtering is significantly more contested. While several recent theoretical studies have found that the ecological effects of ITV likely limit species coexistence (Barabás et al. 2016, Hart et al. 2016), empirical analyses are often conflicting (for a thorough review, see Turcotte and Levine 2016). Reconciling this diverse array of findings is a complex task, but necessary to build a synthetic framework of how ITV shapes the assemblage of ecological communities. My study in Chapter 2 highlights several aspects in which analyses may misestimate the influence of ITV on communities' assembly and resulting biodiversity.

A primary example of these nuances is that the size and diversity of a community's species-pool will determine the degree to which ITV maintains diversity. Although ITV often improves the predictive capabilities of trait-based analyses in high-diversity communities (Cornwell and Ackerly 2009, Jung et al. 2010, 2014), a growing body of work also suggests that it may help facilitate the persistence of low-fitness species in low-diversity communities (Crutsinger et al. 2006, Hughes et al. 2008, Kraft et al. 2014, Siefert et al. 2015, Crawford et al. 2019). "Individual-variation theory" (*sensu* Violle et al. 2012) predicts that this effect will emerge as long as viable niches along a given trait axis are left unoccupied within the community. While high-diversity communities are more likely to have fully-occupied trait axes, low-diversity communities may not. In this case, variation in a species' traits may enable it to fill this empty niche space, bypassing the abiotic and biotic filters present. This insight reconciles a discrepancy between previous literature investigating ITV's influence on biotic filtering and ours: Although Barabás et al. (2016a) found that ITV limited species coexistence in their "saturated" model communities, the analysis presented here suggests that, while the diversity-effects of ITV are marginal in saturated communities, they may be substantial in low-diversity communities. This idea, consistent with niche theory (MacArthur and Levins 1967), has so far been largely supported by empirical evidence (Hulshof et al. 2013, Siefert et al. 2015).

This research also undermines the use of pairwise invasion analysis as a tool to investigate how ITV mediates the community assembly. It suggests that, although ITV increases the invasive capacity of even the least fit species, this added competitive ability may fail to translate into increased abundance within real communities. Indeed, only the competitively average species—those that will often persist regardless—truly benefit from the inclusion of trait variation. Also suggestive of this dichotomy is our analysis of the PFTs' traits, which indicates that different traits vary dramatically in their relative importance in mediating persistence and abundance. Further, this importance changes significantly over our gradient of ITV. At the heart of this insight is the difference between "persistence" and "abundance." Although a species may be able to, in principle, persist at low density within a community, true coexistence will only emerge when it can achieve a high-enough population to overcome the risk of extinction from demographic stochasticity (Kendall and Fox 2002) and environmental fluctuation (Ido Filin and Ovadia 2007). This finding is highlighted by a recently proposed concept, "coviability," which was coined to suggest that the ability for two species to locally coexist is often more stochastic and temporally-fleeting than modern coexistence theory can readily capture (Jeltsch et al. 2019). Rather than focusing purely on whether two species can coexist permanently, we should acknowledge and embrace the stochastic nature of coexistence, testing mechanisms that may enhance species coviability and thus increase the likelihood that they can coexist for a given time. Recognizing the limitations of pairwise invasion analyses is an initial step towards understanding the need for new, though potentially less mathematically-satisfying, lenses through which to consider these complex community assembly mechanisms.

Lastly, studies testing the influence of ITV on competitive interactions are only just beginning to explicitly incorporate the concept of space (Uriarte and Menge 2018, Crawford et al. 2019, Banitz 2019). Contrary to previous studies incorporating ITV into mathematical models that assume averaged competition and a spatially homogeneous environment (Barabás et al. 2016, Hart et al. 2016), each of these studies has found that ITV can increase diversity, despite employing a diversity of methodologies. The first example of these studies, Uriarte and Menge (2018), incorporates the concept of space—modeled by two patches—into the same mathematic model (Beverton and Holt 1957) as that of Hart et al. (2016). If one considers a scenario in which dispersal between the two sites is limited, the authors find that the better competitor on each site will accrue most of the benefits from the inclusion of ITV, consistent with Hart et al. (2016). However, when one introduces some degree of cross-patch dispersal, the inferior competitor will benefit more, assuming it specializes in the most fertile habitat. The authors note that these results indicate that the level of dispersal will be vital to the efficacy of ITV in promoting coexistence, as when the dispersal is too high, the superior competitor once again disproportionately, simply proliferating in both patches. This finding is consistent with a key result from our analysis, as ITV predominately benefitted coexistence in low-diversity communities. Adding dispersal into these communities from species at the high-end of the competitive hierarchy would swamp any additional diversity mediated through ITV. Introducing the concept of space into analyses of ITV can clearly shift its influence from negative to positive.

The inclusion of spatial and temporal resource heterogeneity is another crucial aspect of coexistence that is underappreciated within the ITV-literature. So far, only one study has explored the influence of ITV on coexistence in a spatially-heterogeneous context (Banitz 2019), finding that ITV can considerably increase diversity when it is spatially-structured itself. When spatially-structured, ITV causes responses in individuals' traits that are persistent for a given habitat condition (Moran et al. 2016). This, in effect, can drive a storage effect, bolstering species' populations in hostile habitats. Future work with the IBC-grass model could further explore these ideas.

This disparity between different types of analyses describing how ITV mediates biotic interactions, with spatially-implicit studies suggesting a net-negative effect while spatially-explicit studies suggest the opposite, is a strong argument for embracing the coviability framework and for greater investment in analyses based on individual-based modeling. Because individual-based models are—compared to mathematical models—"embarrassingly" spatially-explicit, they are a natural medium through which to explore how these subtle diversity mechanisms emerge and persist. For example, future analyses of ITV could consider how an individual's competitive neighborhood shifts with intraspecific-trait variation, potentially enhancing the "stochastic dilution effect," (Wang et al. 2016) wherein some individuals, blessed with good fortune, find themselves in a relatively uncompetitive neighborhood. Although this effect—if considered from a Chessonian perspective—may be transient, in real communities it may support the local presence of rare species for generations. And, if combined with other mechanisms, such as source-sink dynamics, they may further promote these rare species’ persistence. Adding ITV to this general mechanism could increase the pathways through which an individual could arrive in a beneficial neighborhood.

Although our simulation is spatially-explicit, our study’s consideration of how space changes the influence of ITV was not fully elaborated. Examining this limitation is a critical challenge for future research, especially in terms of quantifying more clearly how ITV mediates the individuals’ competitive interaction milieu. One modern tool, spatial point-pattern analysis (Wiegand and Moloney 2004, 2013), would be especially interesting to employ for this purpose, as it cleverly utilizes null models to isolate the impacts of spatial arrangement and neighborhood effects on target individuals. Through such analysis, future research could determine exactly how a plant-individual’s neighborhood affects its fitness, and critically, how ITV alters this relationship.

In summary, our incorporation of ITV into the IBC-grass model and subsequent analysis of its impact on community coexistence challenges a significant number of precepts within functional ecology and traditional coexistence theory. Our work joins a growing consensus of literature stressing that intraspecific trait variation matters. Indeed, its influence on ecological interactions, such as competition and facilitation, is likely underestimated (Des Roches et al. 2018, Raffard et al. 2019) and may pervade natural communities. Functional ecologists would be wise to consider including it into their future analyses. These analyses must be thoughtfully designed, however, and should avoid a myopic focus on classical coexistence theory that dismisses a wealth of possibly complementary coviability mechanisms in favor of mathematical tractability.

5.2 Belowground herbivory mediates the diversity and resilience of grasslands

Our study of belowground herbivory's interaction with disturbance began as a broad investigation, parameterizing aspects that define many disturbances, as well as facets of the environment and the herbivores themselves (Chapter 3). We found that belowground herbivores may be important, but underappreciated, mediators of disturbance in grassland communities. But, this analysis also confronted us with deep questions to investigate further: Why do belowground herbivores undermine biodiversity, and why does their influence intensify with higher resources belowground? To isolate this complex relationship, we shifted focus to a disturbance that is caused by an increase in resources belowground—eutrophication (Chapter 4). We then answered these questions by mechanistically comparing how both belowground herbivores and eutrophication can change plant competition. Our results indicate that the impact of belowground herbivores is surprisingly like that of eutrophication, in that herbivores shift competition aboveground by increasing the quantity of belowground resources relative to plant root biomass.

In this section, I will synthesize the results of Chapters 3 and 4, first drawing inferences on how belowground herbivory shapes the plants' competitive dynamics—and eventually their biodiversity—and then focusing on how this effect mediates the impact of various disturbances on the plant community. Throughout, I will compare this behavior to belowground herbivores' commonly studied cousins, herbivores aboveground.

5.2.1 The mechanism through which belowground herbivory impacts grassland competition

A central finding within Chapter 3 of this dissertation is that belowground herbivores have a significantly greater impact on nutrient-rich communities than on nutrient-poor communities. This effect is observed as both a marked decrease in plant diversity during assembly and a significant increase in the impact of the disturbance itself. This connection suggests that belowground herbivores may be a contributing mechanism to one of the longest-standing questions in ecology: Why do nutrient-rich systems tend to reflect lower species diversity (Pigott and Taylor 1964, Tilman 1987)?

The contemporary theories that have emerged over the past decades explain this relationship through either 'niche dimensionality' (Harpole and Tilman 2007, Harpole et al. 2016), wherein a reduction of limiting resources leads to competitive exclusion, or through the 'light asymmetry hypothesis' (Newman 1973, DeMalach et al. 2016, 2017), wherein an increase in resources belowground leads to an increase in—asymmetric—aboveground competition. Although both theories are likely valid, and their effects likely present, their relative importance is a matter of intense debate (DeMalach and Kadmon 2017, Harpole et al. 2017). From the latter theory (light asymmetry), several studies have suggested that aboveground herbivores may be a countervailing force, reducing the asymmetry aboveground and therefore increasing biodiversity (Borer et al. 2014, Anderson et al. 2018, Hautier et al. 2018). Our study (Chapter 4) is the first of its kind showing how belowground herbivores also fit into this framework.

The underlying premise of the light asymmetry hypothesis stems from the publication of Newman (1973), but most recently DeMalach et al. (2016) demonstrated the potential strength of its effect, initially by proposing a model that illustrates how asymmetric aboveground competition interacts with belowground resource availability to drive community trait patterns commonly associated with eutrophication. They found that even a small degree of asymmetry in aboveground competition could shift the community towards large species because it compounds the fitness of individuals that can rapidly outgrow—and therefore overshadow—their neighbors. With scarce belowground resources, however, the importance of this asymmetry is marginal because plants are competing symmetrically belowground (Weiner et al. 1997, Schwinning and Weiner 1998). Following this theoretical model, they experimentally manipulated the asymmetry of aboveground competition in natural communities and showed that light asymmetry was the main mechanism behind the negative diversity effect of nutrient enrichment on species richness (DeMalach et al. 2017).

Our model is consistent with this pattern: With eutrophication, the fastest-growing, most competitive plant species prevail. However, furthering these results, we find in Chapter 4 that incorporating aboveground herbivores within IBC-grass reduces this competitive asymmetry and therefore maintains diversity in nutrient-rich communities—mirroring contemporary theory and empirical analyses. Mechanistically, since aboveground herbivory tends to increase the availability of ground-level light, it decreases the competitive asymmetry between large, fast-growing plants, and their smaller, slowing growing competitors (Borer et al. 2014, Anderson et al. 2018). In other words, aboveground herbivores buffer grassland diversity when belowground resources are not limiting and aboveground competition is high.

Our studies build on this general framework. Because the plant community's competition belowground is often symmetric (Schwinning and Weiner 1998, Berntson and Wayne 2000, Blair 2001, Lamb et al. 2009), when belowground herbivores feed on this compartment's biomass they fail to reduce any asymmetry between the dominant and subordinate species, as no asymmetry between the largest and smallest plants exists to be reduced, thus undermining any potential to promote diversity. Indeed, our study (Chapter 4) indicated that they may have the opposite effect because they reduce the amount of root biomass competing for belowground resources and thus mitigate belowground competition. This reverberates aboveground by increasing the amount of shoot competition, eventually decreasing diversity through competitive exclusion. This novel result suggests that belowground herbivory may exacerbate the effects of eutrophication on grassland biodiversity.

One important feature of this finding is that even belowground herbivores that are selective towards dominant species will not support the diversity of the plant community. This is likely because, within the IBC-grass model, any reduction in the largest individuals' fitness is overshadowed by the corresponding reduction in belowground competition *per se*. This also suggests, however, that belowground herbivory may be a diversity mechanism if belowground competition were, indeed, to be asymmetric. As reviewed in Chapter 4, and further discussed in the following section of this discussion, there is some empirical evidence indicating that asymmetric competition belowground is possible (Weiner 1990, Rajaniemi 2003, Rajaniemi et al. 2003). When it is asymmetric, belowground competition may be mitigated in much the same way as aboveground competition, by minimizing the relative fitness differences between small and large plants. Depending on the strength of asymmetry belowground and aboveground, as well as the relative strength of the herbivory itself, a different competitive environment may emerge.

One limitation of the analysis presented in this thesis is that it did not attempt to increase the asymmetry of belowground resource competition. Therefore, one cannot explicitly test the hypothesis that belowground herbivory would increase diversity if belowground competition was asymmetric. In principle, however, this should not alter our central conclusions. This is because plant competition aboveground is asymmetric, and therefore provides a useful metaphor for understanding what would occur if belowground competition were to be asymmetric. The exact magnitude of these effects will undoubtedly change with the specific traits that underlie them, as asymmetry in the aboveground compartment being controlled by the plants' growth form and size, and asymmetry in the plants' belowground compartment may be controlled by potential traits such as their belowground morphology (Wijk and Bouten 2001) or uptake kinetics (Raynaud and Leadley 2004, Rewald and Leuschner 2009) in addition to their size. However, although the magnitude may differ, the direction is likely the same. In other words, it is likely the case that any asymmetry *per se*—regardless of the compartment—would behave qualitatively the same in its reaction to herbivory. However, it is necessary to validate this hypothesis with future work.

In summary, the efficacy of belowground herbivory to support diversity will depend on the nature of competition belowground. In most cases, since the herbivores exploit plants that are competing symmetrically for belowground resources, they will not increase diversity. Indeed, our results indicate that they may often promote competitive exclusion. This occurs as the herbivores increase the pool of belowground resources available to the plant community, shifting competition from belowground to aboveground, symmetric to asymmetric. In a larger context, given that nutrient enrichment is nearly ubiquitous in grassland ecosystems (Wesche et al. 2012, Isbell et al. 2013a, b), and that root herbivores are nearly omnipresent within them (Cyr and Face 1993, Zvereva and Kozlov 2012, Kozlov and Zvereva 2017), our results suggest that the frequently documented, marked decline in grassland diversity (Tilman et al. 2002, Harpole and Tilman 2007, Isbell et al. 2013a, b, Hautier et al. 2015) is partially explained by the interaction of these two—distinct—processes.

5.2.2 Is competition for belowground resources commonly symmetric?

In the previous section, I demonstrated how belowground herbivory may exacerbate the negative effects of nutrient enrichment in grassland ecosystems. Our results suggest that this effect emerges from their shared mechanism: Belowground herbivory will—like nutrient enrichment—increase the ratio of belowground resources to root biomass. Unless belowground competition is asymmetric, the magnitude of this effect will likely dominate any competing effects, such as that of preferential herbivory. In the following section, I will consider the likelihood that this assumption broadly holds, and consequences for my main findings if it does not.

While symmetry in plants' competition belowground is often reported within the theoretical (Schwinning and Weiner 1998) and empirical (Weiner et al. 1997, Casper and Jackson 1997, Berntson and Wayne 2000, Cahill, Jr. and Casper 2000, Blair 2001, Wettberg and Weiner 2003, Lamb et al. 2009) literature, a growing body of work suggests that this is not always the case. One promising mechanism inducing asymmetry in belowground competition arises when nutrients are patchily distributed in the soil matrix. When this is the case, fast-growing, precise foraging species may find and exploit these nutrient-rich patches before their smaller, slower-growing counterparts (Casper and Jackson 1997, Rajaniemi 2003, Hutchings et al. 2003). This initial asymmetry in competitive ability compounds with time, increasing the size and relative abundance of dominant species, eventually decreasing species diversity and shifting the community towards competitive plant functional types (Rajaniemi et al. 2003).

There are several other mechanisms through which belowground competition could tip into asymmetry. Some plants, for example, may compete asymmetrically for resources in the vertical root dimension (Schenk 2006), with root systems near the surface receiving more water and nutrients (Wijk and Bouten 2001). It is also possible that plants' uptake kinetics could shift competition towards asymmetry, particularly in wet soils when nutrients are highly diffuse (Raynaud and Leadley 2005, Rewald and Leuschner 2009). Species with efficient uptake kinetics will absorb resources significantly more quickly than their less-efficient counterparts (Raynaud and Leadley 2004). As these individuals convert nutrients to biomass, this advantage in nutrient uptake may compound over time, eventually leading to the competitive exclusion of the weaker species.

However, despite evidence of belowground competitive asymmetries in natural communities, for belowground herbivores to benefit a plant community under asymmetric competition, they must be preferential towards the dominant PFTs. In Chapter 3 of this dissertation, we confront this question. Although belowground herbivory (regardless of its preferentiality) decreases diversity compared to no herbivory at all, relative to the presence of purely generalist herbivory (i.e. directly proportional to root biomass), even small degrees of herbivore preference towards dominant plant species increases diversity. This suggests that, if plant competition belowground is asymmetric, a relatively small degree of preference in the feeding preferences of belowground herbivores may increase plant diversity. Therefore, understanding to what degree belowground herbivores feed preferentially in natural communities is an important question to answer, and contemporary empirical analyses are beginning to do so.

In principle, a 2012 meta-analysis found that generalist herbivores are the most predominant source of biomass-loss belowground, with specialist herbivores contributing significantly less (Zvereva and Kozlov 2012). However, if generalist herbivores tended to select plants with larger root systems, diversity-promoting effects may still arise. The feeding preferences of root herbivores have begun to generate more interest (Schallhart et al. 2012, Sonnemann et al. 2013, Wallinger et al. 2014). Nevertheless, significantly fewer studies of root herbivores exist compared to their foliar counterparts. Within this subject, species of the genus *Agriotes*, or wireworms, are one of the most studied examples. This is because they are nearly ubiquitous (Parker and Seeney 1997, Jedlička and Frouz 2007) and, as external root chewers, they may be one of the most damaging sources of belowground herbivory (Zvereva and Kozlov 2012). They are broadly considered generalists but may vary their diet throughout the year to favor some species over others (Wallinger et al. 2014). Overall, they may tend to eat plants with high biomass, growth rates, and tissue quality (Sonnemann et al. 2012, 2015). Depending on the strength of this tendency, such generalist herbivores may shift the influence of belowground herbivory overall in ways that are beneficial for grassland diversity.

If a grasslands' plant community is competing asymmetrically for belowground resources, and herbivores are preferentially consuming the roots of the dominant plant species, this root herbivory may counteract the negative consequences of eutrophication. In this scenario, the effects of root herbivores may mirror those of their aboveground counterparts, reducing the fitness of the dominant species and thus boosting plant diversity. Although this mechanism (which increases diversity) would compete with diversity-impacts of an increased abundance of nutrients relative to root biomass (which decreases diversity), the combined impacts of preferential herbivory acting on asymmetric competition could perhaps emerge as the more powerful force. Therefore, if our assumption of symmetrical belowground competition is unsupported, the eventual diversity impacts of belowground herbivory could conceivably be largely reversed.

Quantifying the symmetry of belowground competition may help reconcile disparities between empirical studies, which suggest that belowground herbivores decrease (Brown and Gange 1989a, b, Fraser and Grime 1999) or increase (De Deyn et al. 2003, Stein et al. 2010, Borgström et al. 2017) diversity. For example, since Stein et al. (2010) conducted their study in a grassland with nutrient-poor soil, root competition may have tilted towards asymmetry and, therefore, the removal of any size-preferential herbivores could have led to lower species richness and evenness. This possibility strongly argues that future analyses investigating belowground herbivory should consider the nature of competition belowground.

5.2.3 How belowground herbivory impacts the resilience and succession of grasslands

Belowground herbivores are not only important mediators of grassland community diversity, but they also represent an important class of trophic interactions that determine the resilience of these communities and guide their diversity-response to a wide variety of disturbance events. Both Chapters 3 and 4 of this dissertation detailed how root herbivory mediated the resilience of grassland communities to disturbance. Chapter 3 focused on a generic disturbance (the death of random plant-individuals), considering a broad range of the system's parameters such as the timing of disturbance, its intensity, the presence of a seed bank and amount of belowground resources for the grassland community, and the preferences of the root herbivores themselves. Chapter 4 focused more specifically on the disturbance of eutrophication, discussed in more detail in the previous section of this chapter. In this section, I will synthesize these two analyses to show how the type, intensity, and timing of the disturbance interplays with belowground herbivores to drive succession in our model grasslands.

Consistent across both types of disturbance, the most important determinant of root herbivory's influence on a grassland community is the amount of resources belowground. In both studies, belowground herbivory was significantly less consequential in mediating the post-disturbance succession of low resource grassland communities (Chapter 3) and exacerbated the plant community's negative reaction to eutrophication (Chapter 4). Given this result, belowground herbivores may be a more important driver of diversity in high resource grassland systems. However, the type of disturbance also mediates the belowground herbivores' effects. For example, with eutrophication alone, belowground herbivores exacerbated its effect (Borgström et al. 2017) and increased the time it took for the plant community to return to recovery to its previous community (Chapter 4). But, should that community be disturbed by the death of some percentage of the resident plants, it appears that belowground herbivores—if present—will increase diversity by disproportionately affecting the remaining individuals, thus giving new species from the meta-community space and resources to flourish for a time.

A variety of other parameters in our simulated grasslands shaped the impact of belowground herbivores on grassland diversity. For example, we found that the grassland community was more resilient to our stochastic disturbances when they retained some "memory" of the previous years' community (Chapter 3). This memory could emerge either through a long-term seed bank or because the disturbance occurred after the seeds had already dispersed. Through either of these mechanisms, a representative sample of seeds from the previous community partially outweighs the gains in biomass made by the surviving plants-individuals (Miller et al. 2012). This slows the rate through which the community shifts to their new state.

Seed banks may, therefore, buffer grasslands' resilience to Anthropogenic disturbances. Unfortunately, contemporary research suggests that grasslands' seed banks may be insufficiently long-lived to fulfill this role (Bekker et al. 1997, Klaus et al. 2018). In addition, since eutrophication tends to deplete grassland seed banks (Basto et al. 2015), their buffering-capacity may be further undermined. Future analyses of these dynamics should incorporate time horizons that are sufficiently long to capture the influence of eutrophication on these dynamics (Kidd et al. 2017).

Although belowground herbivores, in principle, lower species richness and evenness by shifting the plants' competitive interactions aboveground, they will not necessarily reduce diversity after disturbance. Since our random disturbance regime (Chapter 3) led to a relative increase in herbivory pressure towards the largest remaining plant-individuals, newly recolonizing rare-species are given a reprieve. These complex interactions, with belowground herbivory shaping diversity in a context-dependence process, demand further empirical examination.

In summary, belowground herbivory is likely to reduce biodiversity in grasslands generally. Moreover, while they may exacerbate the negative effects of eutrophication events, if preferential in their feeding preference, they may support diversity immediately after disturbances that impose individual plant mortality, assuming seed addition is present. This is because the heightened feeding pressure will disproportionately impact the largest individuals, which in high-resource communities will tend to be the largest, fastest-growing species. However, this effect pales in comparison to the negative consequences of belowground herbivory when belowground competition is symmetric. In other words, although belowground herbivores may support diversity during post-disturbance succession, the plant community's diversity will generally be much lower with herbivores than without.

5.3 Biodiversity and stability in grassland ecosystems: A synthesis

Human-mediated environmental change threatens the health and diversity of grasslands worldwide (Wesche et al. 2012, Harrison et al. 2015). Predicting how these ecological systems will change with increasing land-use management demands a deep understanding of their underlying community assembly processes, but also an effective framework describing how these processes will shift under stress.

My results further develop our understanding of each of these processes. In the second chapter of my thesis, I provide evidence that ITV can be a critical factor contributing to grassland diversity, but its benefits are not distributed evenly. Competitively average species benefit only in low diversity communities. Researchers seeking to understand the effects of ITV on their systems should embrace the concept of coviability (Jeltsch et al. 2019) and move away from more traditional pairwise analyses, as the effect of ITV in mediating invasion is not equivalent to its effect in mediating abundance. In the third chapter of my thesis, I showed that belowground herbivores can dramatically shift the trajectory of grassland succession after intense disturbances. Indeed, in the fourth chapter, I showed that they synergistically interact with eutrophication to reduce diversity by shifting competition aboveground. The synthesis of these two chapters presents strong evidence for the efficacy of belowground herbivores—even at "background" levels (Zvereva and Kozlov 2012, Kozlov and Zvereva 2017)—in controlling plant species diversity through their indirect effect of increasing aboveground competition. Of course, as noted in the previous section, this effect is highly dependent on the symmetry of belowground competition, which has itself been inadequately studied.

In summary, my thesis leverages state-of-the-art simulation modeling to delve into the feedback between grassland communities and the ecological processes that mediate their assembly. Further developing these ideas will be critical to navigating biodiversity loss as human population growth stresses these natural and semi-natural ecosystems. Enriching our body of ecological theory promises to help conservation practitioners understand where leverage is to be found in meeting their biodiversity targets.

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7. **Declaration**

This cumulative dissertation comprises three scientific studies (chapters 2 – 4), which were prepared as independent manuscripts and are published (chapter 2) or in review (chapters 3 and 4) in international, peer-reviewed journals. As I prepared the manuscripts in cooperation with my co-authors, they are written in the first-person plural. As the leading author of all manuscripts, I developed the model extensions and experimental design, as well as conducted the analyses and wrote the text for all chapters. All co-authors provided feedback during the completion of each analysis and preparation of each paper. This dissertation has not been previously submitted to any other university.

Michael S. Crawford (PhD candidate)

Prof. Florian Jeltsch (supervisor)

8. Appendix

For simplicity, all three ODD documents (Overview, Design concepts, and Details, Grimm et al. 2006) have been collected into one unified document. Therefore, while citations of "Supplemental Material A," will always refer to the unified ODD document throughout this dissertation, all references of the proceeding supplements (B, C, D, etc.) are chapter-specific. The appendix is therefore divided into four sections: The ODD (8.1), and then all supplements pertaining to the second chapter (8.2), the third chapter (8.3), and finally the fourth chapter (8.4).

8.1 Supplemental Material A: Overview, Design concepts, and Details (ODD) protocol

The individual-based community grassland model (IBC-grass)

8.1.1 Detailed model description

This model description follows the ODD protocol (Overview, Design concepts, and Details) for describing individual-based models (Grimm et al. 2006, Grimm et al. 2010). The description of the original model by May et al. (2009) is coloured black, while changes made for the second chapter's analysis are colored in red, the third's are in blue, and the fourth's are in green. Two submodels, belowground herbivory and seed addition, are used within both the third and fourth chapters' analyses.

8.1.2 Purpose

The model is designed to evaluate the response of plant functional type diversity towards aboveground grazing under different local environmental conditions and differentiated assumptions about plant-plant competition.

8.1.3 State variables and scales

The model includes the entities seeds, individual plants, and grid cells (Table A1). Seeds are described by the state variables position, age, and mass. Plant individuals are characterized by their position, the mass of three plant compartments (shoot, root and reproductive mass), the duration of resource stress exposure, and they are classified as a certain PFT with specific trait attribute parameters (see May et al. 2009 for the parameterization for the PFTs). If intraspecific trait variation is enabled, each plant additionally has its own set of functional traits, derived through from their PFT's trait mean. Spatially, plants are described by their "zone-of-influence" (ZOI), i.e. a circular area around their location (Schwinning and Weiner 1998, Weiner et al. 2001). Within this area the individual can acquire resources and if the ZOIs of neighboring plants overlap, the individuals will only compete for resources in the overlapping area. For the three-compartment model version we consider two independent ZOIs for a plant's shoot and root, representing above- and below-ground resource uptake and competition. The ZOIs radii are determined from the biomass of the corresponding plant compartment.

In order to simplify spatial calculations of resource competition, ZOIs are projected onto a grid of discrete cells. Grid cells represent 1 cm². The state of a grid cell is defined by two resource availabilities, above and below ground. To avoid edge effects, periodic boundary conditions were used, i.e. the grid essentially was a torus. Through periodic boundaries, we ensure that dispersal limitation is the same for individuals in the center and at the edge of the simulated area. A model's time step corresponds to one week; a vegetation period consisted of 30 weeks per year, and simulations were run for 100 years in chapter 2, 300 years in chapter 3, and 300 years in chapter 4.

8.1.4 Process overview and scheduling

The processes resource competition, plant growth and plant mortality are considered within each week of the vegetation period. Seed dispersal and seedling establishment are limited to certain weeks of the year (Fig. A2, A3, A4). Grazing events occur randomly with a fixed probability which is constant for all weeks. Two processes, winter dieback of above-ground biomass and mortality of seeds are only considered once a year, at the end of the vegetation period (Fig. A2, A3, A4). Plant's state variables are synchronously updated within the subroutines for growth, mortality, grazing and winter dieback, i.e. changes to state variables are updated only after all model entities have been processed (Grimm and Railsback 2005).

8.1.5 Design concepts

Basic concepts

The model represents trait-offs in the plants' traits, and it focusses on plant function types (PFT), not on predefined species. Community assembly is mimicked by starting with all possible combinations of trait combinations and letting the final community composition assemble itself. Different modes of competition, i.e. asymmetric and symmetric, are implemented for above- and below-ground competition, respectively. Adaptive resource allocation is implemented (see below, design concept "Adaptation").

Emergence

All features observed at the community level, such as community composition and diversity, emerged from individual plant-plant interactions, grazing effects at the individual scale, and resource availability.

Adaptation

In the submodel representing plant growth and above- and below-ground competition, plants adaptively allocate resources to shoot and root growth in order to balance the uptake of above- and below-ground resources (see below, Submodels – Plant growth and mortality).

Interactions

Competitive interactions between plant individuals were described using the ZOI approach.

Stochasticity

Seed dispersal and establishment, as well as mortality of seeds and plants are modelled stochastically to include demographic noise. Grazing events occur randomly during the vegetation period and the affected plants are chosen randomly, but the individual's probability of being grazed depends on plant traits (see Submodels – Grazing). A plant's exact trait values will be varied from their PFT's mean trait values (see Submodels – Intraspecific trait variation).

Observation

In order to describe community diversity and composition the individual numbers of all PFTs are recorded each year in week 20 directly before seed germination in autumn. These data are used to calculate annual values of Shannon diversity, which contains more information about the distribution of relative abundances among PFTs than the number of surviving PFTs only. Additionally, the overall above- and belowground biomasses are recorded to distinguish the responses of type richness and standing biomass. If desired, the simulation can also output state variables for each individual, each year. These data include the above- and belowground biomass for the individual, its current stress level, its exact location, and its varied trait values.

8.1.6 Initialization

Initially, 10 seedlings of each PFT is randomly dispersed onto the grid. Their germination probability was set to 1.0 to assure equal initial population sizes of all PFTs. A spatially and temporally homogenous distribution of resources (both above- and below-ground) was used in all simulation experiments.

8.1.7 Input

The model does not include any external input of driving environmental variables.

8.1.8 Submodels

Competition

Following the ZOI approach, plants compete for resources in a circular area around their central location point. To relate plant mass to the area covered (A_{shoot}), we extended the allometric relation used by (Weiner et al. 2001)

$$A_{shoot} = SLA \cdot (LMR \cdot m_{shoot})^{\frac{2}{3}} \qquad \text{(A1)}$$

where SLA is a constant ratio between leaf mass and ZOI area and m_{shoot} is vegetative shoot mass (compare Tables A1 and A2). The LMR is introduced to describe different shoot geometries and is defined as the proportion of photosynthetically active (leaf) tissue to the total (shoot) tissue (Fig. A1). The allometric relationship between the amount of photosynthetic biomass and the area of the ZOI is consistent with the model of Weiner et al. (2001), eq. 1, and presents sigmoidal growth in the absence of competition. Given the phenomenological nature of this relationship, we follow Weiner et al. 2001 and omit unit-rectifying constants from this and each subsequent equation within the model. Only the former is considered for the calculation of the ZOI size. These circular areas are projected onto a grid of discrete cells. Grid cells thus contain the information by which plants they are covered, so that resource competition can be calculated cell by cell. The resources within a cell are shared among plants according to their relative competitive effects (β_i). The resource uptake (Δres) of plant *i* from a cell with resource availability ($\mathrm{Res}_{\mathrm{cell}}$) covered by n plants is thus calculated as

$$\Delta \mathrm{res}_i = \frac{\beta_i}{\sum_{j=1}^{n} \beta_j} \cdot \mathrm{Res}_{\mathrm{cell}} \cdot \qquad \text{(A2)}$$

Calculating β_i in different ways allows including different modes of competition (Weiner et al. 2001). We assume that the relative competitive ability of a plant is correlated with its maximum growth rate in the absence of resource competition. Therefore, β_i is proportional to maximum resource utilization per unit area covered (g_{max}), see Submodel: Plant growth and mortality and Table A2), In the case of size-symmetric competition, β_i simply equals g_{max}:

$$\beta_i = g_{max} \qquad \text{(A3a)}$$

In the case of partially size-asymmetric competition β_i is a function of plant mass and shoot geometry:

$$\beta_i = g_{max} \cdot m_{shoot} \cdot LMR^{-1} \qquad \text{(A3b)}$$

The inverse of LMR is used, because plants with a lower fraction of leaf tissue are considered to be higher and thus show a higher competitive ability by overtopping other plants (Fig. A1). In this way, plants with equal g_{max} receive equal amounts of resources from one unit of area irrespective of their mass or height in the case of size-symmetric competition, while larger and higher plants receive a higher share of resources in proportion to their shoot geometry traits in the case of partially asymmetric competition (Schwinning and Weiner 1998, Weiner et al. 2001). The resource uptake of one plant within one week can then be determined by summing the results of Eq. (A2) over all cells covered by the plant.

To include differences between intra- and interspecific competition, individuals of the same PFT are considered as conspecifics and those of different PFTs as heterospecifics. The relative competitive ability βi of one plant is then determined as a decreasing function of the number of plants belonging to the same PFT (n_{PFT}) and covering the same cell:

$$\beta_i = g_{max} \cdot \frac{1}{\sqrt{n_{PFT}}} \tag{A3c}$$

Eq. (A3c) is used for size-symmetric competition instead of Eq. (A3a). In the case of size asymmetry, plant mass and geometry are taken into consideration according to Eq. (A3b). This approach represents a situation where intraspecific competition is increased relatively to interspecific competition and therefore implicitly includes niche differentiation of resource competition at the cell scale, which has been known as an important factor for species coexistence (Chesson 2000, Silvertown 2004). In the model analysis, versions with and without niche differentiation were compared in order to test if this assumption for competition at the cell scale translates into a different behavior at the community scale (results see May et al. 2009).

Plant growth and mortality

Plant growth only depends on the resources (Δres) that the plant acquired during the current time step. In the absence of competition, plants show sigmoidal growth (Hunt 1982). Therefore, we again adapted the allometric growth equation used by Weiner et al. (2001) to the description of plant geometry used here:

$$\Delta m = g \cdot \left(\Delta res - SLA \cdot LMR^{\frac{2}{3}} \cdot g_{max} \cdot \frac{m_{shoot}{}^{2}}{m_{max}{}^{\frac{4}{3}}} \right) \tag{A4}$$

where g is a constant conversion rate between resource units and plant biomass and m_{max} is the maximum mass of shoot or root, respectively. In addition, the maximum amount of resources that is allocated to growth each week is limited by a maximum resource utilization rate given by g_{max} [resource units/cm²] multiplied by ZOI area [cm²]. If Eq. (A4) yields a negative result, Δm is set to zero and thus negative growth is prohibited. The terms were designed in Weiner et al. (2001) such that: 1) growth is proportional to the resources available to the plant, scaling with the ZOI area, 2) without competition, growth is sigmoidal, 3) the equation is as simple as possible.

Growth of reproductive mass is restricted to the time between weeks 16 – 21. In this period, a constant fraction of the resources (5% for all PFTs) is allocated to growth of reproductive mass (Schippers et al. 2001, Kahmen 2004), and reproductive mass is limited to 5% of shoot mass in total. The same resource conversion rate (g) is used for reproductive and vegetative biomass.

Eqs. (A1) – (A4) are applied to shoot and root ZOIs independently, with the difference that for root growth the factor LMR is always one. We assume that the minimum uptake of above- and below-ground resources limits plant growth (Lehsten and Kleyer 2007) and introduced adaptive shoot-root allocation in a way that more resources are allocated to the growth of the plant compartment that harvests the limiting resource (Shipley and Meziane 2002, Weiner 2004). For resource partitioning, we adopt the model of Johnson (1985) and the fraction of resources allocated to shoot growth is calculated as

$$\alpha_{\text{shoot}} = \frac{\Delta \text{res}_B}{\Delta \text{res}_B + \Delta \text{res}_A} \tag{A5}$$

where Δres_A is above-ground and Δres_B is below-ground resource uptake. This transport-resistance partitioning model was taken from Johnson 1985 (eq. 16) which relates the root:shoot ratio to the C:N ratio in the plants. Eq. A5 ensures that the ratio of total resources taken up (both above- and belowground) going to the shoots is equal to the rate of resources taken from the soil. For the roots, the proportion is vice versa. This keeps the growth of both compartments balanced.

Plants suffer resource stress if their resource uptake (in any layer) is below a fixed threshold fraction (thr_{mort}) of their optimal uptake, which is calculated as maximum resource utilization times ZOI area. That means each week the condition $\Delta res < thr_{mort} \cdot A_{\frac{shoot}{root}} \cdot g_{max}$ is evaluated and if it is true either for shoot or root the plant is considered as stress exposed during this week. Consecutive weeks of resource stress exposure (w_{stress}) linearly increase the probability of death

$$\text{p}_{\text{mort}} = \text{p}_{\text{base}} + \frac{\text{w}_{\text{stress}}}{\text{surv}_{\text{max}}} \tag{A6}$$

where surv_{max} is the maximum number of weeks a plant can survive under stress exposure and p_{base} is the stress independent background mortality of 0.7% per week corresponding to an annual mortality rate of 20% (Schippers et al. 2001). It's possible for p_{mort} to exceed 1, but the plant will be killed that time step.

Dead plants do not grow and reproduce anymore, but they still can shade others and are therefore still considered for competition in the one-layer model and for at least above-ground competition in the two-layer model. Each week the mass of all dead plants is reduced by 50% and they are removed from the grid completely as soon as their total mass decreases below 10 mg.

Aboveground herbivory

Grazing is modelled as partial removal of an individual's above-ground biomass. The frequency of grazing is specified by a constant weekly probability (p_{graz}) of a grazing event. Grazing is a process that acts selectively towards trait attributes such as shoot size and tissue properties. Therefore, for each plant the susceptibility to grazing (s_{graz}) is calculated as a function of shoot size, geometry and PFT-specific palatability (palat).

$$s_{graz} = m_{shoot} \cdot LMR^{-1} \cdot palat \tag{A7}$$

The probability for each plant to be grazed within one week is derived by dividing individual susceptibilities by the current maximum individual susceptibility of all plants (in other words, the susceptibility of the most-susceptible plant). All plants are checked for grazing in random order. In case a plant is grazed, 50% of its shoot mass and its complete reproductive mass are removed. The random choice of plants is repeated without replacement, until 50% of the total (above-ground) biomass on the whole grid has been removed. When all plants have been checked for grazing once, but less than 50% of the total above-ground biomass has been removed, grazing probabilities for all individuals are calculated once more based on Eq. (A7) and the whole procedure is repeated until 50% of above-ground biomass has been removed or until a residual biomass is reached which is considered ungrazable. This fraction is set to 15 g/m² following (Schwinning and Parsons 1999). This allows a plant individual to be grazed never or several times during one week with a grazing event.

In addition to stochastic grazing, each year at the end of the vegetation period 50% of the above-ground mass of all plant individuals is removed to mimic vegetation dieback in winter.

Intraspecific trait variation

Intraspecific trait variation (ITV) was modelled by varying each new individual's functional trait values. This was accomplished through adding to each trait value a random variate, drawn from a truncated Gaussian distribution with a mean of 0 and standard deviation of ITVsd, and normalized to the trait's mean value. We truncate at -1 and 1 to ensure that no trait garners a negative value. After drawing a variate from this distribution, it is multiplied by the trait's mean and then added to the mean trait value. This results in a normal distribution with the mean being the PFT's mean trait value, and the coefficient of variation being ITVsd. Positively tied traits are modified by the same variate while negatively tied traits are varied inversely by negating the variate for one of the traits. Table A4 illustrates the process of varying these traits for one individual plant, and Figure A4 presents a sample census of the populations' trait values for one selected trait, with and without trait variation.

Every process inside the model uses the plants' new trait values with the exception of seed germination. The germination algorithm uses a weighted lottery to simulate seed competition. It tallies the number of seeds of each PFT on a given cell and weights each sum based on its PFT's mean seed size. This data is used to probabilistically determine which PFT germinates and occupies the square. For pragmatic runtime considerations, we did not introduce ITV into this algorithm.

Belowground herbivory[1]

Belowground herbivory was implemented such that each time step some percentage of the extant biomass is removed from each of the plants, with a gradient of preference in root size ranging from generalist to preferential (i.e. disproportionally eating larger root systems). This herbivory algorithm is intended to reflect the influence of belowground, invertebrate herbivores, such as those belonging to the genus *Agriotes*, one of the most

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[1] *The belowground herbivory submodel is used within both the third and fourth thesis chapters.*

abundant root herbivores in Europe. As this genus generally tends to eat plants with high biomass and growth rates (Sonnemann et al. 2012, 2015), we refrain from explicitly modelling the plants' roots palatability.

The feeding need at week t, n_t, is calculated as a defined percent (feeding rate, f) of that week's expected root mass, which is estimated by averaging each previous week's total realized root biomass R_i for the previous w weeks,

$$n_t = f \cdot \frac{\sum_{i=t-w}^{t-1} R_i}{w} \qquad \text{(A8)}$$

For this analysis, the feeding rate (f) is 0.1 per week, potentially lower than the typical belowground herbivory pressure (Zvereva and Kozlov 2012), but equal to the aboveground herbivory pressure commonly used in IBC-grass. The number of weeks used to estimate the expected root mass, w, is 10. Both parameters are held constant in the following analysis.

The biomass to be removed from each individual's root mass ($g_{i,t}$) is calculated each week as:

$$g_{i,t} = \left(\frac{r_{i,t}}{R_t}\right)^{\alpha} \cdot n_t \qquad \text{(A9)}$$

where $r_{i,t}$ is the expected root mass of individual i in week t and R_t is the week's realized total root mass, which may differ from the expected root mass (Fig. A3). R_t differs from R_i in eq. A8 in that R_i refers to the total realized root biomass on week i (and ranging backwards by w weeks), whereas R_t refers to the total realized root biomass on the current week. The parameter α represents the generality of the herbivory; set at $\alpha = 1$, $g_{i,t}$ will equal the plant's root mass ($r_{i,t}$) in proportion to the total root mass (R_t) at time t. Above 1, α will increase the preference of the herbivores to disproportionally prefer large root systems (Sonnemann et al. 2013). If the biomass to be removed from a plant is larger than its total root mass (which may occur, based on the distribution of plant biomasses and α), the plant is killed and the overshoot biomass remains in the feeding need (n_t), to be removed from other plants.

The amount of edible biomass will be significantly reduced immediately after the disturbance in Chapter 3 (Figure A6), but a large number of herbivores will remain in the system. During these initial few weeks, when there is less root biomass available to the herbivores than their feeding need, we leave a small amount of the total root biomass ungrazed to mimic a feeding response wherein the herbivores would have to spend more time searching for the remaining biomass.

Disturbance

Disturbance was modelled parsimoniously, as the death of some percentage of the plant individuals, chosen randomly. When a plant is killed, its above- and belowground biomass is left to degrade normally (see Plant growth and mortality). The disturbance occurs once during the simulation after a "burn-in" period of 100 simulation years, either directly before or directly after seed dispersal, and does not impact any dispersed seeds or the root herbivores. With only a transient seed bank, a complete disturbance of the community before seed dispersal will therefore result in the community being "reset" entirely through immigration, while a complete disturbance after seed dispersal will mean that the "memory" of the community's previous species abundance distribution is also present, potentially decreasing the time it takes for the community to recover. The type seed bank is parameterized into two types: transient and long-term. Transient seed banks exist for only one year, so that the seeds dropped during the last year have a chance to establish in the current year. In long-term seed banks, the seeds are able to persist for three years, barring germination or overwintering mortality (with a probability of 0.5 per year).

Eutrophication

Eutrophication was simulated as an increase in belowground resources (BRes) from the baseline resource rate. Therefore, in IBC-grass a eutrophication intensity of 10 would translate to an increase in belowground resources of 10 BRes for the duration of the experiment. Immediately after the experimental period, the belowground resources return to their pre-eutrophication level for 100 simulation years, for the analysis of the plots' recovery. For this analysis we increased the amount of belowground resources by 50% over their baseline levels (Weiss et al. 2014), increasing from 60 to 90 BRes during the experimental period.

Seed addition[2]

External seed input takes place in week 20, when all plants disperse their seeds. All PFTs of the regional PFT pool (containing 86 PFTs) are thereby considered as seed source. Seeds are set to the grid by randomly assigning coordinates. The number of seeds added per year per PFT is constant, i.e. if the number of seeds is 1, one seed per PFT per year will be added to the grid.

Seeds added through this pathway must compete to germinate with the seeds that are already present in that grid cell's seed bank. Further, as with all seeds, if their grid cell is overshadowed no seeds will germinate.

Seed addition was used into this version of the simulation to re-incorporate lost species after eutrophication events. Because IBC-grass operates on a "closed systems," any species lost from the community will remain absent unless they are added externally. To mimic long distance seed dispersal from other communities, and thus facilitate the conditions that enable recovery to occur, we use a modicum of seed dispersal per year in the present analysis (10 seeds/PFT/year).

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[2] *The seed addition submodel is used within both the third and fourth chapters of this thesis.*

Trade-offs

Within IBC-grass, submodels (Section 8) are built upon the plants' state variables (e.g. shoot biomass, root biomass) as well as their trait values. These trait values, (e.g. LMR, m_{max}, g_{max}, and SLA) are critical to understanding the trade-offs within the model, defined by the submodels' equations. Below we further explore these trades-offs by specifically addressing the impacts of each of their component traits on each fundamental equation.

Growth form

LMR: LMR defines the growth form of an individual. A high value represents a rosette growth form—low to the ground but almost entirely composed of photosynthetic biomass. Its importance emerges in the equations defining the amount of photosynthetic area available to the individual (A1), asymmetric competition (A3b), conversion of resources to biomass (A4), and herbivory (A7).

In defining photosynthetic biomass (A1), LMR is multiplicative; a low leaf-mass ratio reduces the amount of light gathering biomass. A value of 1 means the entire shoot biomass can gather resources.

In defining asymmetric competition (A3b), the inverse of LMR is used because plants with a lower fraction of leaf tissue (lower LMR) are considered to be higher—more erect—than those with high LMR values—rosettes.

LMR is incorporated into the plant growth submodel (A4) through the utilization of the allometric relation between mass, and growth form (LMR), and SLA. It is incorporated into the loss term, helping to define the maintenance costs of the plant. Within the equation, LMR helps to define the ZOI of the plant. Plants with larger ZOIs (of which LMR is a component) suffer a higher maintenance cost than those with small ZOIs.

LMR factors into grazing in a similar matter as in competition; higher plants are more susceptible to grazing than lower plants. The equation (A7) reflects this by using the inverse of the LMR.

ZOI size — grazing susceptibility

SLA: SLA defines the ratio between leaf mass and ZOI area. In other words, a plant that has a high SLA is able to gather more aboveground resources per mg shoot mass. This relation is incorporated into the competition (A1) and plant growth submodels (A4).

In the competition submodel (A1), SLA is multiplied by the total photosynthetic biomass to produce the ZOI area (A_{shoot}). This ZOI area then determines how many grid cells the plant overlaps and can therefore gather resources from.

In the plant growth submodel (A4), SLA helps to define the ZOI of the plant. The maintenance cost (loss term) of the relation includes this ZOI, meaning that plants with larger ZOIs must spend more resources maintaining this photosynthetic biomass than their smaller ZOI competitors.

Palat: Palatability is positively correlated to SLA and is integral to calculating the susceptibility of a plant towards grazing. Plants with larger body mass, more erect growth form, and more palatable leaves are more susceptible to grazing.

Growth rate — stress tolerance

g_{max}: g_{max} reflects maximum number of resources a plant can uptake per week per grid cell. Therefore, plants with a high g_{max} are able to take up a larger amount of resources per time step than their competitors. It is incorporated into the two versions of competition (A3a, A3b) as well as the intraspecific competition (A3c) and plant growth (A4).

In size-symmetric competition (A3a), the competitive ability of a plant is directly related to its g_{max}. In size-asymmetric competition, a plants competitive ability is related to its g_{max}, its size, and its growth form (LMR). Larger plants are considered dominant to small plants, and high plants (low LMR) are considered to overshadow low plants (high LMR).

In intraspecific competition (A3c), the number of intraspecific competitors overlapping that same grid cell reduces the g_{max} of a plant on that grid cell.

In plant growth (A4), the g_{max} of a plant helps to define its maintenance cost (loss term). This behaviour operates under the assumption that higher growth rates are generally correlated to higher maintenance costs.

$surv_{max}$: $surv_{max}$ is negatively correlated to g_{max}. the defines the stress tolerance of a plant. An integer, it represents the maximum number of weeks a plant can survive without meeting its maintenance costs. The probability of mortality linearly increases with each of these weeks.

Maximum plant and seed size — dispersal ability

m_{max}: The maximum size of the plant is positively correlated to its seed size and incorporated into the plant growth submodel (A4). It is a component of the loss term which defines the maintenance cost of the plant. It is allometrically related to the current size of the plant, in such a way that plants near their m_{max} spend more resources on maintenance costs than do plants far from their $m_{max.}$

m_{seed}: The mass of a seed is directly correlated to the plant's maximum size (m_{max}), and negatively correlated to the mean dispersal distance of the seed ($mean_{disp}$). The value defines the relative probability that the seed will germinate, versus the other seeds on that grid cell, as well as the initial biomass of the newly established plant.

$mean_{disp}$: Mean dispersal distance is negatively correlated to maximum plant size and seed size and is integral in defining the dispersal kernel of the plant. Plants with high $mean_{disp}$ are able to disperse farther than those with lower $mean_{disp}$. Seed dispersal is based on a log-normal distribution, where both the mean and variance parameters are equivalent—this ensures that large seeds have short dispersal distances with little variance. Small seeds, vice versa, disperse far with a longer tail.

8.1.9 References

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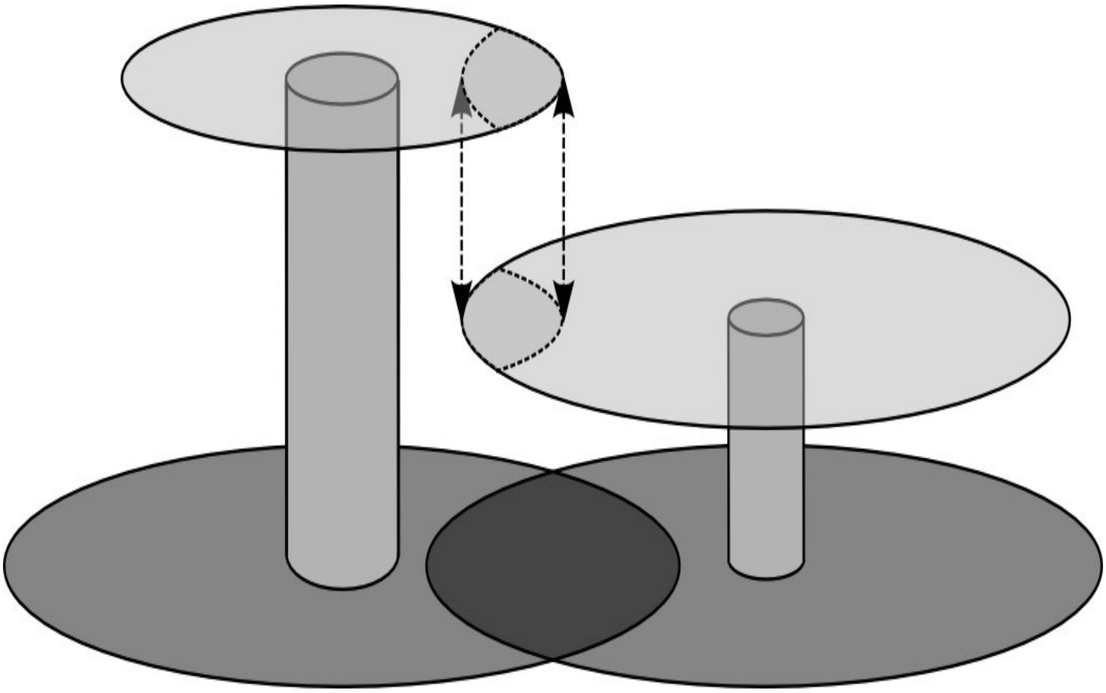


Figure A1. Illustration of the “zone-of-influence” (ZOI) approach including above- and below-ground competition and different shoot geometries. Above- and below-ground “zones-of-influence” are shown as light and dark grey circles, respectively. Stems and support tissue are represented as grey cylinders. Plant individuals compete for resources in the areas of overlap only (arrows indicate the area of above-ground competition). The plant to the left has a lower ratio of leaf mass to shoot mass (LMR) and thus a smaller above-ground ZOI. In return its competitive ability for above-ground resources (light) is higher as it is able to shade the plant to the right.

Table A1. Model state variables

State variable	Unit	Description
Plants		
m_{shoot}	mg	vegetative shoot mass (leaves + stems)
m_{root}	mg	root mass
m_{repro}	mg	reproductive mass (seeds)
w_{stress}	weeks	duration of resource stress exposure
PFT ID	-	identification number for plant functional type
Plant ID	-	Identification number for the individual plant
Seeds		
m_{seed}	mg	seed mass
age	years	time since release from mother plant
Cells		
Res_A	units/cm²	above-ground resource availability
Res_B	units/cm²	below-ground resource availability

Table A2. PFT parameter values

Symbol	Description	Unit	Value
Vegetative traits			
LMR	ratio of leaf mass to total shoot mass	mg/mg	**
SLA	above-ground ZOI area per leaf mass	cm²/mg	**
c_{root}	below-ground ZOI area per root mass	cm²/mg	1.0
g	conversion rate resource units to biomass	mg/resource unit	0.25
g_{max}	maximal resource utilization per time step and ZOI area (equal for shoot and root*)	resource units/cm²/ week	**
thr_{res}	Threshold fraction of g_{max}considered as resource stress	-	0.2
$surv_{max}$	maximal survival time under resource stress exposure	weeks	**
m_{max}	maximum plant mass (equal for shoot and root*)	mg	**
palat	palatability – susceptibility towards grazing	-	**
Generative traits			
m_{seed}	mass of a single seed	mg	**
$mean_{disp}$	mean of dispersal distance	m	**
std_{disp}	standard deviation of dispersal distance	m	**
p_{germ}	germination probability	-	0.5
t_{disp}	time of seed dispersal	week of the year	21
t_{germ}	time of seed germination	week of the year	1 – 4 21 – 25

**PFT specific values, see May et al. 2009

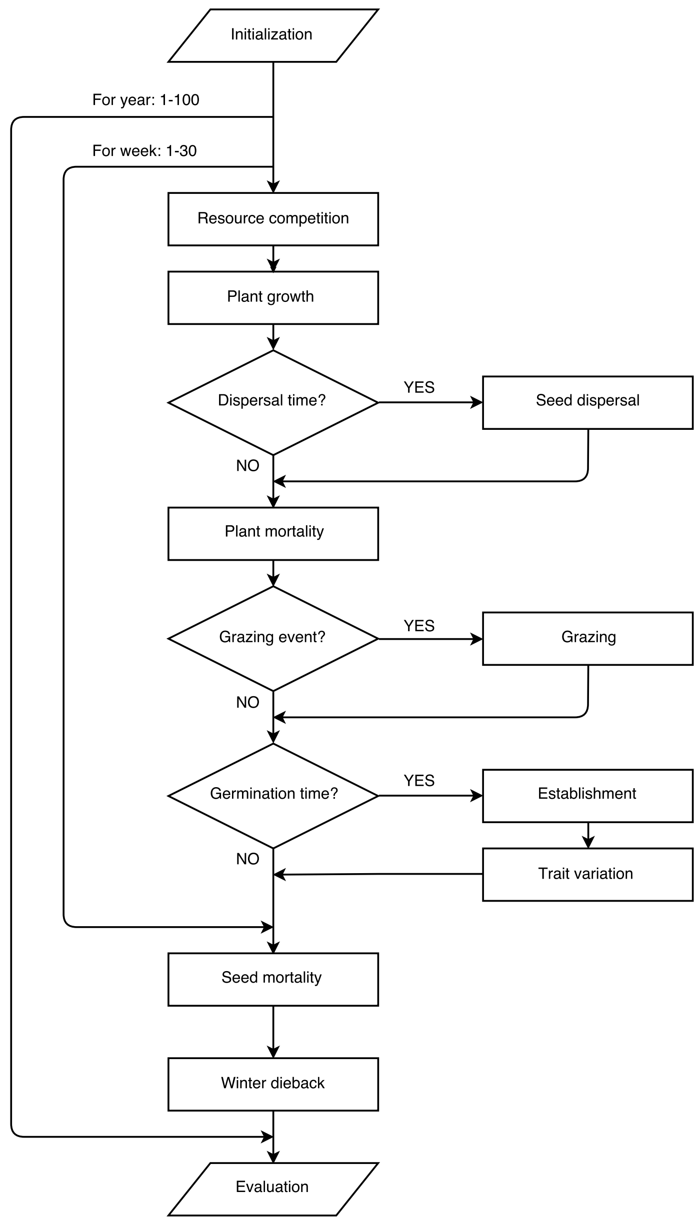


Figure A2. Flow-chart representing process scheduling in the grassland model. Resource competition, plant growth and mortality are executed each week, while seed dispersal and seedling establishment are restricted to certain weeks of the year (see Table A2). Grazing events occur stochastically with a fixed probability per week. Seed mortality and winter dieback are only considered once at the end of each year. State variables of all plants are updated synchronously after each process. Simulations were run for 100 years with 30 weeks vegetation period per year.

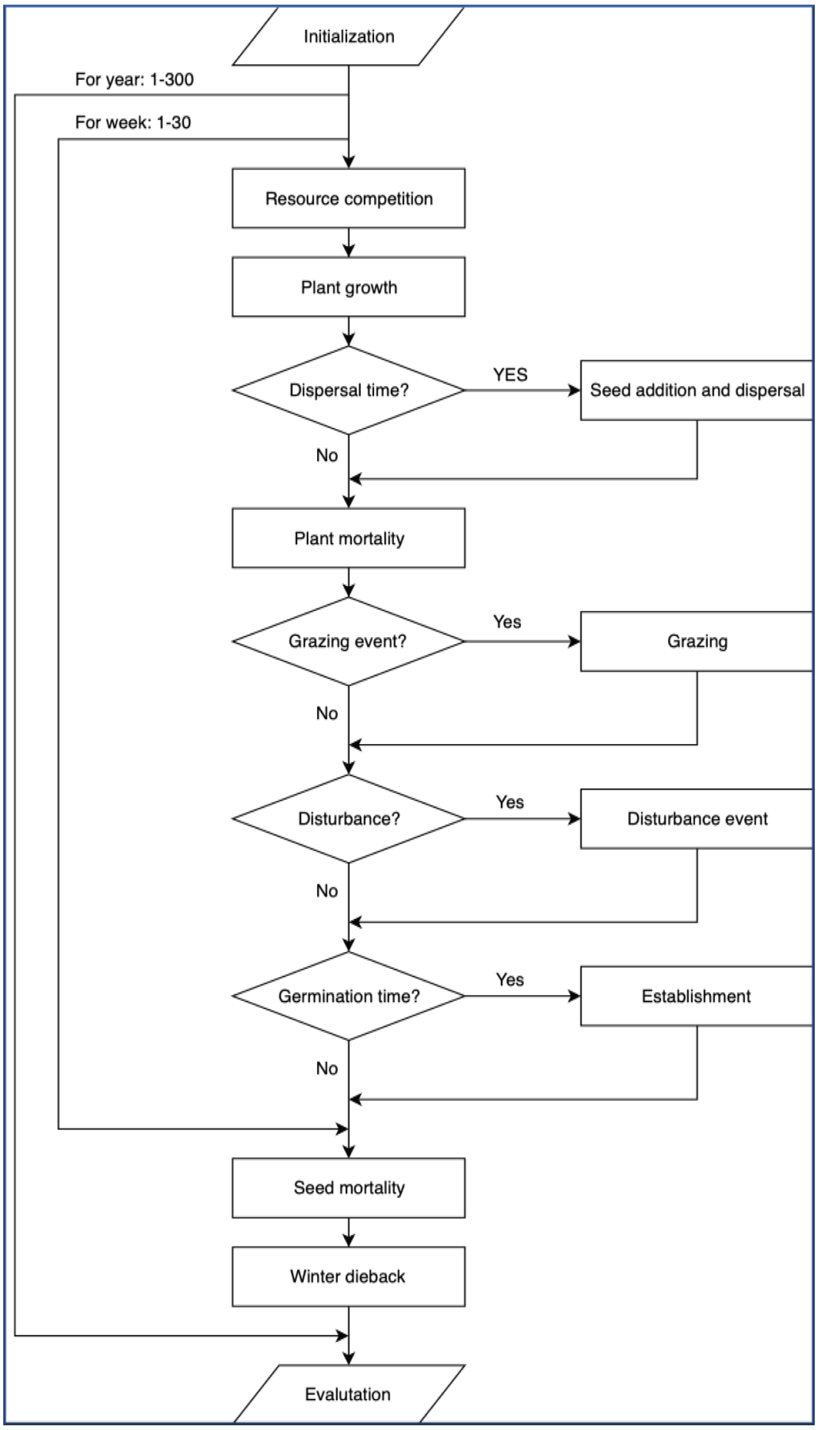


Figure A3. Flow-chart representing process scheduling in the grassland model. Resource competition, plant growth and mortality are executed each week, while seed dispersal and seedling establishment are restricted to certain weeks of the year (see Table A2). Grazing events occur stochastically with a fixed probability per week. Seed mortality and winter dieback are only considered once at the end of each year. State variables of all plants are updated synchronously after each process. Simulations were run for 100 years with 30 weeks vegetation period per year.

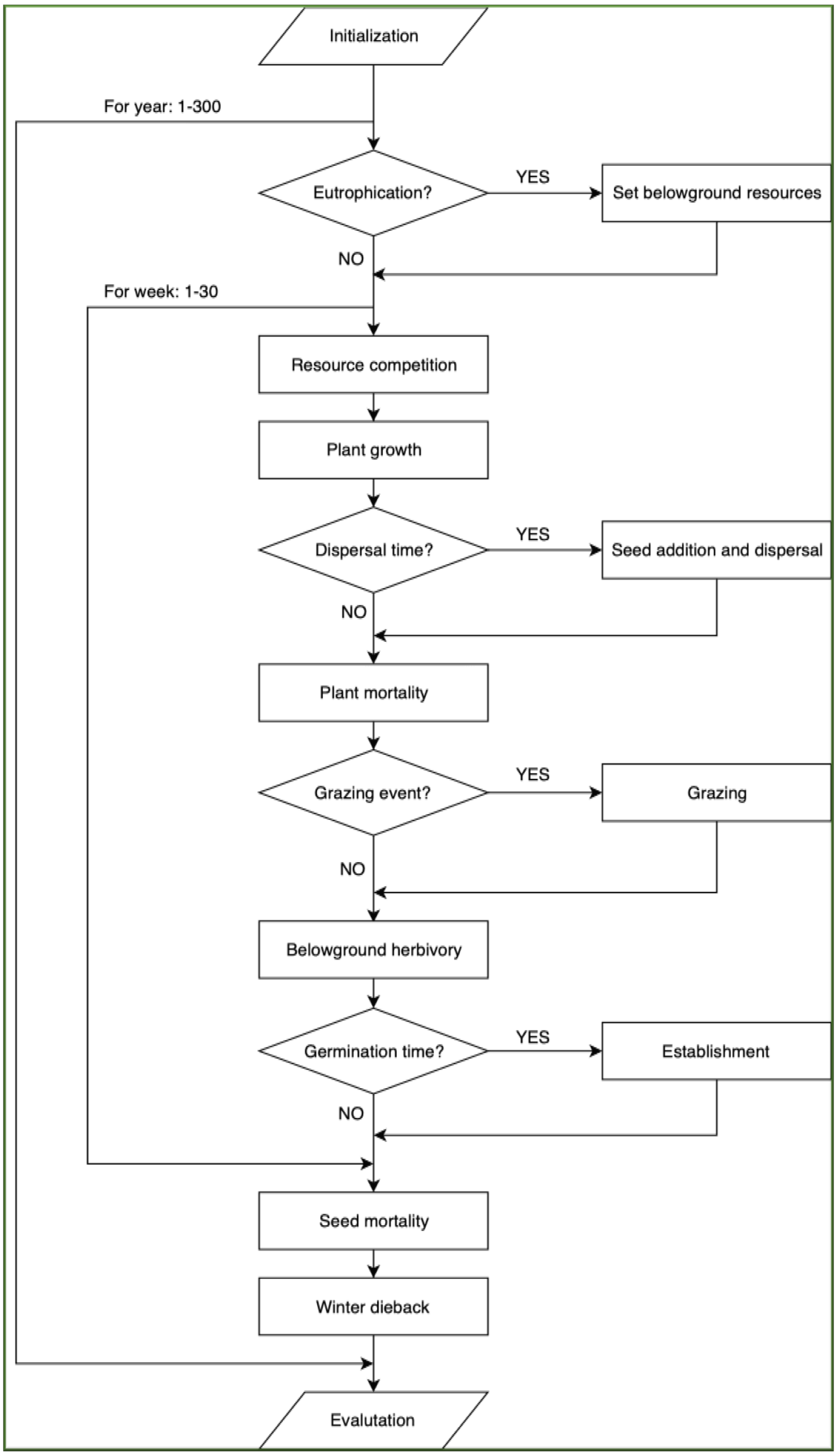


Figure A4. Flow-chart representing process scheduling in the grassland model. Resource competition, plant growth and mortality are executed each week, while seed dispersal and seedling establishment are restricted to certain weeks of the year (see Table A2). Grazing events occur stochastically with a fixed probability per week. Seed mortality and winter dieback are only considered once at the end of each year. State variables of all plants are updated synchronously after each process. Simulations were run for 100 years with 30 weeks vegetation period per year.

Table A3: Adding intraspecific variation to an individual plant's traits with an ITVsd of 0.5. Each plant has four sets of traits: "Growth form," determining whether the plant grows as a rosette or erect pattern; "Max plant size," describing its maximum biomass, but also its seed size and dispersal kernel; "Resource response," determining how the plant responds to resource stress, which is inversely correlated to how well it competes with other plants; and "grazing response," which documents how palatable the plant is to grazers. Each trait set is composed of multiple correlated sub-traits. To derive an individual plant's new, varied trait value, a random number is drawn from a Gaussian distribution with a standard deviation of ITVsd and normalized to the PFT's mean trait value. This normalized modifier is then added to the PFT's mean trait value. Each correlated sub-trait uses the same modifier, though the direction of the correlation is maintained.

Set	**Trait**	**Description**	**Sample mean trait value**	**Sample variate (*ITVsd* = 0.5)**	**Tied variation direction**	**Varied trait value**
Growth form	*LMR*	e.g. rosette or erect	0.75	-0.4922944	NA	0.3807792
Max plant size	m_{max}	Max plant size	5000 mg	-0.1805448	+	4097.276
	m_{seed}	Seed mass	1 mg	-0.1805448	+	0.8194552
	$mean_{disp}$	Mean dispersal distance	0.1 m	-0.1805448	-	1.180545
	std_{disp}	Standard deviation of dispersal distance	0.1 m	-0.1805448	-	0.1180545
Resource response	g_{max}	Maximal resource utilizations per time step and ZOI area	20 resource units/cm^2/ week	0.5275132	+	30.55026
	$surv_{max}$	Maximum survival time under resource stress exposure. Whole number.	6 weeks	0.5275132	-	3
Grazing response	palat	Palatability – susceptibility to grazing	0.5	0.1906902	+	0.5953451
	SLA	Above-ground ZOI area per leaf mass.	0.75	0.1906902	+	0.8930177

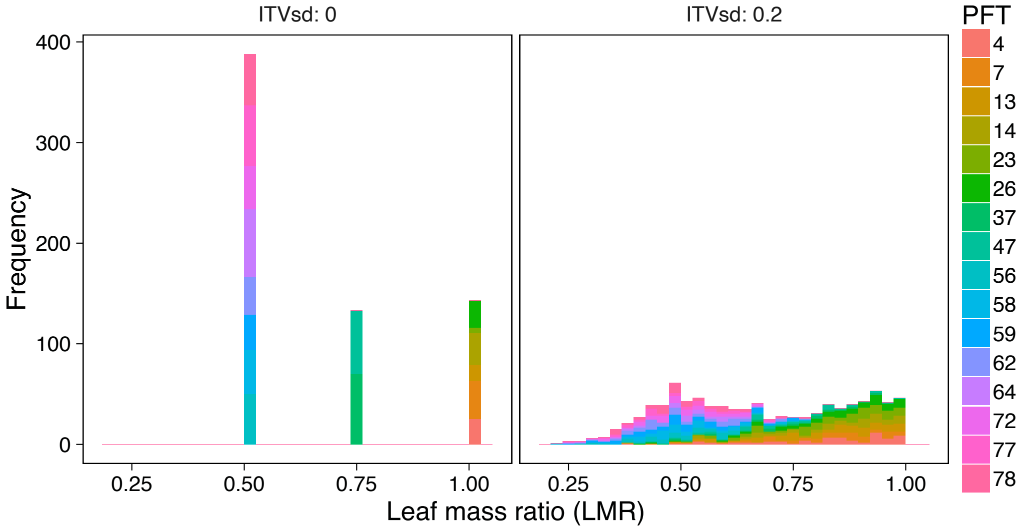


Figure A5. Population trait values for each PFT in one simulation run with an ITVsd of 0 and of 0.2. Without intraspecific variation, the "Leaf mass ratio" (LMR) trait was centered on three trait means: 0.50, 0.75, and 1.00. With intraspecific variation, there is much more variation in each PFT's traits, with individuals garnering LMRs above and below their PFT's trait mean. Those PFTs with an original LMR of 1.00 were only able to vary down, as a value above 1.0 would not make biological sense.

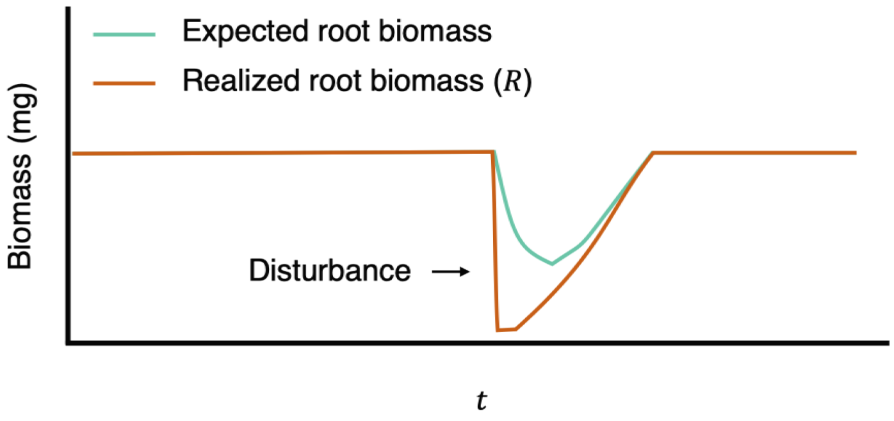


Figure A6: A conceptual figure of equation A8. If there is less root mass available than the root herbivores need, the feeding response is triggered in which the herbivores will leave some percentage uneaten. As the realized root biomass gradually increases, the expected root biomass and realized root biomass will begin to equalize.

8.2 Intraspecific trait variation increases diversity in a trait-based grassland model

8.2.1 Supplemental Material B: Random Forest parameterizations

Pairwise Random Forest model parameterization: Variable importance over ITVsd

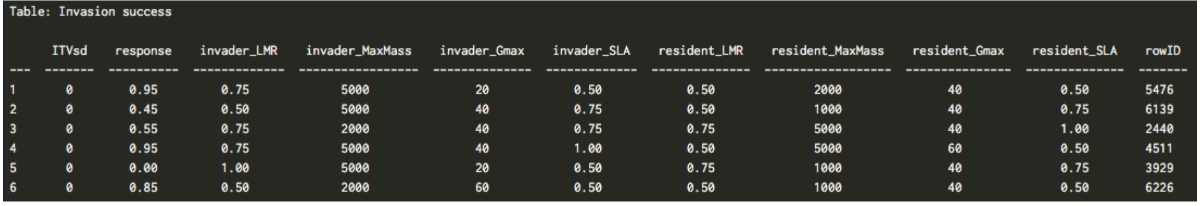
Eleven different Random Forests (R, randomForest version 4.6-12), one per level of *ITVsd*. Forests were trained on a randomly sampled 70% of the total dataset, stratified by *ITVsd*, and tested against the remaining 30%.

The response variable would be binary in the case of invasion success or integer in the case of final abundance.

Formula = *response* ~ *invader_LMR* + *invader_MaxMass* + *invader_Gmax* + *invader_SLA* + *resident_LMR* + *resident_MaxMass* + *resident_Gmax* + *resident_SLA*
ntree = 1024
mtry = 3

Below is a sample from the dataset, as well as metadata for the two sets of random forests, one with invasion success as the response variable, and the other using abundance. The reported meta-data are the R-squared and correlation coefficient to the testing datasets.

Table 1.1: Sample of pairwise invasion dataset



```
Table: Invasion success

     ITVsd   response   invader_LMR   invader_MaxMass   invader_Gmax   invader_SLA   resident_LMR   resident_MaxMass   resident_Gmax   resident_SLA   rowID
---  -------  ----------  ------------  ----------------  -------------  ------------  -------------  -----------------  --------------  -------------  -------
1      0        0.95         0.75            5000              20           0.50          0.50             2000               40            0.50        5476
2      0        0.45         0.50            5000              40           0.75          0.50             1000               40            0.75        6139
3      0        0.55         0.75            2000              40           0.75          0.75             5000               40            1.00        2440
4      0        0.95         0.75            5000              40           1.00          0.50             5000               60            0.50        4511
5      0        0.00         1.00            5000              20           0.50          0.75             1000               40            0.75        3929
6      0        0.85         0.50            2000              60           0.50          0.50             1000               40            0.50        6226
```

A random sample of 6 invasions. For this table, the response is equal to the invading PFT's invasion success rate.

Figure 1.2: Metadata for variable importance: invasion success

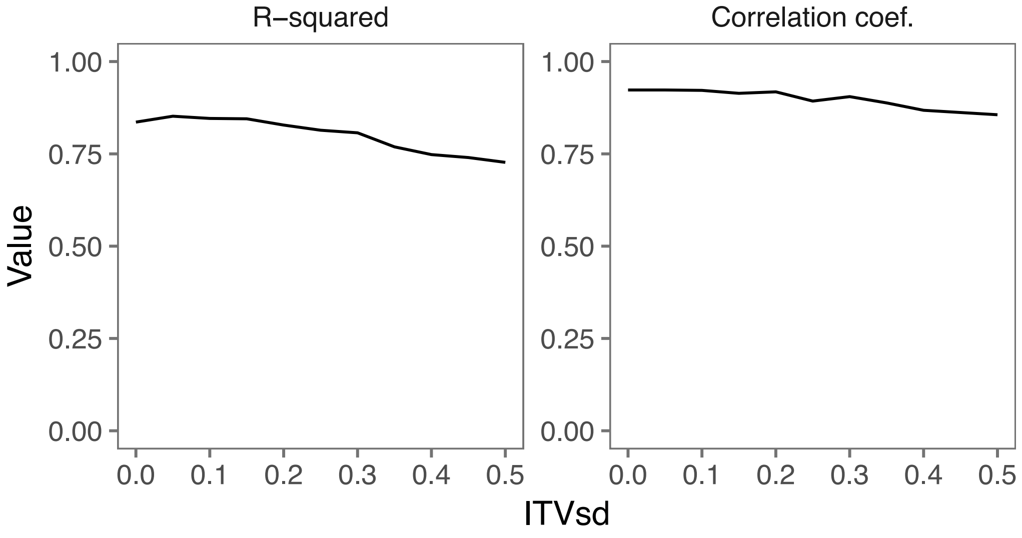
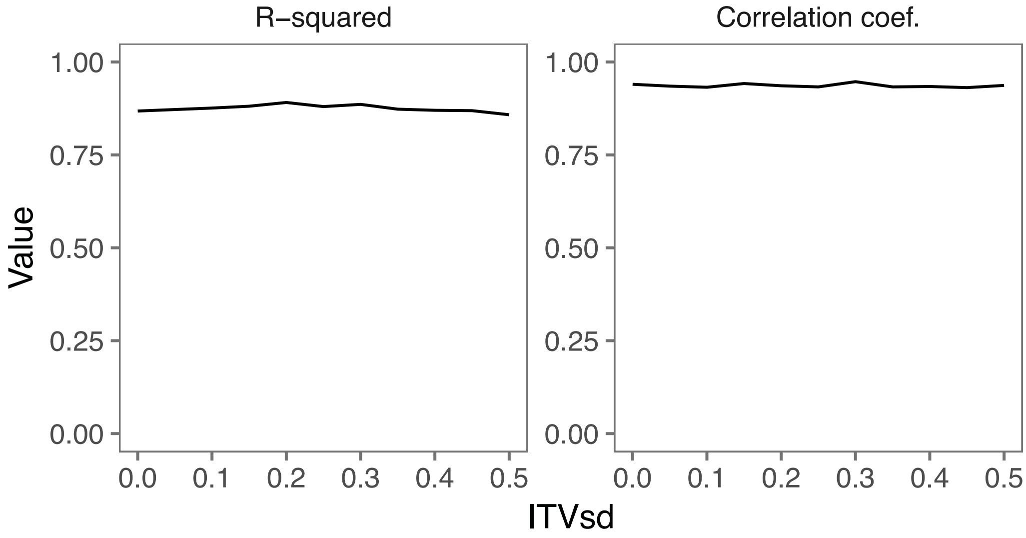


Figure 1.3: Metadata for variable importance: abundance



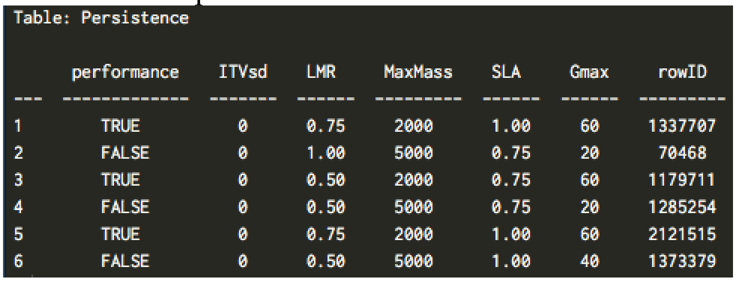
Community Random Forest model parameterization: Variable importance over ITV

Eleven different Random Forests (R, randomForest version 4.6-12), one per level of *ITVsd*. Forests were trained on a randomly sampled 70% of the total dataset, stratified by *ITVsd*, and tested against the remaining 30%.

The response variable would be binary in the case of persistence or integer in the case of final abundance.

formula = *performance* ~ *LMR* + *MaxMass* + *SLA* + *Gmax*
ntree = 1024
mtry = 2

Table 2.1 Sample of dataset



```
Table: Persistence


     performance    ITVsd    LMR     MaxMass     SLA     Gmax     rowID
---  -------------  -------  ------  ---------  ------  ------  ---------
1        TRUE          0     0.75      2000      1.00     60     1337707
2        FALSE         0     1.00      5000      0.75     20      70468
3        TRUE          0     0.50      2000      0.75     60     1179711
4        FALSE         0     0.50      5000      0.75     20     1285254
5        TRUE          0     0.75      2000      1.00     60     2121515
6        FALSE         0     0.50      5000      1.00     40     1373379
```

A randomly selected sample of the 2.2 million (2,200,000) row dataset used to derive variable importance over a shifting ITVsd. Performance was measured as the PFT’s final population or presence/absence at the end of the simulation run. Analysis was stratified by ITVsd, so each sub-forest contained 200,000 rows, because there were 11 different levels of ITVsd.

Figure 2.2 Metadata for variable importance: persistence

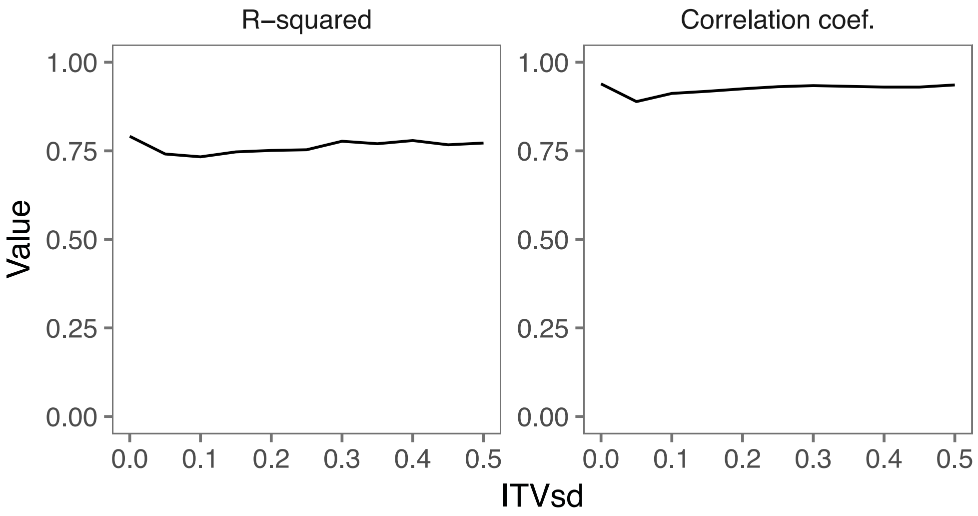
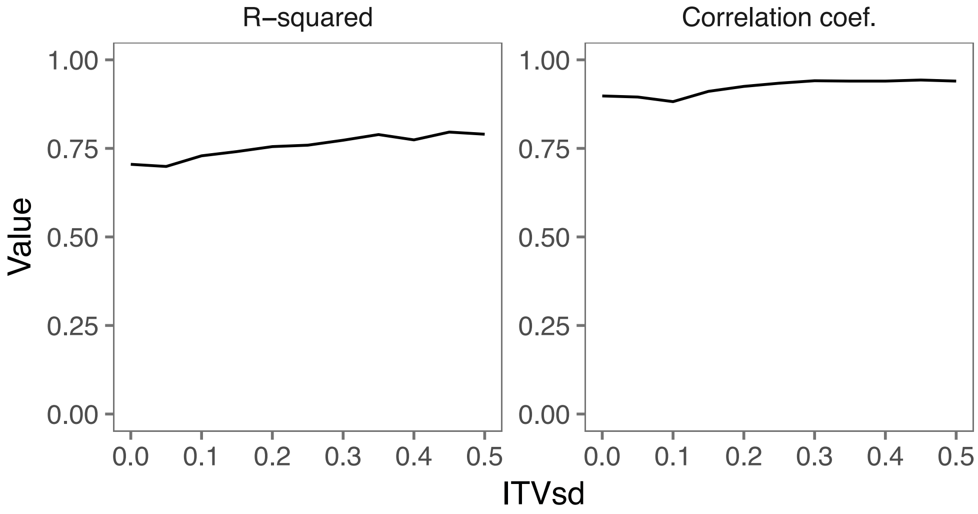


Figure 2.3: Metadata for variable importance: abundance



8.2.2 Supplemental Material C: Testing different diversity measurements

Methods

In addition to Shannon diversity—reported in the main manuscript—we also tested both richness and evenness for their relationship with ITV. To calculate evenness, we used probability of interspecific encounter (PIE, Hulbert 1971; Chase and Knight 2013). Probability of interspecific encounter is an intuitive measurement of evenness: it is the probability that, given two individuals are sampled from the population, these two individuals are of different species. A value of "0.5" would indicate that there is a 50% chance those two individuals are different species.

Using these other metrics, we also run the equivalent statistical analyses as those in the main manuscript, to ensure that the patterns reported with Shannon diversity are equivalent to those with richness and PIE. For each, we first derive a linear mixed-effect model investigating how the metric changes with increasing ITV, with both the slope and intercept subject to a random effect based on the community identifier. Then, we use the coefficients from this model (i.e. each communities' slope and intercept) in a linear model, seeking to understand the trends of how the communities respond to higher ITV

We used the same dataset for all three of the diversity metrics, composed of 250 communities with 16-PFTs each. We ran 50 replicate simulations for all eleven values of ITVsd.

For reference, the graph of Shannon diversity derived with this 16 PFT is also included in this supplement. It is differentiated from that shown in the main manuscript (i.e. Fig. 3B) in that it has significantly more communities and levels of ITVsd. It should be noted that this dataset—with 250 16-PFT communities—is used for all statistical models in this manuscript.

Results

We find agreement between Shannon diversity, Richness, and PIE.

Shannon diversity of the 16-PFT communities behaves consistently with the main manuscript's Fig. 3B (Fig. 1A). Median richness climbs from 6 PFTs persisting after 100 years without ITV to 9 PFTs persisting with an ITVsd of 0.5 (Fig. 1B). Median PIE increases much more gradually, an effect dwarfed by its relative change in variance with increasing ITV (Fig. 1C).

The model predicting the change in richness based on ITV with the community as a random effect—for both slope and intercept—shows a positive increase (marginal R^2: 0.17; conditional R^2: 0.60). The other different model, predicting PIE, also shows an increase (marginal R^2: 0.380, conditional R^2: 0.15). Comparing these models, the community identity holds more sway in determining the change in richness than it does the change in PIE. Conversely, ITV explains change in PIE significantly more than it does change in richness.

The linear models using the model parameters (i.e. the slope and coefficient for each community) of richness and PIE are in general agreement. For richness, the linear model estimates a slope of -1.05 over the ITV levels ($R^2 = 0.26$, Fig. 2B). For PIE, the slope is significantly steeper, -1.53, and explains significantly more variance ($R^2 = 0.78$, Fig. 2D).

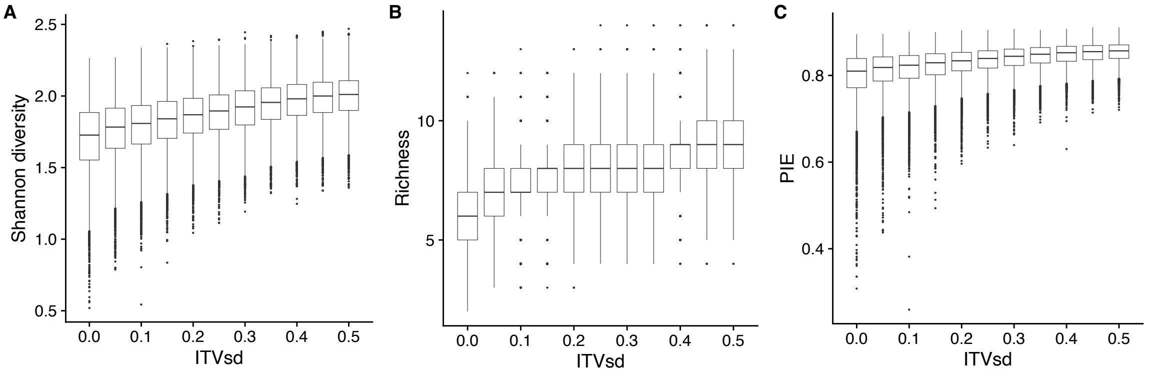


Fig. 1: 16-PFT community data decomposed into two diversity components: A) richness and B) evenness, measured as the probability of interspecific encounter (PIE).

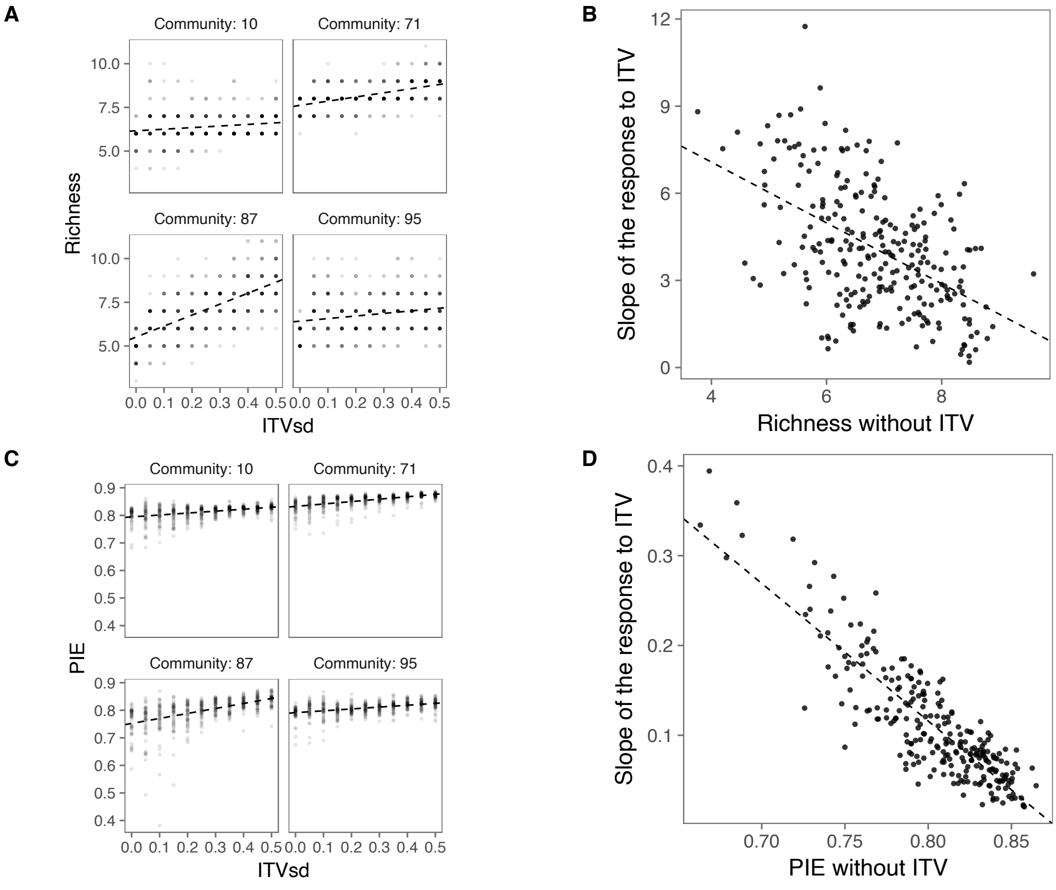


Fig. 2: From top left: A) slopes and intercepts of the response in richness of four sample communities to an increased ITVsd, B) a linear model showing the regression parameters (slope and intercept) of the linear mixed-effect model for richness C) slopes and intercepts of the response in evenness (PIE) of the four sample communities, D) a linear model of the regression parameters for PIE.

8.2.3 Supplemental Material D: Simulation results without intraspecific negative density dependence

Motivation

In IBC-grass, intraspecific negative density dependence (INDD) is an important extra stabilizing component that drives species richness in the model. INDD reflects, for example, species-specific predators or pathogens. While traits are the only mechanism through which the fitness hierarchy is established for a given abiotic condition, without this INDD richness falls to one species over the simulation length (100 years). This added stabilization enabled IBC-grass—prior to the inclusion of ITV—to successfully simulate the trait distributions and community dynamics recognizable for a given abiotic condition (i.e. above- and belowground resource regime as well as grazing intensity).

However, given that this extra stabilization acts on the PFTs rather than the traits, it is important to understand to what degree it interacts with ITV. It is possible that adding ITV to IBC-grass could enable weaker PFTs to garner more beneficial trait values without penalizing them through their closer proximity to the other species in that location on the trait axes. It is therefore critical to understand the influence of ITV without this extra stabilization.

Methods

Mirroring the main simulation batches, we ran a set of simulations varying INDD for 250 communities—generated with 16 PFTs—with 50 replicates per level of ITV. To understand how the influence of ITV changes based on the presence or absence of INDD, we calculated three diversity indices over time: Shannon diversity, richness, and probability of interspecific encounter (PIE, which is equivalent to Simpson's diversity). We then analyzed how these diversity metrics change within the simulation.

Results

We find that without stabilization (INDD) ITV continues to be an important additive effect to all diversity indices (Fig. 1, 2, 3), but its efficacy degrades over the first 50 years of the simulation. Regardless of ITV, without stabilization richness ultimately falls to one or two species (Fig. 2).

For the first 25 years without INDD, Shannon diversity remains high as the amount of ITV is increase (Fig. 1). Over time, however, its effectiveness degrades and, by the year 100, diversity is near 0 regardless of the amount of ITV. With INDD its effect is permanent for the duration of the simulation.

Richness is the most impacted in IBC-grass without INDD (Fig. 2), increasing the median richness by as much as 4 species after 25 years. As the simulations reach past the fifty-year point, however, diversity falls back towards one or two species regardless. With added INDD the ITV-driven increase in richness lasts for the entire least 100 years.

With INDD, the variation in the communities' PIE values decreases with increasing ITV (Fig. 3). This effect is not present without stabilization, and by the end of the simulation (100 years), evenness is very low as there is usually one or at more two species present.

Conclusion

INDD is an important component of the model, ensuring realistic community assembly (Weiss et al. 2014) through one specific form of a stabilizing mechanism. Although by removing the model's INDD component ITV's efficacy decreases over the course of 50 years, ITV's positive effect on diversity can still be observed and is thus not dependent on INDD.

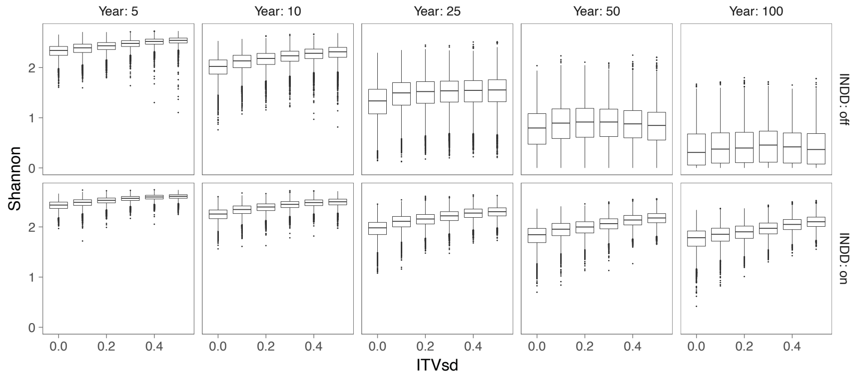


Fig. 1: The impact of stabilization through INDD on the plant communities' Shannon diversities over time for varying levels of ITVsd. Each level of ITVsd contains 50 replicates of all 250 communities.

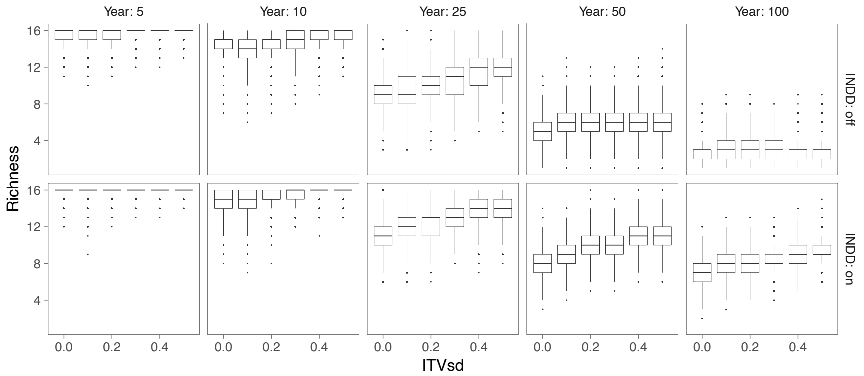


Fig. 2: The impact of stabilization through INDD on the plant communities' richness over time for varying levels of ITVsd. Each level of ITVsd contains 50 replicates of all 250 communities.

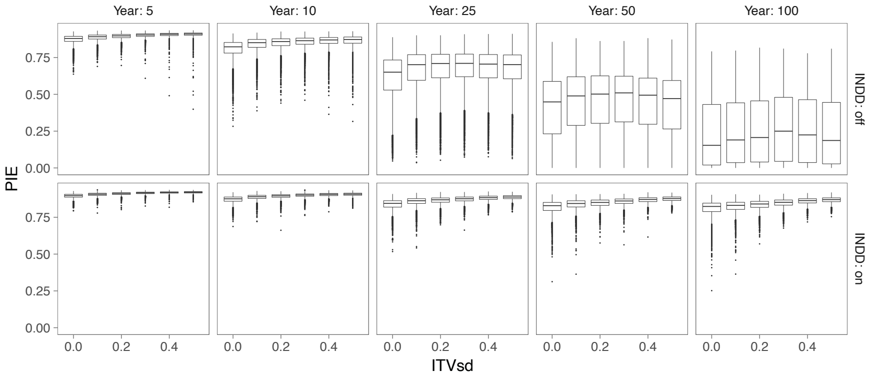


Fig. 3: The impact of stabilization through INDD on the plant communities' PIE over time for varying levels of ITVsd. Each level of ITVsd contains 50 replicates of all 250 communities.

8.2.4 Supplemental Material E: Partial dependency plots

Methods

Given their high dimensional nature, it can often be difficult to tease apart the relationships between the response variable and explanatory variables (features) in random forests. However, partial dependence plots are a reliable way to visualize the associations between the random forest's features (i.e. explanatory variables) and the response variable, by choosing a set of target features and plotting the how the model prediction changes across them, while marginalizing the values of the other features. To derive these plots, we used the R package "pdp" (Greenwell 2017). The random forests used included ITV as a predictor variable. For all random forests, 30% of the total dataset was withheld for validation.

Results

Partial dependence plots of pairwise invasion: Predicting invasion rate

Variable importance plots (Fig. 6 in main manuscript) suggested that the invader's LMR is unimportant in driving invasion, and this is mirrored in the partial plots: there is very little difference in the random forest's predicted invasion rate with different LMR values (Fig. 1A). Resident LMR does play a roll, also seen in the variable importance plots. Low LMR residents are significantly easier to invade than medium and high LMR residents. Low LMR PFTs have less photosynthetic biomass and smaller ZOIs.

The invader's m_{max} is unimportant. Residents with a high m_{max} were easier to invade than their low- m_{max} counterparts, potentially indicating that low m_{max} PFTs are tightly packed and resist their invaders more easily (Fig. 1B).

Gmax was the only trait that mattered from the invaders' perspective: Low Gmax PFTs are much less likely to invade (Fig. 1C). Resident Gmax is also an important trait. Interestingly both low and high Gmax residents are invaded more easily than their medium Gmax counterparts until middle ranged of ITV, in which high Gmax PFTs become slightly easier to invade.

While invader SLA is unimportant, resident SLA is the most important trait in the invasion dataset (Fig. 1D). Low SLA individuals, perhaps because of their small ZOI leaving uncovered space for invaders to germinate, are much easier to invader than their low and high SLA competitors. Like Gmax, there is a nonlinearity between medium and high SLA PFTs, wherein the high SLA PFTs become easier to invade with increasing ITV.

Partial dependence plots of pairwise invasion: Predicting abundance

The LMR trait is largely consistent from both the abundance and pairwise perspective: low LMR species are significantly easier to be evaded (Fig. 2A).

m_{max} is significantly different from the invader's perspective: Contrary to the pairwise plots, invader m_{max} is of critical importance and becomes even more important with increasing ITV (Fig. 2B). Low m_{max} plants display much higher abundances than their high m_{max} counterparts. This is logical, given that the spatial extent is fixed at 1 m^2, and large plants would simply take up more space than their smaller competitors. Again, large residents generally tend to enable larger populations of invaders.

Unlike invasion rate, invader Gmax is relatively uninfluential (Fig. 2C). Interestingly, low Gmax residents enable much larger invader populations to emerge. This is contrary to the invasion rates, in which a low Gmax is much less differentiated from the other settings in its effect. This indicates that the effect of Gmax is less important for invasion than it is for the competitive processes which occur after establishment, implying that most species repel invasion through reducing the invader's ability to germinate new seedlings.

The impact of SLA is largely concurrent between invasion and abundance (Fig. 2D). The primary difference occurs in the invader SLA, which shows more differentiation between the levels: low SLA PFTs generally see higher abundances than their medium and high SLA counterparts. This, again, could indicate that smaller ZOIs enable for larger populations of individuals.

Partial dependence plots of community dynamics: Predicting persistence rate

For persistence, LMR remains uninfluential in driving persistence for the plants (Fig. 3A). m_{max} is one of the most influential traits driving persistence (Fig. 3B). Whereas medium and low sized PFTs persist frequently in the model and improve, large PFTs rarely do. Further, while medium and low PFTs increase in their persistence, high values do not improve. Medium and high Gmax values reliably persist (Fig. 3C). Low Gmax persist very rarely but improve with increased levels of ITV. SLA is generally unimportant for persistence, but high SLA species generally persist less frequently than their low and especially medium SLA counterparts (Fig. 3D).

The main source of variation between traits in predicting persistence with increasing ITV are m_{max} and Gmax. Gmax trades off with m_{max}, initially becoming the most important trait before becoming less important with higher levels of ITV. This likely occurs because of the behavior of both traits: The partial dependency plot shows that an ITVsd of 0.05 leads to a jump in the persistence rate of large (high m_{max}) PFTs. This reduces the distance between the m_{max} traits values and therefore reduces the trait's importance. The Gmax eventually becomes less important, however, and this is likely due to the low Gmax PFTs persisting more often with ITVsd values above 0.25.

Partial dependence plots of community dynamics: Predicting abundance

LMR remains generally unimportant (Fig. 4A). However, m_{max} again gains in importance with ITV (Fig. 4B): While low and medium values are initially similar in their abundance values, with increased ITV low trait values become significantly more abundance. This is likely the primary reason for the trade-off between m_{max} and Gmax. Moreover, there is more differentiation between medium and high levels of Gmax, with medium levels being the most advantageous (Fig. 4C). And lastly, there is a greater difference between low and medium SLAs and their large SLA competitors, but SLA remains unimportant in the variable importance plots (Fig. 4D).

References

Brandon M. Greenwell (2017). pdp: An R Package for Constructing Partial Dependence Plots. The R Journal, 9(1), 421--436.

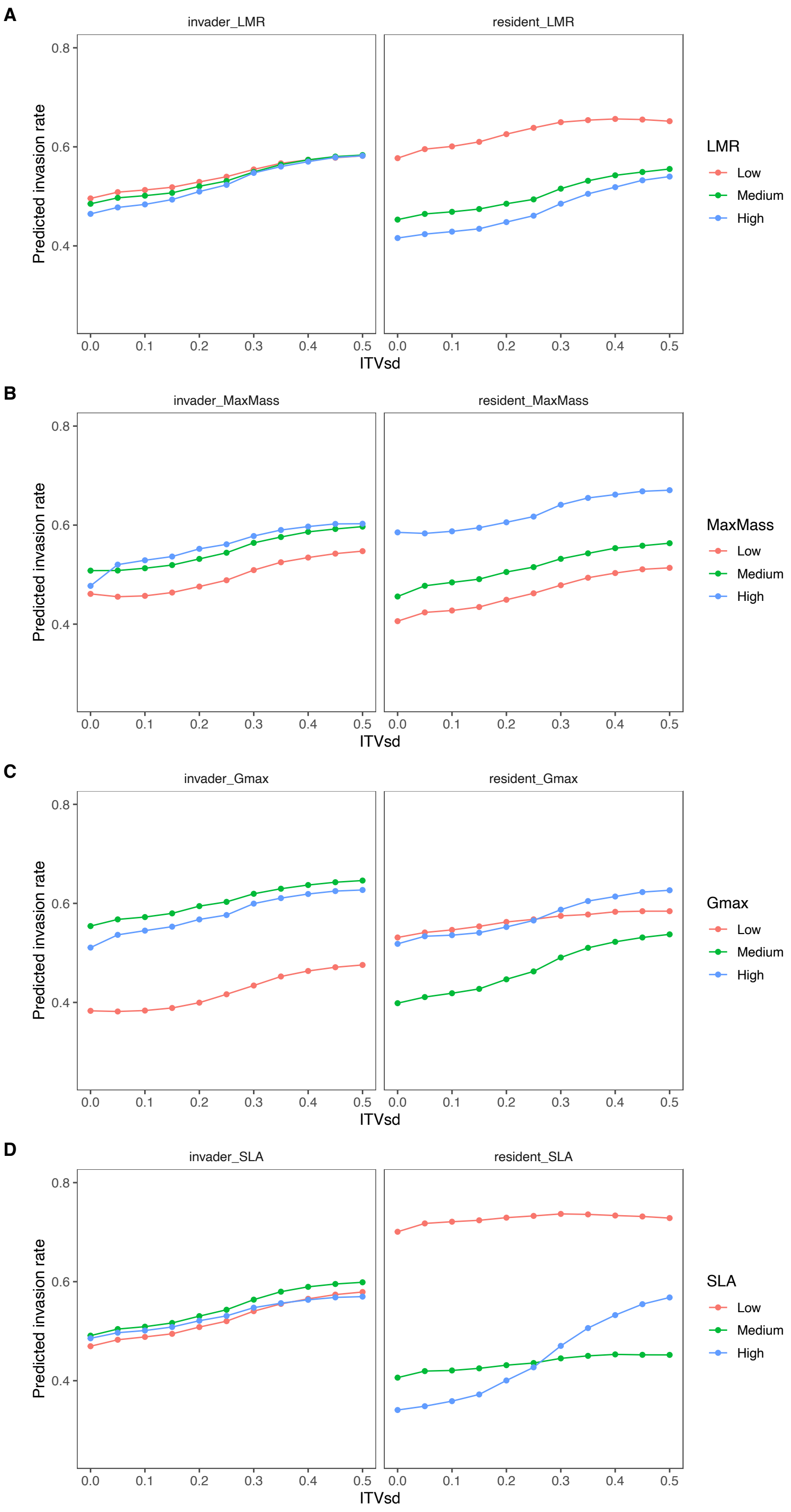


Fig 2. The influence of ITV on the resident's and invader's traits' and their impact the invader's invasion rate. Formula: invasion_rate ~ ITVsd + invader_LMR + invader_MaxMass + invader_Gmax + invader_SLA + resident_LMR + resident_MaxMass + resident_Gmax + resident_SLA | mtry: 3 | ntrees: 1024 | R^2: 0.824 | MSE: 0.011 | correlation to validation dataset: 0.908

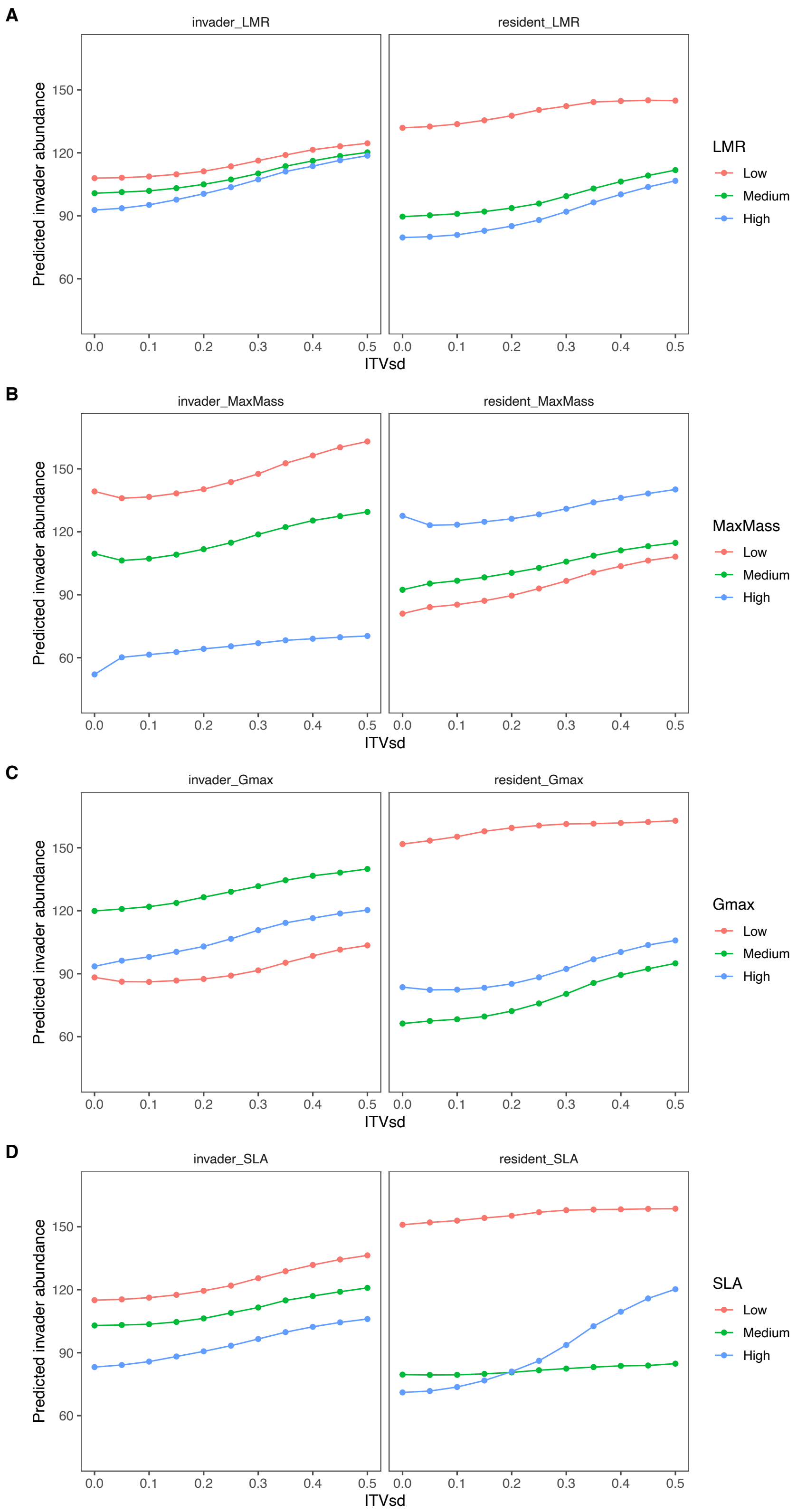


Fig. 2: The influence of ITV on the PFTs' traits' and their impact its abundance. *Formula*: abundance ~ ITVsd + invader_LMR + invader_MaxMass + invader_Gmax + invader_SLA + resident_LMR + resident_MaxMass + resident_Gmax + resident_SLA | *mtry*: 3 | *ntrees*: 1024 | R^2: 0.89 | *MSE*: 841.4 | *correlation to validation dataset*: 0.95

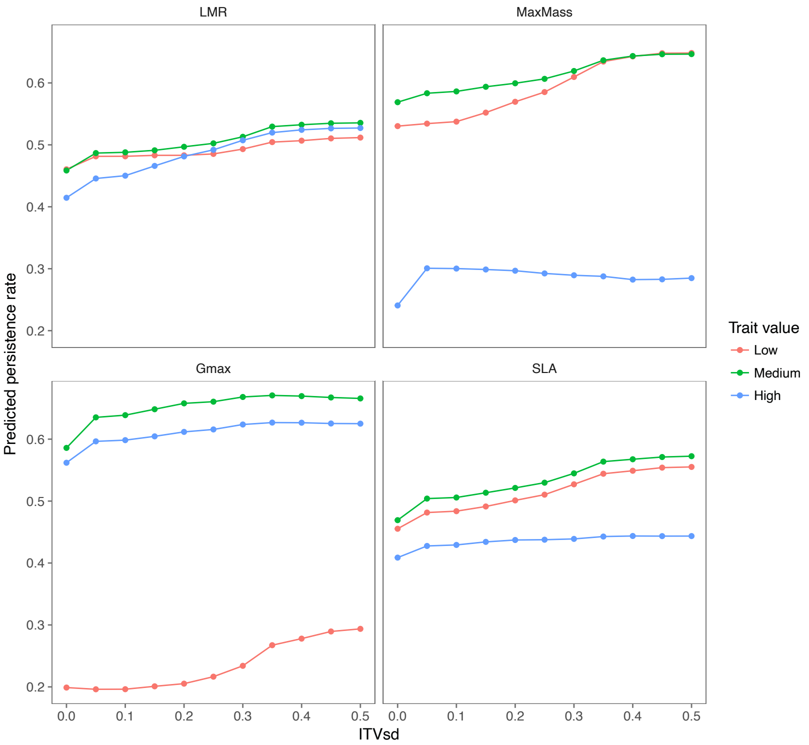


Fig. 3: The influence of ITV on the PFTs' traits' and their impact its persistence rate. *Formula*: persistence ~ ITVsd + LMR + MaxMass + Gmax + SLA | *mtry*: 2 | *ntrees*: 1024 | R^2: 0.73 | *MSE*: 0.5 | *correlation to validation dataset*: 0.92

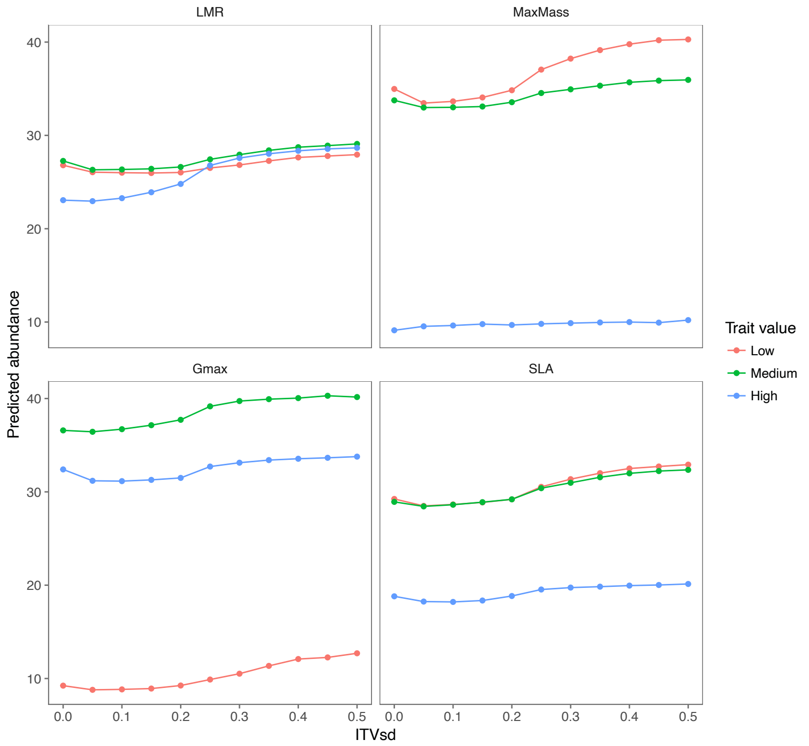


Fig. 4: The influence of ITV on the traits' and their impact the PFTs' abundance. *Formula*: abundance ~ ITVsd + LMR + MaxMass + Gmax + SLA | *mtry*: 3 | *ntrees*: 1024 | R^2: 0.75 | *MSE*: 264.0 | *correlation to validation dataset*: 0.92

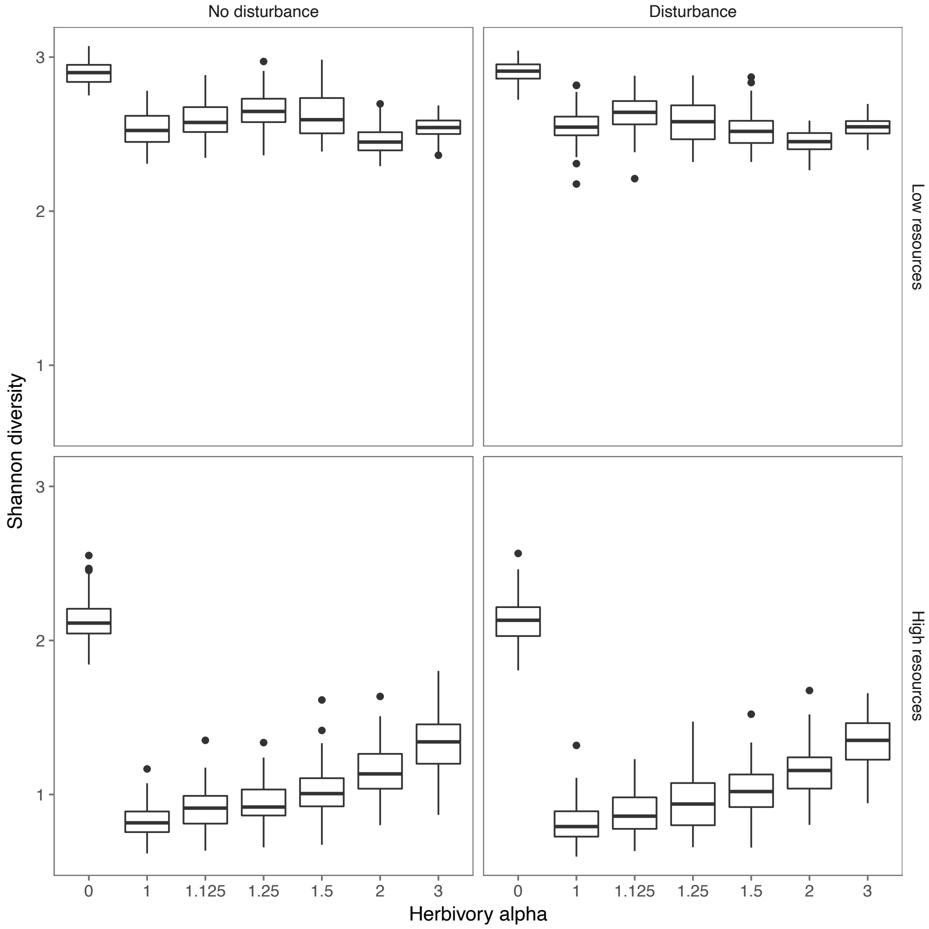
8.3 Root herbivores interact with belowground resources to mediate plant community resilience and succession after disturbance in a grassland model

8.3.1 Supplemental Material B: Sensitivity analyses

Herbivory alpha

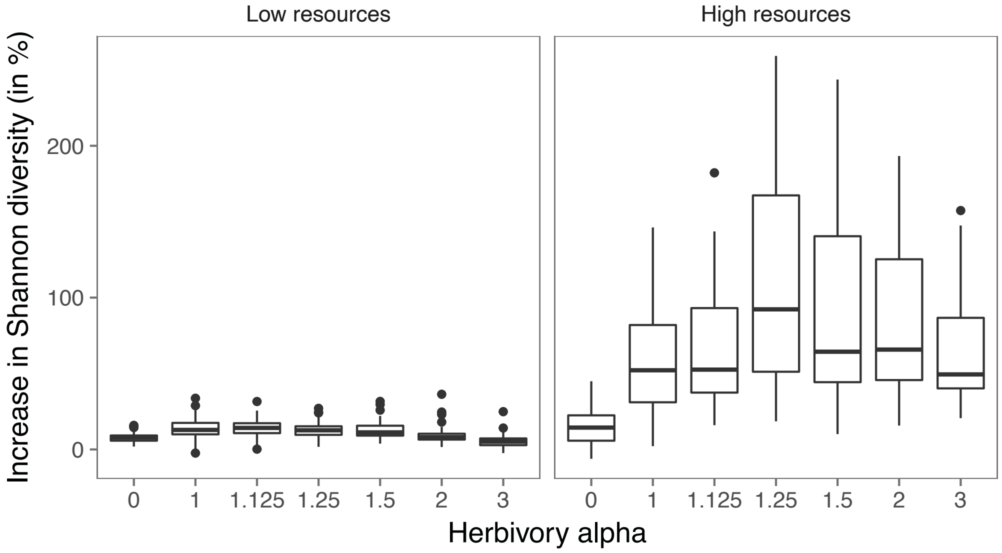
For herbivory alpha, the default value is either 1 (generalist herbivores) or 1.25 (preferential herbivores).

Shannon diversity



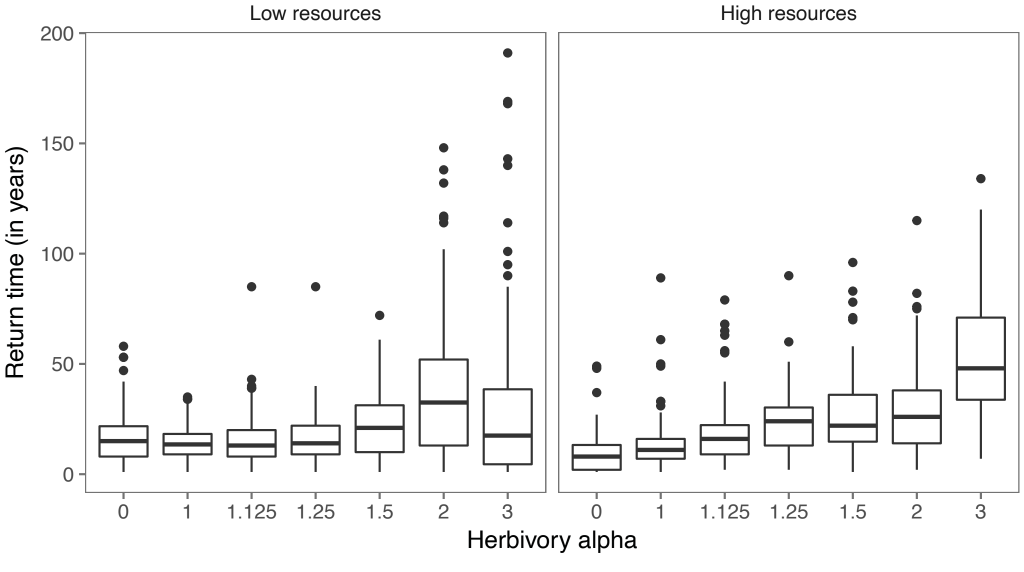
The influence of the herbivores' feeding preference—its "alpha"—on the Shannon diversity at the end of the simulation (i.e. year 300). In high resource scenarios, the presence of herbivory dramatically lowers the Shannon diversity of the plot. However, as the preference of the herbivores becomes more dramatic—the more they prefer to consume larger individuals—the impact on Shannon diversity decreases. Whether or not there is a disturbance does not impact this effect. In low resource scenarios, the impact of herbivores is significantly less. There is a slight drop in Shannon diversity with herbivores, and statistically insignificant pattern though consistent in between the effects of the different alphas.

Resistance



The impact of the different herbivory alphas on the resistance of the plant communities. In low resource scenarios, the preference of the herbivores plays little part in the response of the community to disturbance. However, in high resource scenarios there is a much larger impact. This impact on resistance is greatest with moderate alpha levels, wherein an alpha of 1.25 increases Shannon diversity most.

Recovery

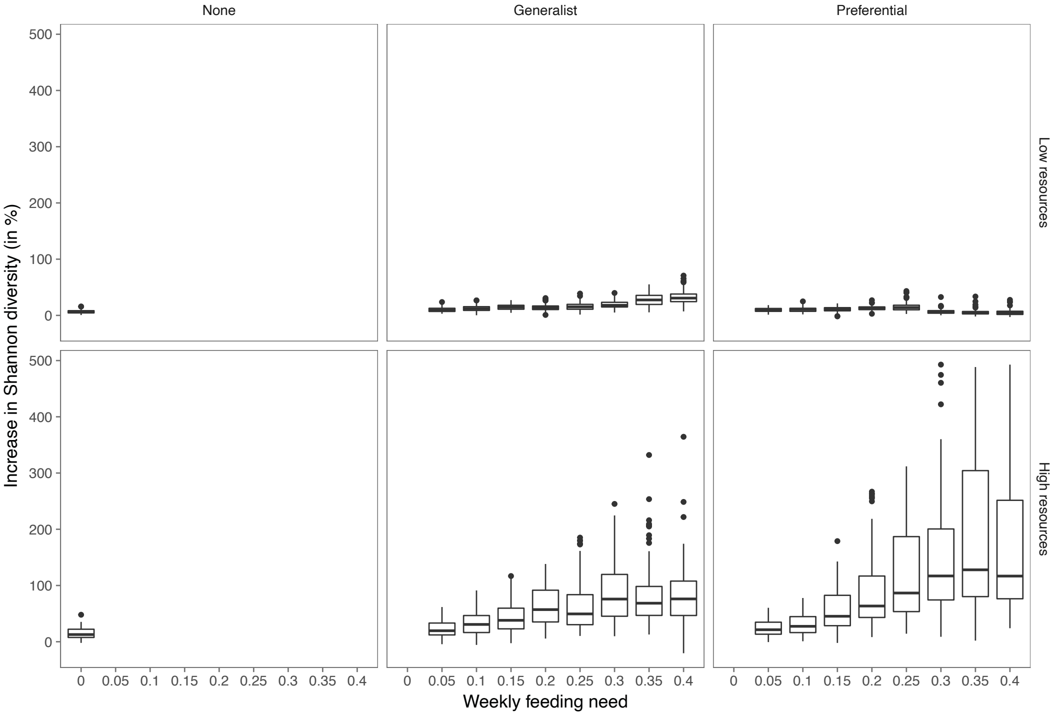


The recovery of both low and high resource scenarios interacts with the herbivory alpha, with higher values tending to increase the time to recover the most in both cases.

Herbivory feeding need

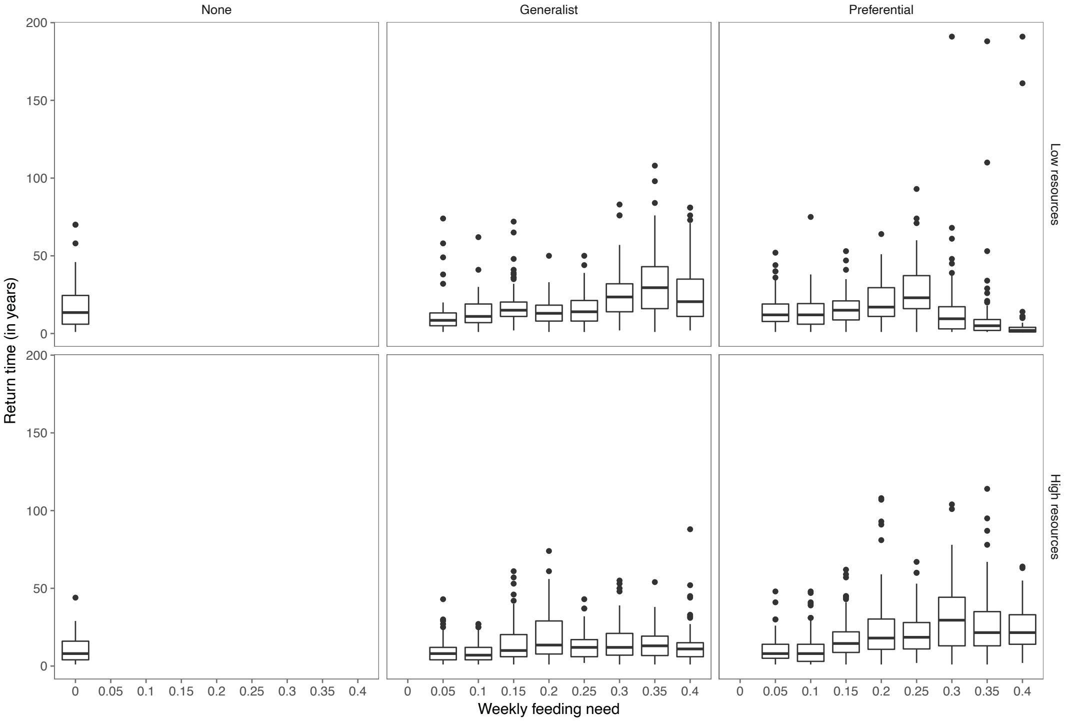
For herbivory feeding need, the value is set at 0.2, or 20% of the total biomass being consumed per week.

Resistance



The impact of the feeding need—how much plant biomass the herbivores consume per week—as well as their preferences on the resistance of the plant communities. In low resource communities, there is little change in the Shannon diversity with increasing feeding needs, regardless of the preferences of the herbivores. In high resource communities, the preferential herbivores more greatly impact the Shannon diversity after disturbance, but regardless of the herbivores' preferences the impact is significant.

Recovery



Unlike resistance, there is a little difference in the distributions of recovery time between low and high resource scenarios. Interestingly, in low resource scenarios preferential herbivores with very high feeding needs have considerably lower return times than their lower-feeding need counterparts.

Herbivory functional response threshold

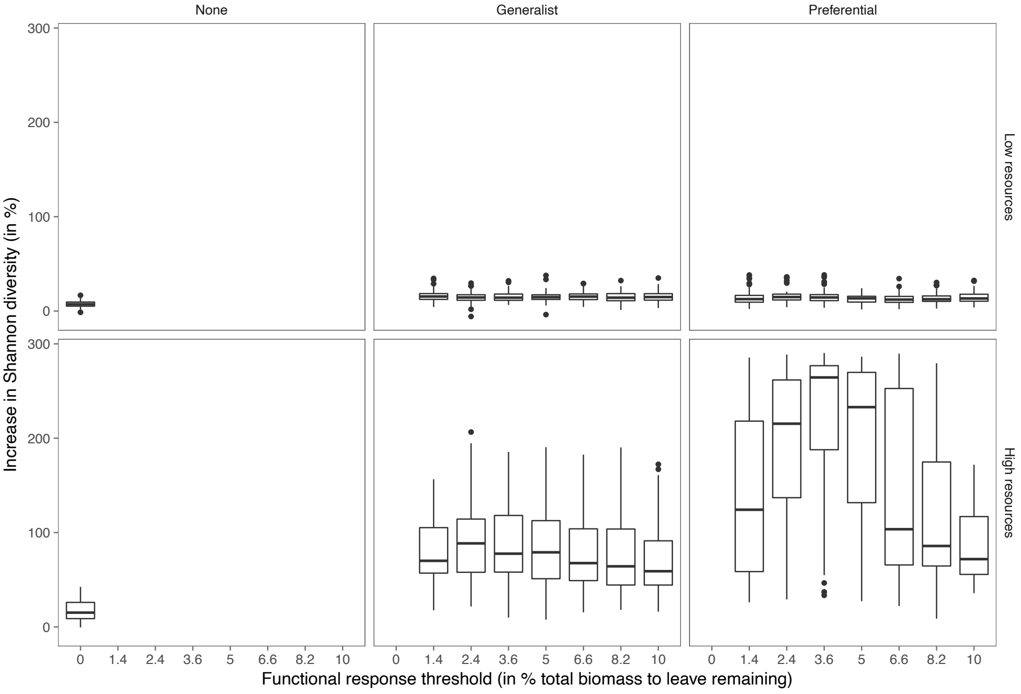
The amount of edible biomass will be significantly reduced immediately after the disturbance (see Supplement A, Fig. A3), but a large number of herbivores will remain in the system. During these initial few weeks, when there is less root biomass available to the herbivores than their feeding need, we leave a small amount of the total root biomass ungrazed to mimic a feeding response wherein the herbivores would have to spend more time searching for the remaining biomass. The threshold (t) is related to the percent biomass left undisturbed (b) and the feeding rate (f) such that:

$$b = 1 - e^{-\frac{f}{t}} \qquad \text{eq. B1}$$

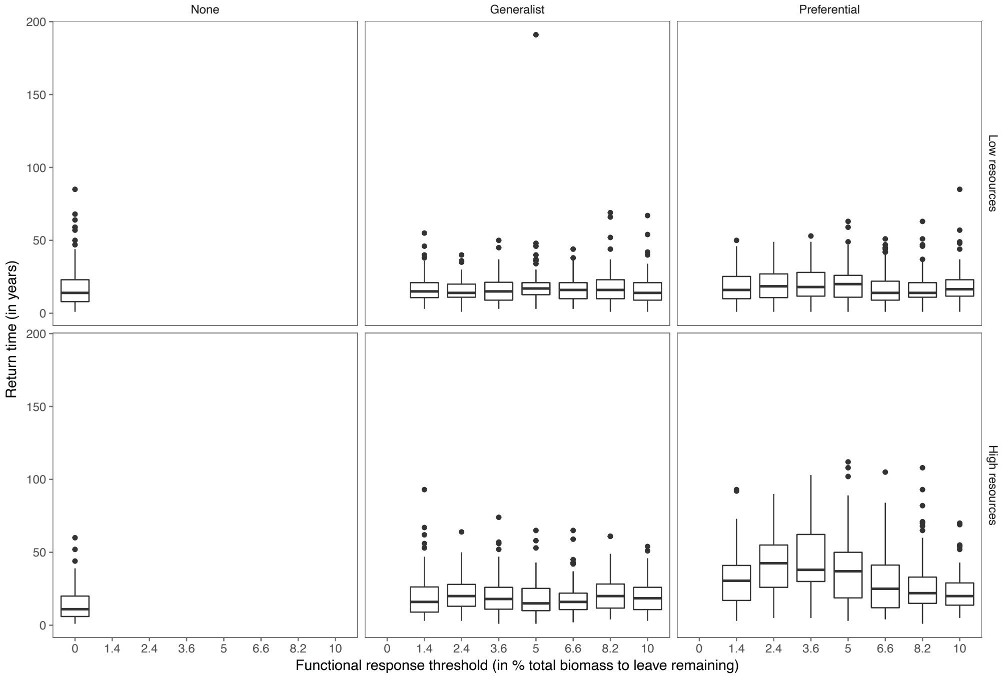
This relation ensures that lower thresholds will leave less biomass undisturbed, but also that larger feeding rates—holding the threshold constant—will also leave less biomass undisturbed. The chosen threshold was 5 percent, or 0.0667616.

The functional response threshold is most impactful for high resource scenarios with preferential herbivory. Of these, moderate thresholds change the resistance and recovery of the plant communities the most.

Resistance



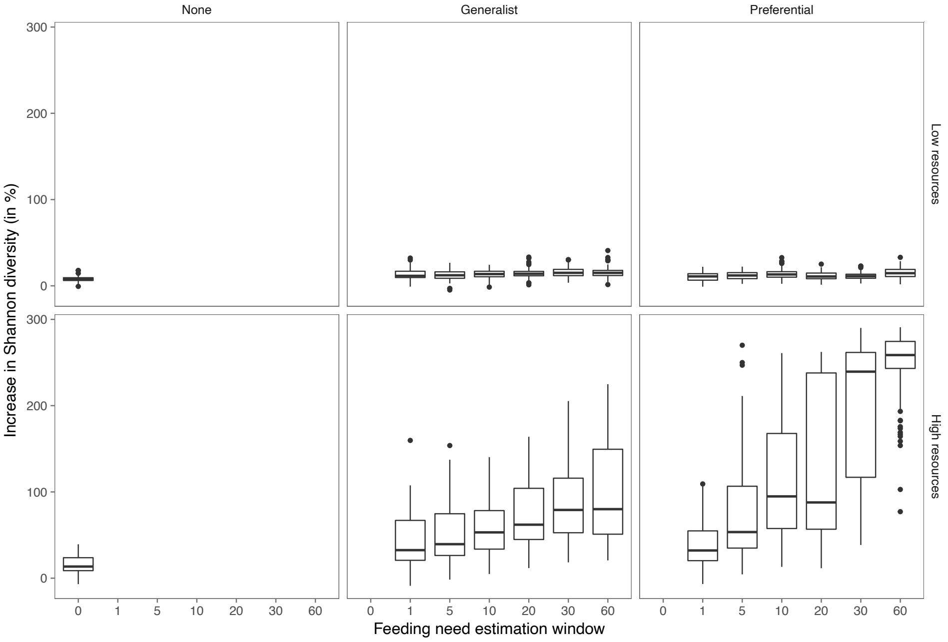
Recovery


None
Generalist
Preferential
Low resources
High resources
Return time (in years)
0
50
100
150
200
0
1.4
2.4
3.6
5
6.6
8.2
10
Functional response threshold (in % total biomass to leave remaining)

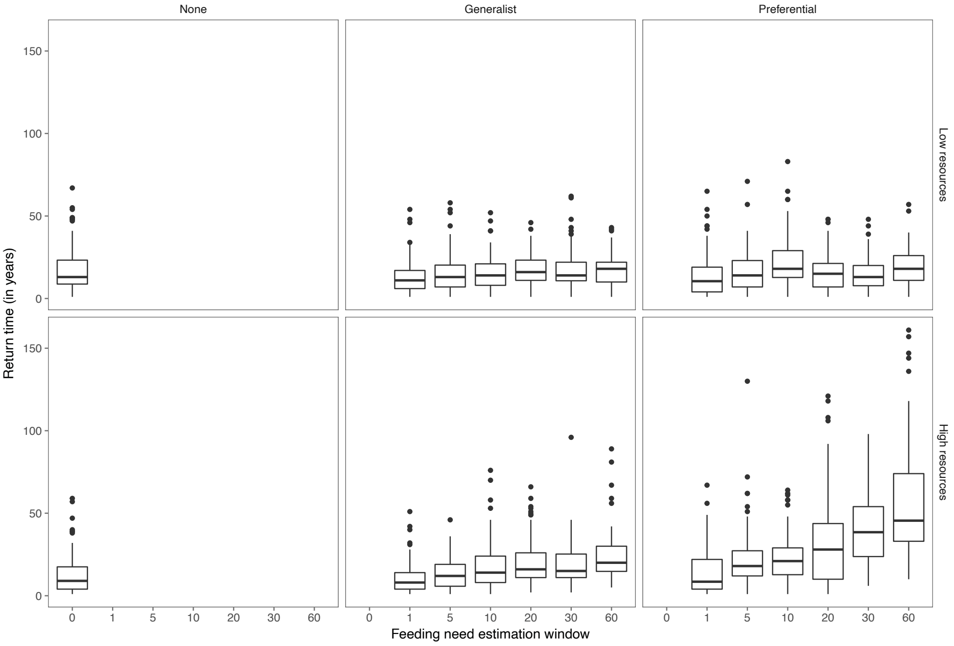
Herbivory window

For high resource scenarios, there is a general increasing trend in which higher weekly windows garner larger increases in Shannon diversity after disturbance. With a two-year window, in which the belowground herbivores take sixty weeks to fully respond to the disturbance, the median increase in Shannon diversity is nearly 300% with preferential herbivory.

Resistance



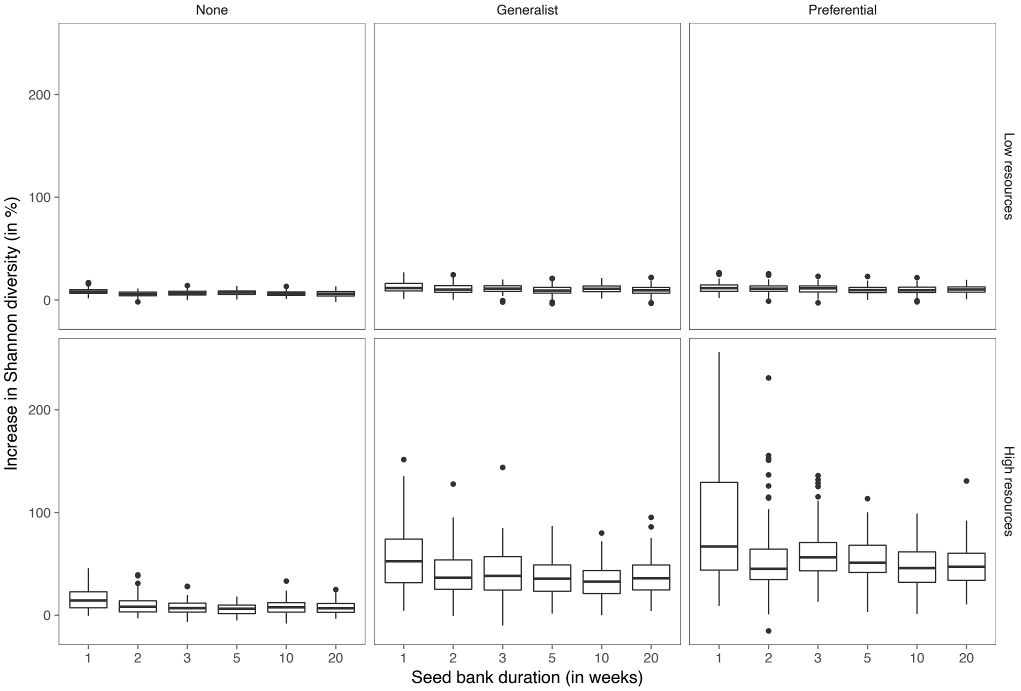
Recovery



Seed bank longevity

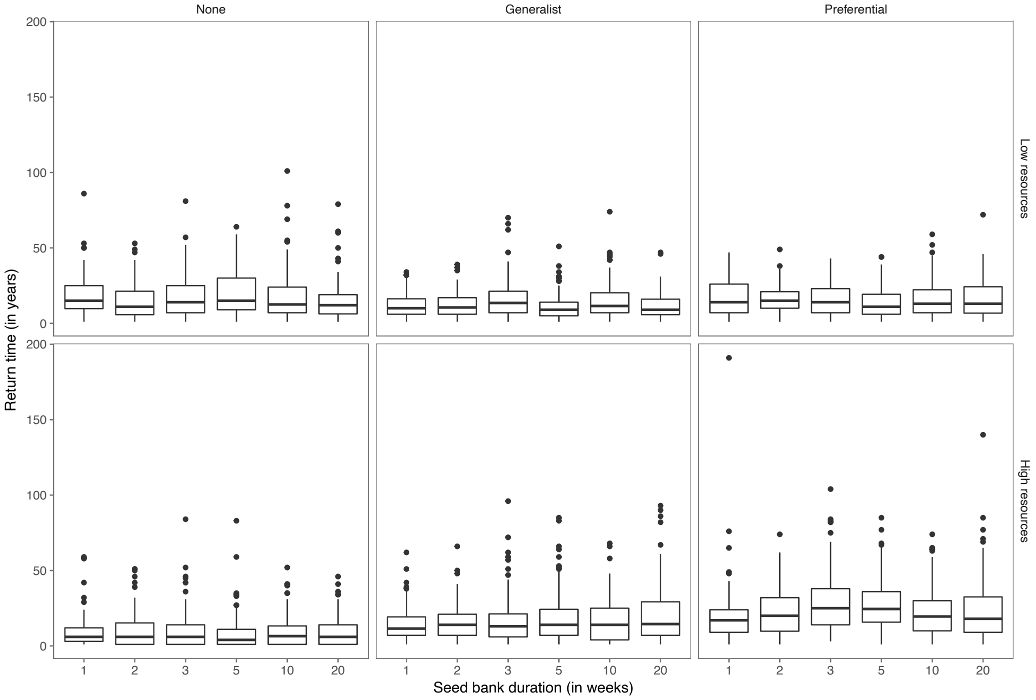
The longevity of the seed bank is set to either 1 (short-term) or 3 (long-term) years.

Resistance



Short-term seed banks are more impacted by herbivores after disturbance than long term seed banks, but there is little difference between a 2- or 3-week seed bank and a 20-week seed bank.

Recovery

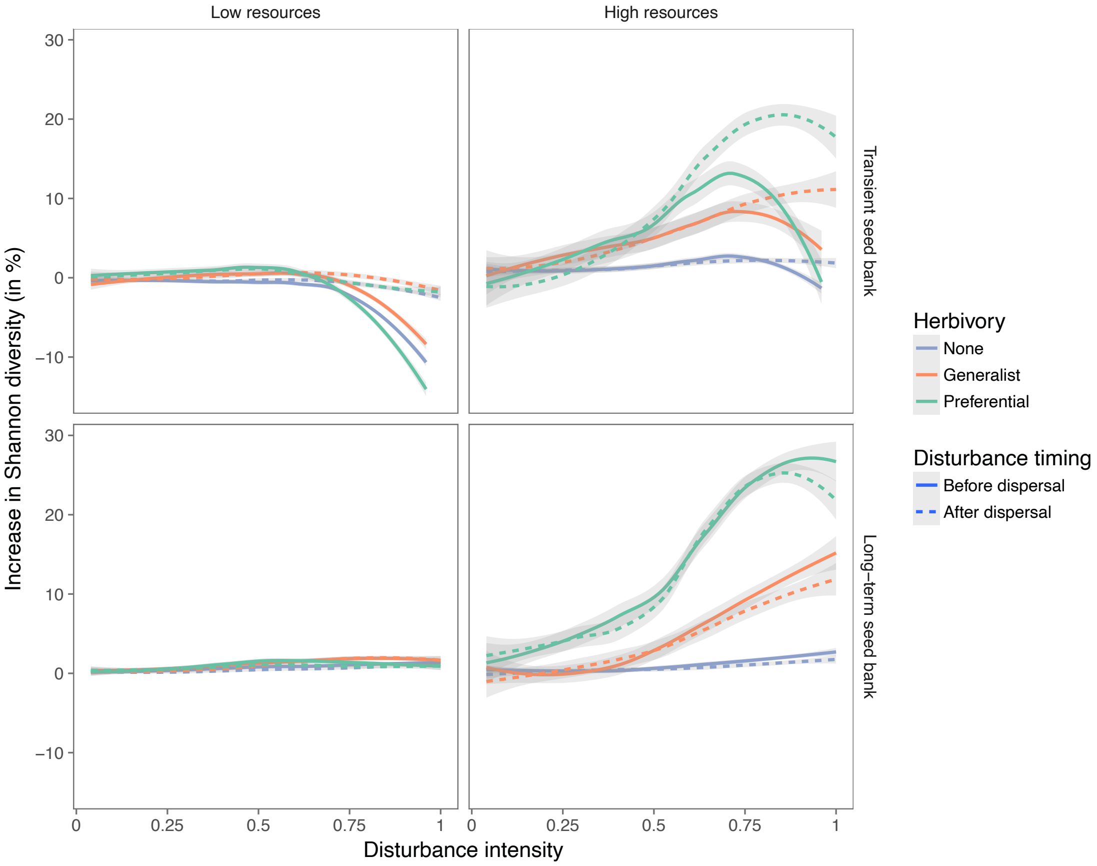


8.3.2 Supplemental Material C: Simulations without seed addition

Introduction

Our base simulations included a relatively low level (Weiss et al. 2014) of seed addition, intended to reflect input from the surrounding plant community. However, real grassland species are variable in their dispersal properties, and the ability for these species to re-enter the disturbed community should not be taken for granted. Therefore, we ran a second set of simulations identical the original, except without seed input. Extinction in this scenario is permanent.

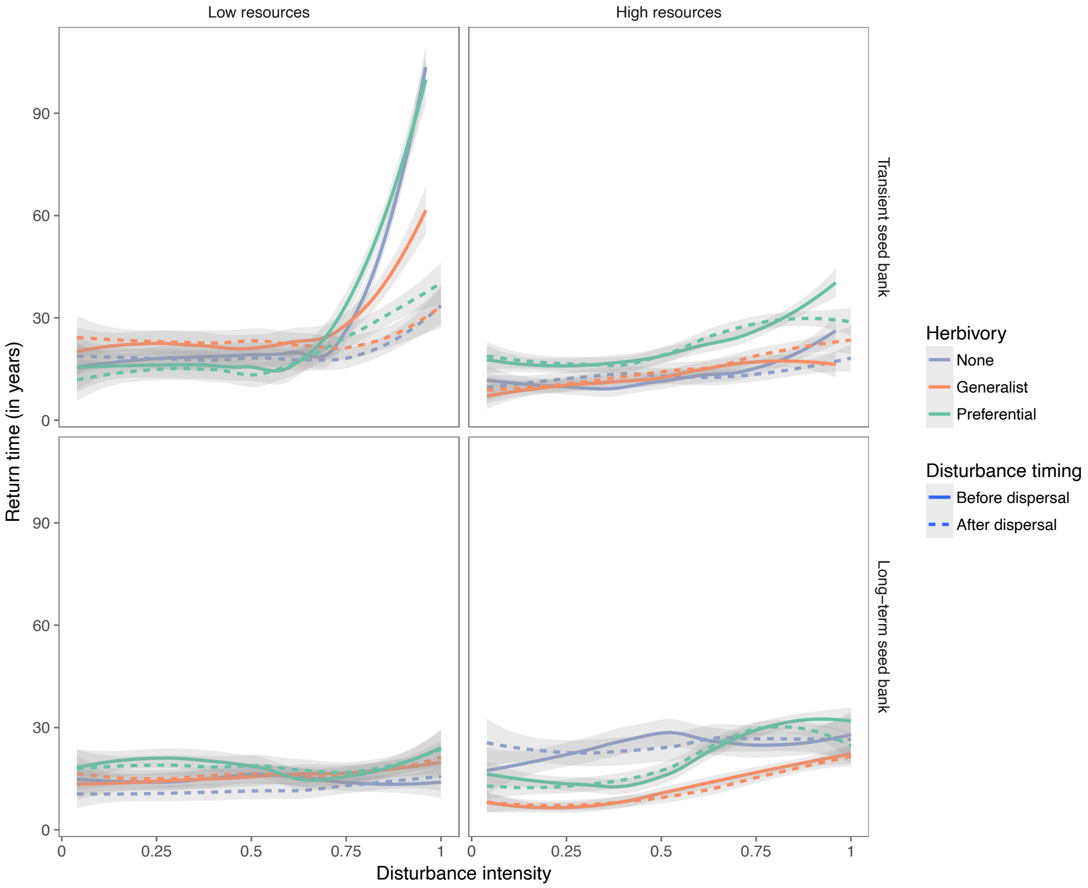
Resistance



The patterns of resistance are similar with to that of the simulations with seed addition except for two main differences. First, whereas low resource grasslands with transient seed banks (upper-right) increase in their Shannon diversity with seed addition, they decrease without it. And second, the “reset” of the simulation in high resource communities with a transient seed bank (upper-left) no longer exists. Those simulations with a long-term seed bank, however, are qualitatively the same, although with greater differentiation between generalist and preferential herbivory in high resource grasslands.

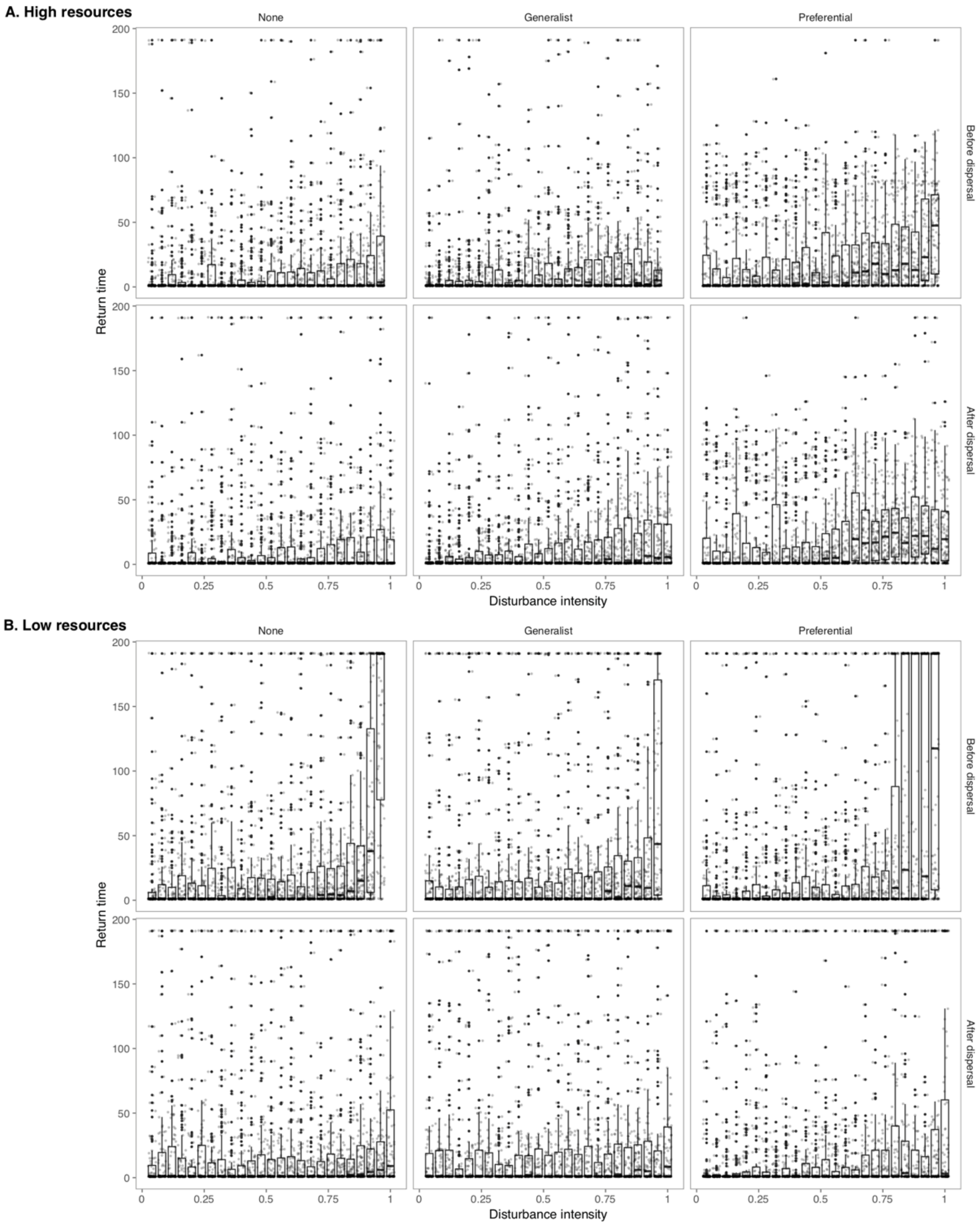
Recovery

LOESS data



Recovery, by contrast, is very different between communities with and without seed addition. With a transient seed bank, the time to return between low resource communities with and without seed addition is qualitatively similar, although intense disturbances without seed addition last roughly twice as long. The hierarchy or herbivory scenarios is slightly different as well, with no clear differentiation between the different settings of herbivory. In high resource scenarios, while the time to return for intense disturbances are roughly the same, low intensity disturbances also take several decades to return. This suggests that external seed addition acts as a stabilizing force within the simulation, counterbalancing the stochasticity that may guide a community towards a different successional pathway, regardless of disturbance and herbivory. Were this to be the case, our measurement of "recovery" in the context of this simulation would be confounded because we measure recovery as the time it takes to return within one standard deviation of the control (no disturbance) scenarios' Shannon diversity. The input of additional seeds may limit the prevalence of stochastic extinctions, therefore reducing the total successional pathways that a community can take regardless of herbivory or disturbance.

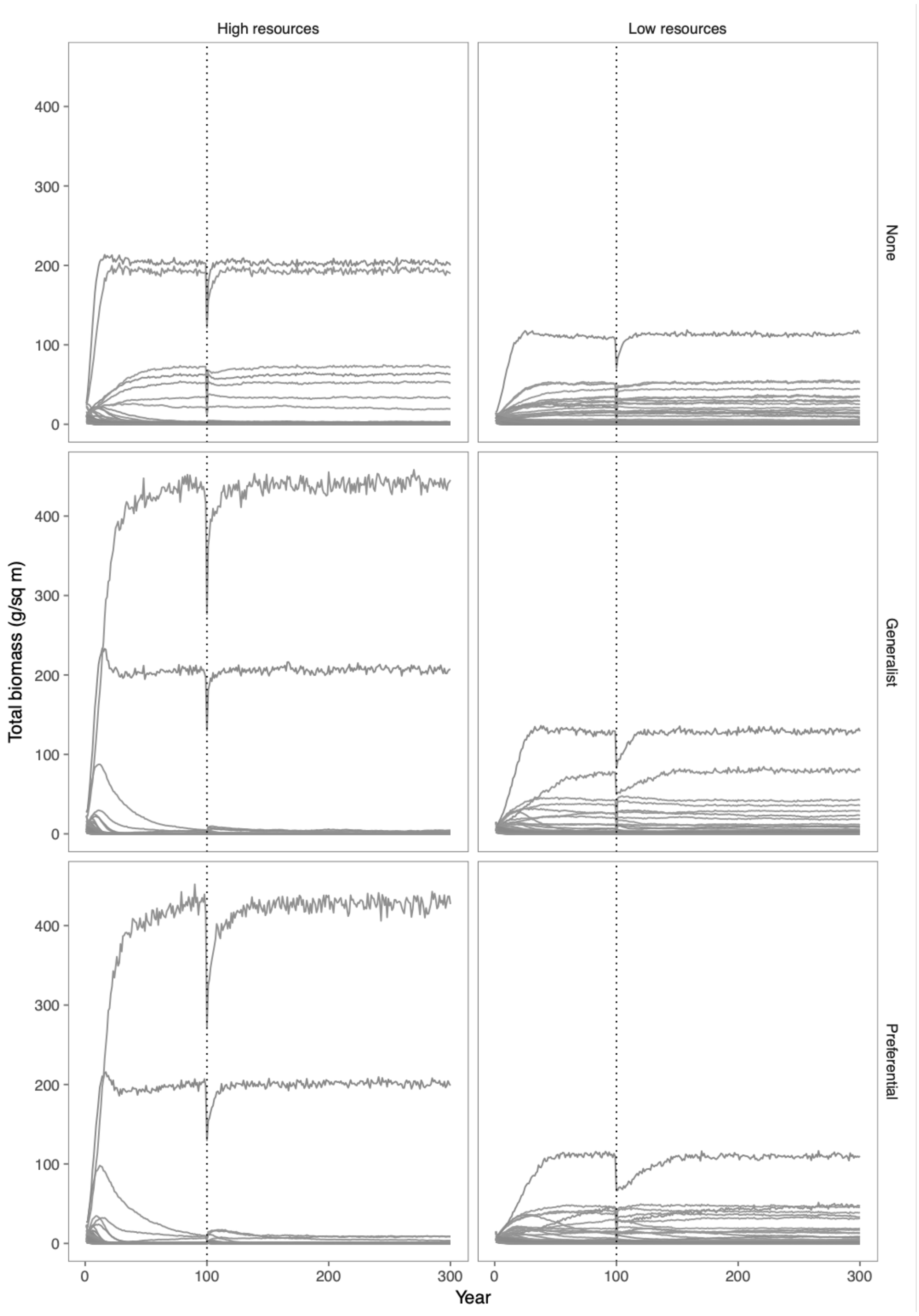
Raw data



The raw dataset for transient seed banks bares this hypothesis out. Even without disturbances and herbivory, a significant number of simulations take dozens or hundreds of years to “return” to the control Shannon diversity. This strongly suggests that the number of possible community states without seed addition is significantly higher than with seed addition. This limits the applicability of our measurement of recovery.

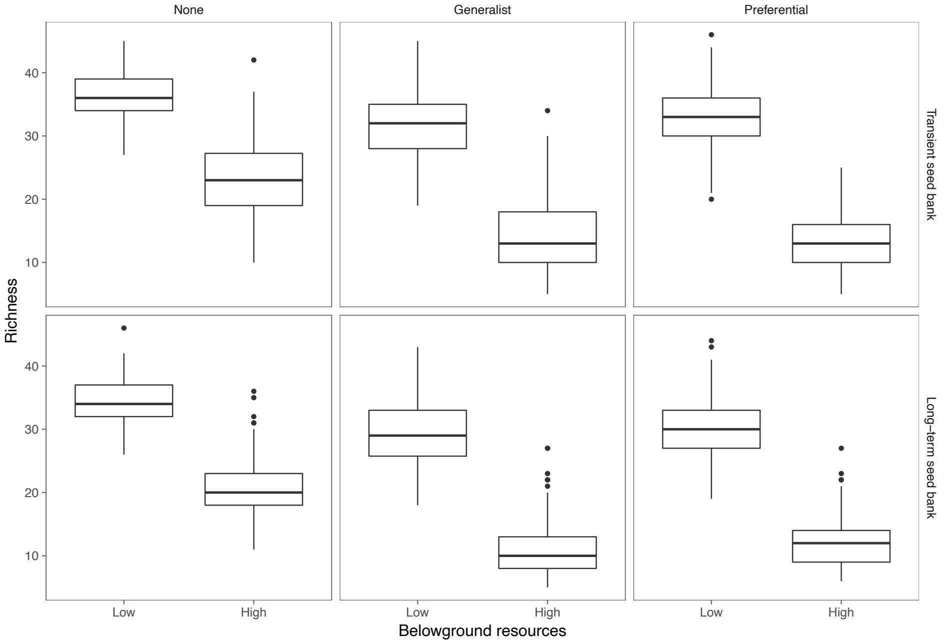
8.3.3 Supplemental Material D: Extra figures

Population dynamics visualization



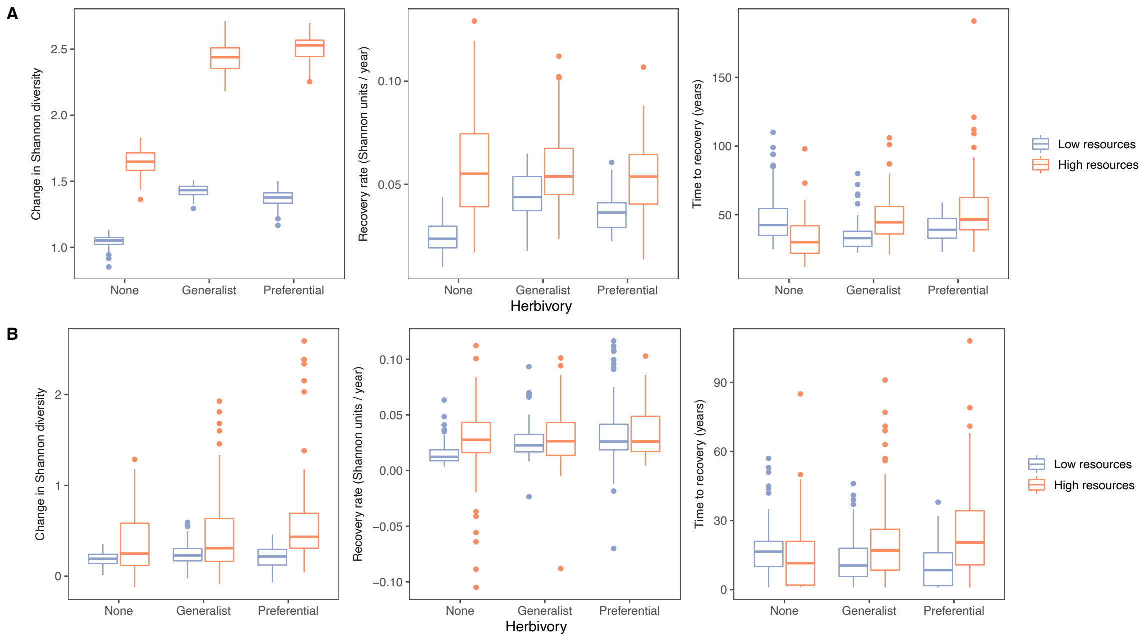
Each PFT—species—is a different line. Disturbances occurred on year 100 and were and intensity of 0.75. Low resource communities have significantly more diversity than high resource communities, and herbivory (generalist or preferential) decreases this richness further.

Species richness



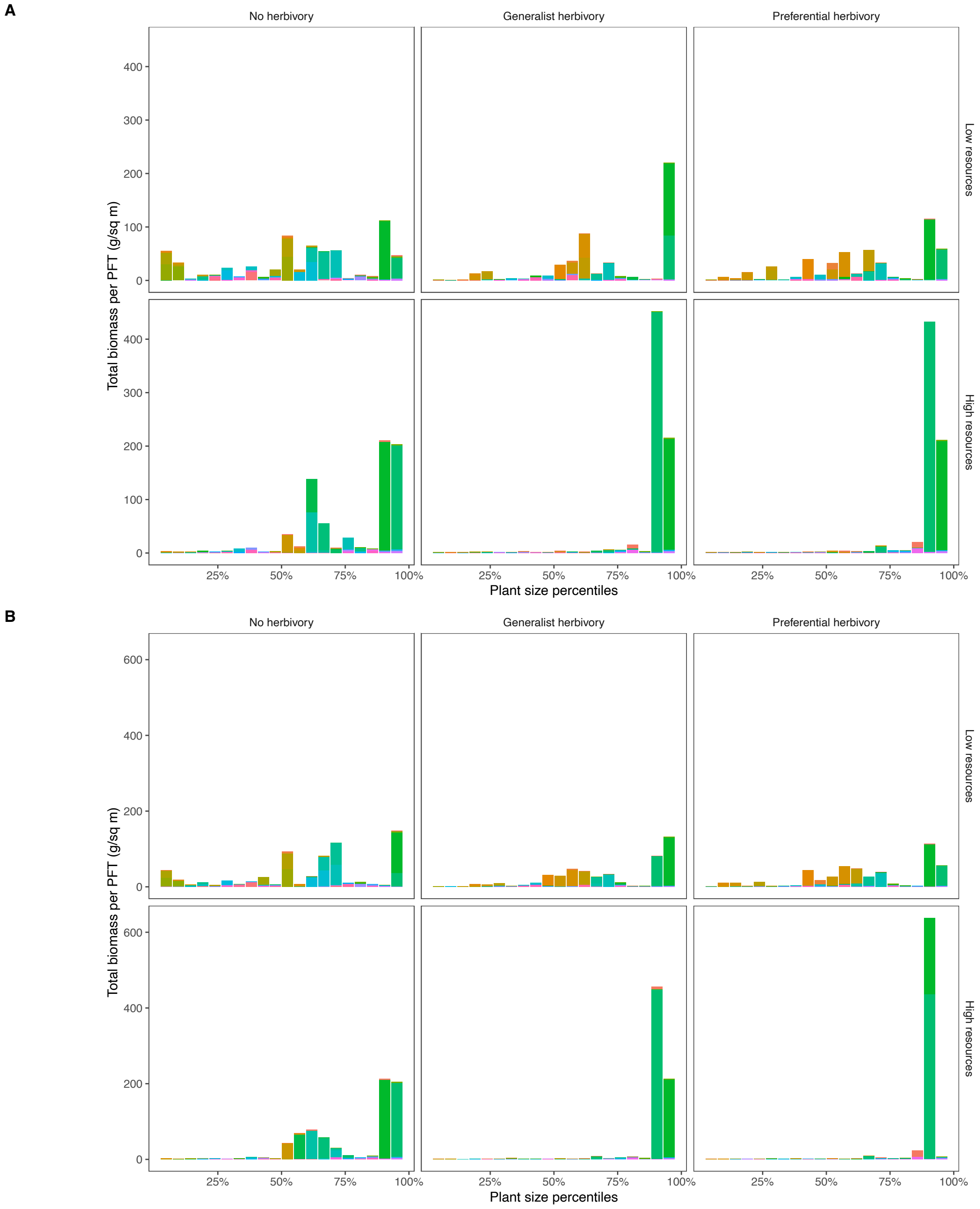
Species richness of our simulation communities without disturbance, measured at year 100. Broadly, high resource scenarios are less rich than low resource scenarios. Further, herbivory of either generalist or preferential type reduces richness regardless of belowground resources or seed bank, although low resource scenarios are considerably less impacted than high resource scenarios. A long-term seed bank reduces the variability between replicates.

Resistance, recovery rate, and time to recover for intense disturbances



Change from no-disturbance control in Shannon diversity, recovery rate (Shannon units / year), and time to recovery for simulations with a disturbance level of 100% mortality and a transient seed bank for grasslands disturbed *before* seed dispersal (A) and *after* seed dispersal (B).

Biomass distributions without disturbance

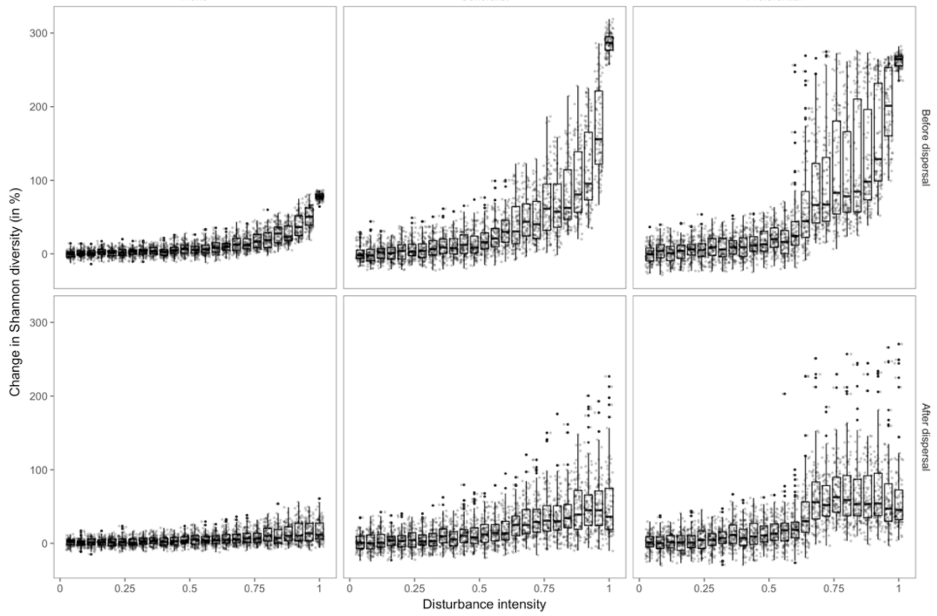


Total biomass per PFT ($g \cdot m^{-2}$) for the control communities, not subject to the disturbance regime. Individuals are divided into their size-classes, with the largest composing the highest plant size percentile. Colors indicated species identity. (A) shows grasslands *with transient seed banks* while (B) reflects grasslands *with long-term seed banks*.

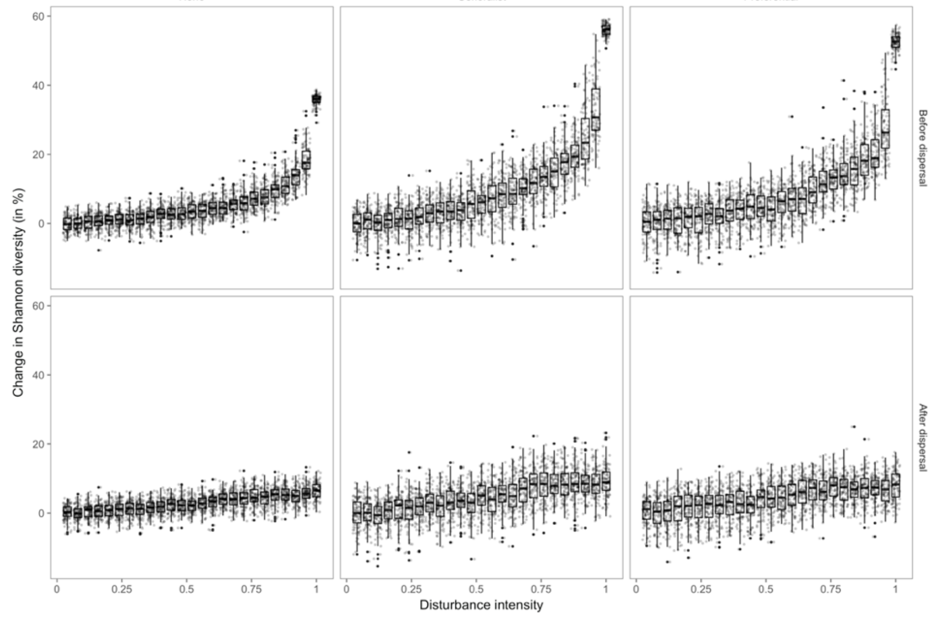
Resistance raw data

Resistance raw data: Transient seed bank

A. High resources

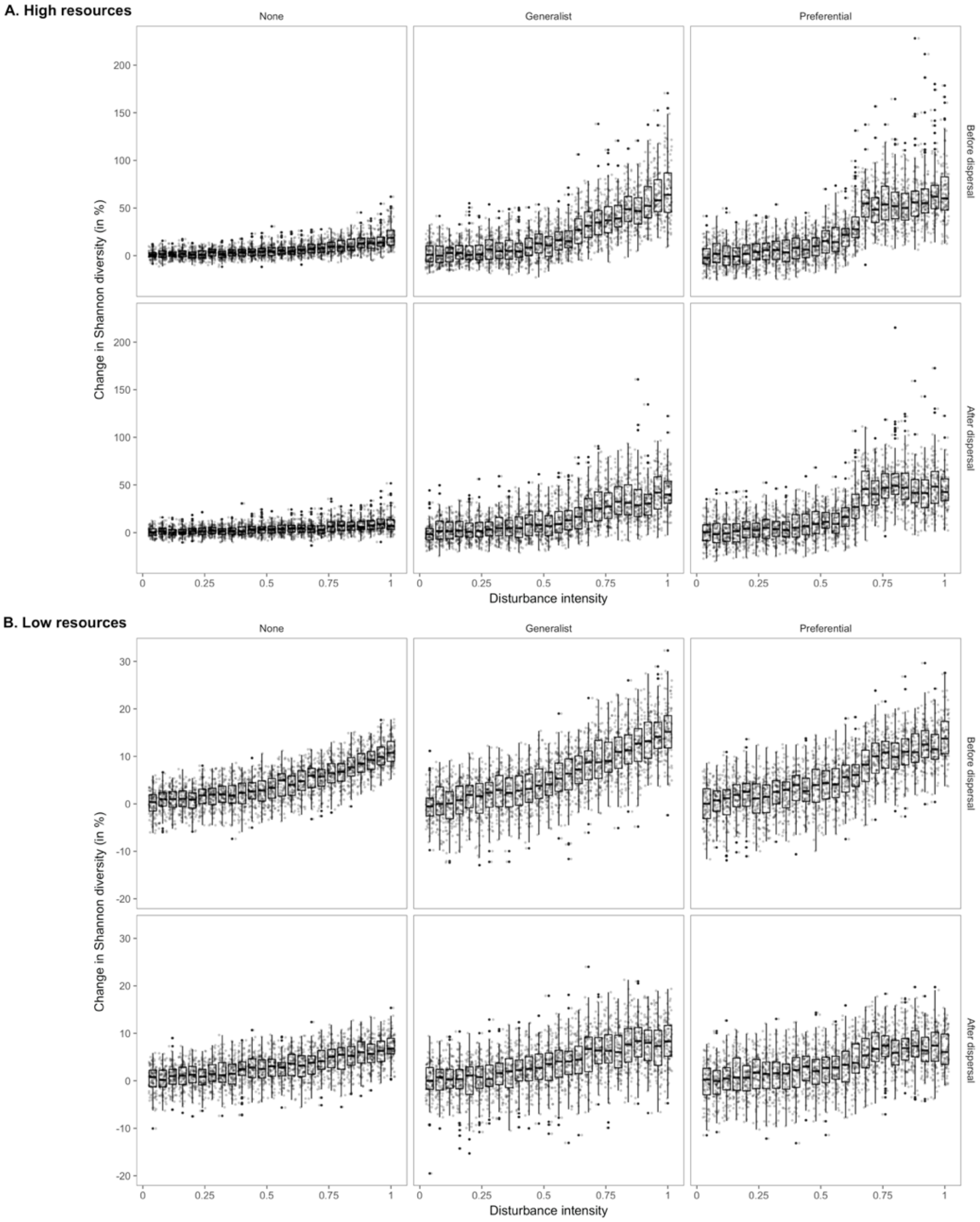


B. Low resources



With a transient seed bank and disturbance before dispersal, there is very little variation between repetitions, as in effect this parameterization is a "reset" to initialization, except with a disproportionately high belowground herbivory pressure. With high belowground resources, the impact of preferential herbivory can, starting with a relatively low disturbance intensity (~ 0.60) lead to dramatically different communities after the disturbance, seen through a very large increase in its skew towards high percent change. Interestingly, although the median change in Shannon diversity is always positive, on a per-replicate basis, small disturbances to many simulated grasslands decrease Shannon diversity in relation to the control—no herbivory—simulations.

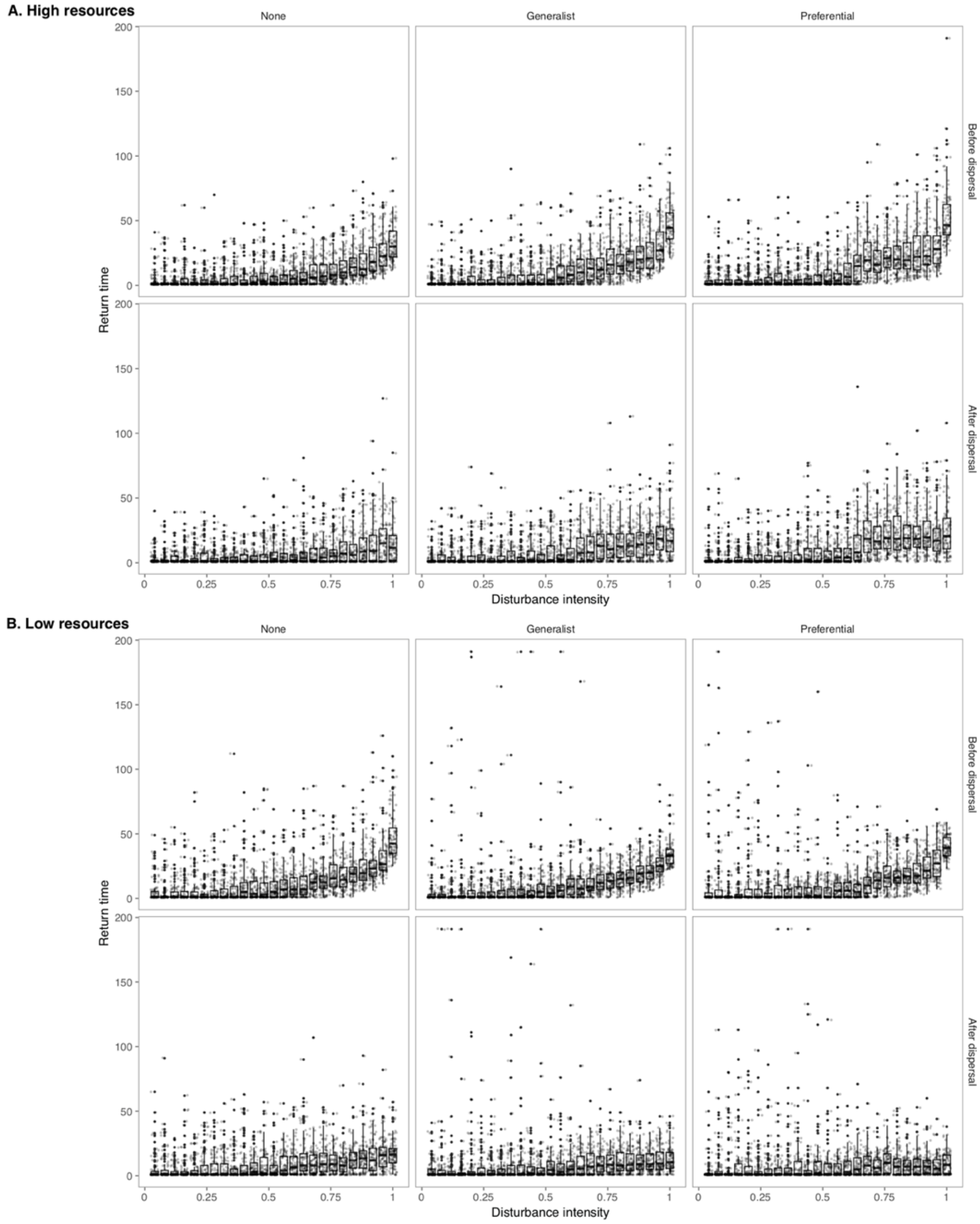
Resistance raw data: Long-term seed bank



With a long-term seed bank, the extreme effects of intense disturbances before dispersal are significantly mitigated, although the general shape of response is consistent, particularly for high resources grasslands. For low resource grasslands, before dispersal disturbances actually only increase in their percent change linearly with disturbance intensity, rather than super-linearly. Moreover, disturbances after dispersal have significantly more replicates Shannon diversity actually decreases in relation to the control—no herbivory—simulations.

Recovery raw data

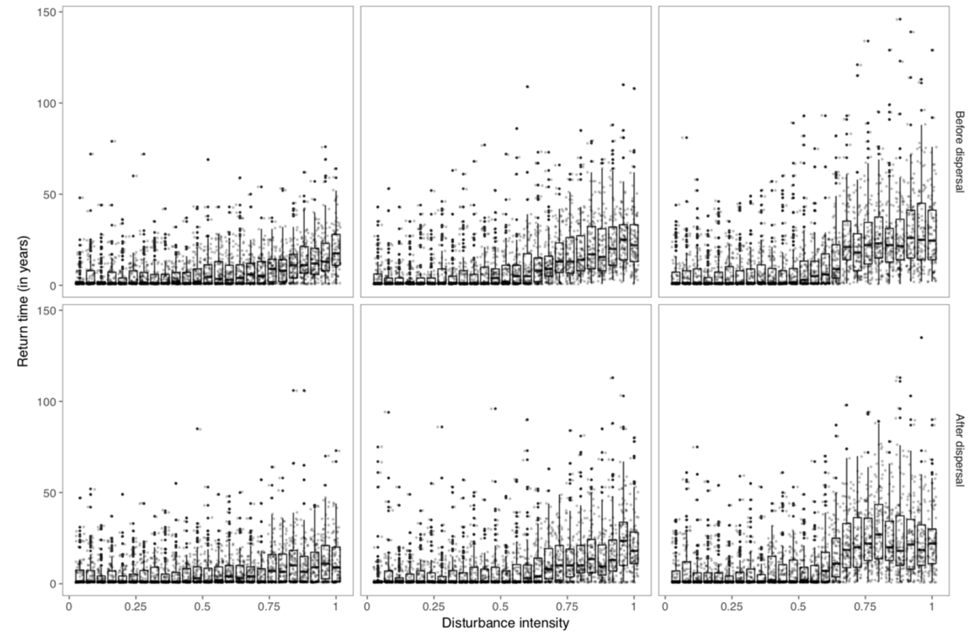
Recovery raw data: Transient seed bank



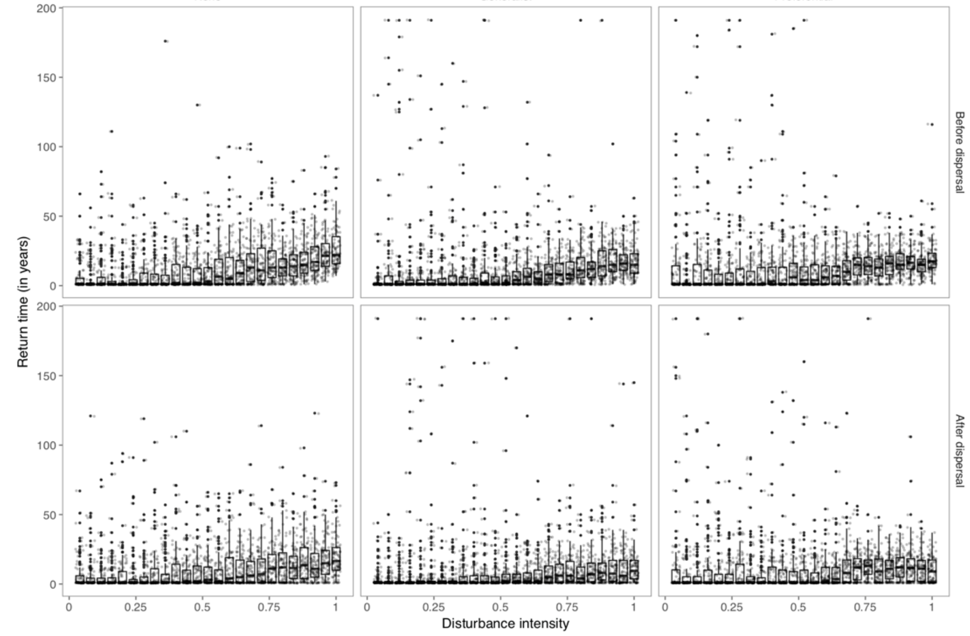
A main aspect discernable only through the raw recovery data is that, primarily with low resource grasslands, a relatively large number of simulations actually take a significantly longer period of time to return to control-diversity. In some cases, they may never return. This indicates that, especially with low-disturbance levels, a small number of communities follow fundamentally different successional pathways than their control—no herbivory—counterparts. Other than this effect, the raw recovery data is generally consistent with the resistance dataset in their pattern.

Recovery raw data: Long-term seed bank

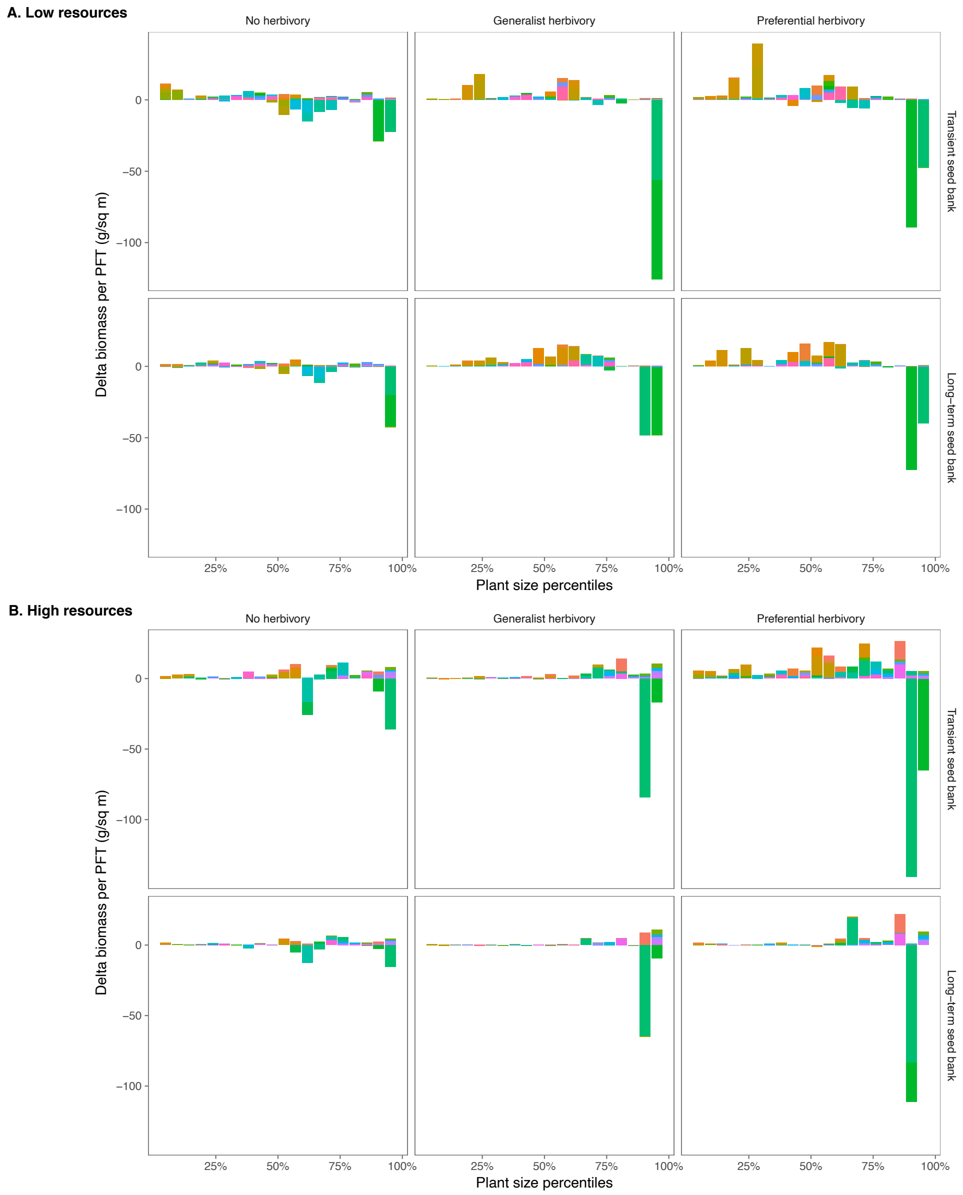
A. High resources



B. Low resources



Plant community size composition: after dispersal disturbance



The patterns of plant community composition were very similar regardless of whether the disturbance occurred before or after seed dispersal. However, disturbances before dispersal were more extreme in their effect. After dispersal, although the “winners” and “losers” were consistent, the changes to their biomass were less pronounced.

8.4 While shoot herbivory mitigates, root herbivory exacerbates eutrophication's impact on diversity in a grassland model

8.4.1 Supplemental Material B: Additional graphs

Replication of Borgström et al. (2017)—Pielou's Evenness (E)

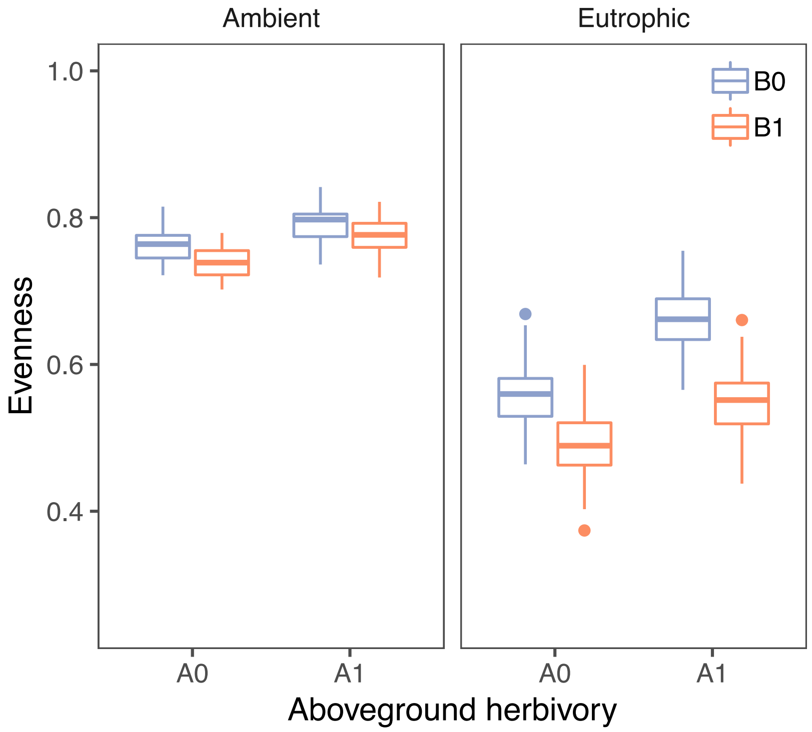


Figure B1: Pielou's evenness after three years of experimental treatment. Borgstrom et al. (2017) calculates Pielou's evenness, rather than Shannon diversity, in their mesocosm experiments. This variable differs from raw Shannon diversity in that it is normalized to log(S), where S is the number of species present in the community. Although numerous differences between study systems will complicate the direct comparison of our data to theirs, the main interactions remain consistent: Aboveground herbivores help maintain diversity, while belowground herbivores and eutrophication generally diminish it. One of the central differences between these two datasets is the dramatically higher evenness seen in the ambient resource simulations. The default resource setting of IBC-grass (60 BRes, 100 ARes) generally leads to rich (~ 40 species/m^2) communities. For ambient resources, while above- and belowground herbivory treatments alter the number of species within the plots, they do not influence the evenness of the resultant communities nearly as much. A0 – Aboveground herbivory removed, A1 – Aboveground herbivory present; B0 – Belowground herbivory removed, B1 – Belowground herbivory present.

Borgström, P., J. Strengbom, L. Marini, M. Viketoft, and R. Bommarco. 2017. Above- and belowground insect herbivory modifies the response of a grassland plant community to nitrogen eutrophication. Ecology 98:545–554.

Effect of herbivore preference on the dominant PFT's total root biomass

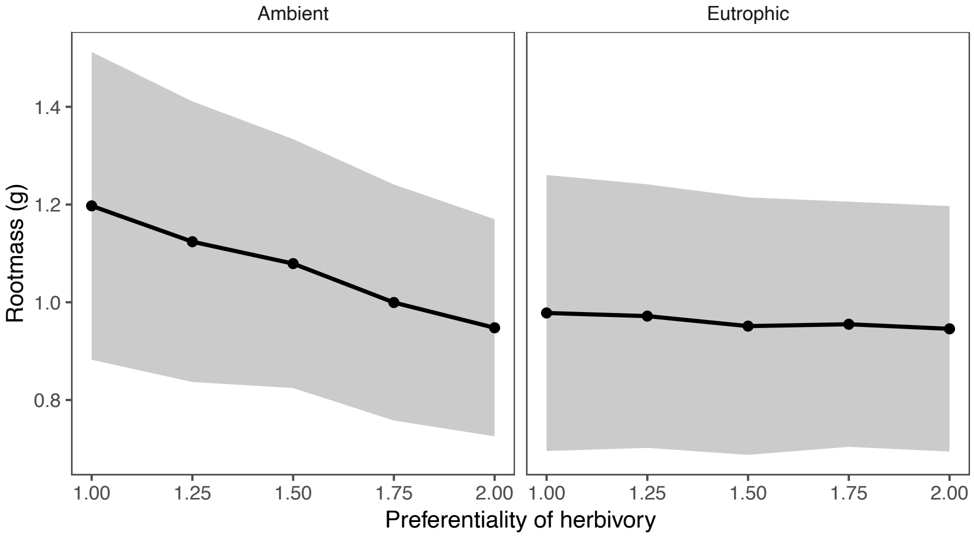


Figure B2: Change in root biomass of the dominant PFT, defined as the PFT with the most root biomass in simulations with generalist belowground herbivores. Ribbons indicate 1σ around the mean.

Standardized test of recovery algorithm

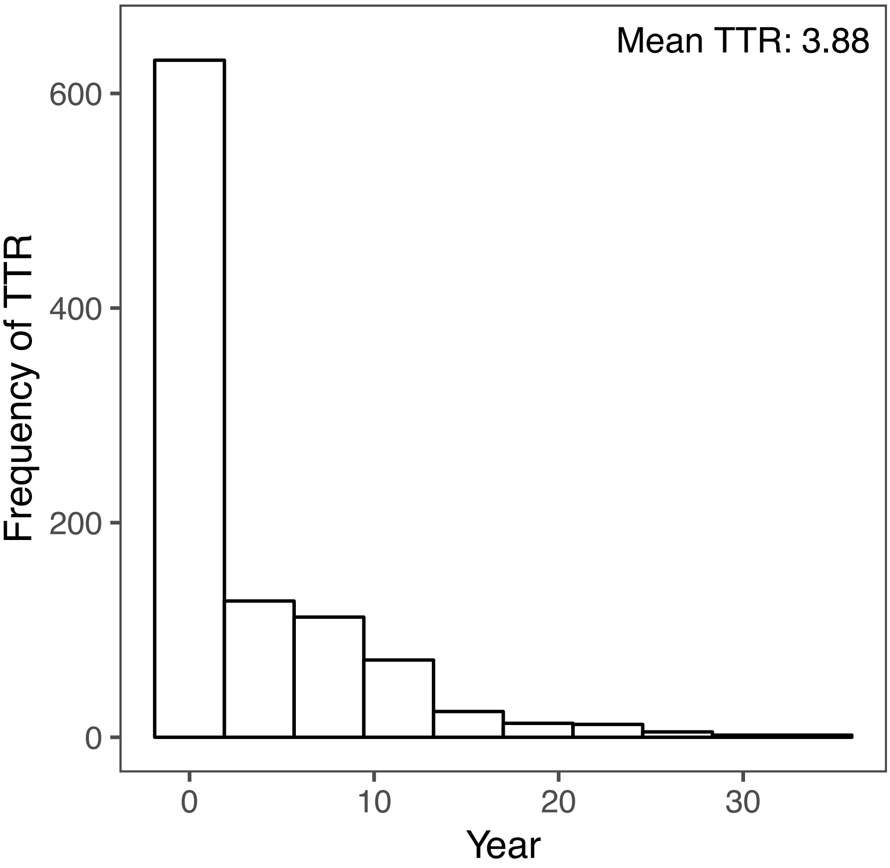


Figure B3: Results of running the recovery algorithm (deriving the TTR) on a timeseries dataset of 1000 replicates derived from sampling a Gaussian distribution ($\mu = 0$, $\sigma = 1$). The average number of years required for a replicate to return to within 2σ of the mean and stay within this window for 10 years was 3.8 years.

Effect of herbivore preference on recovery

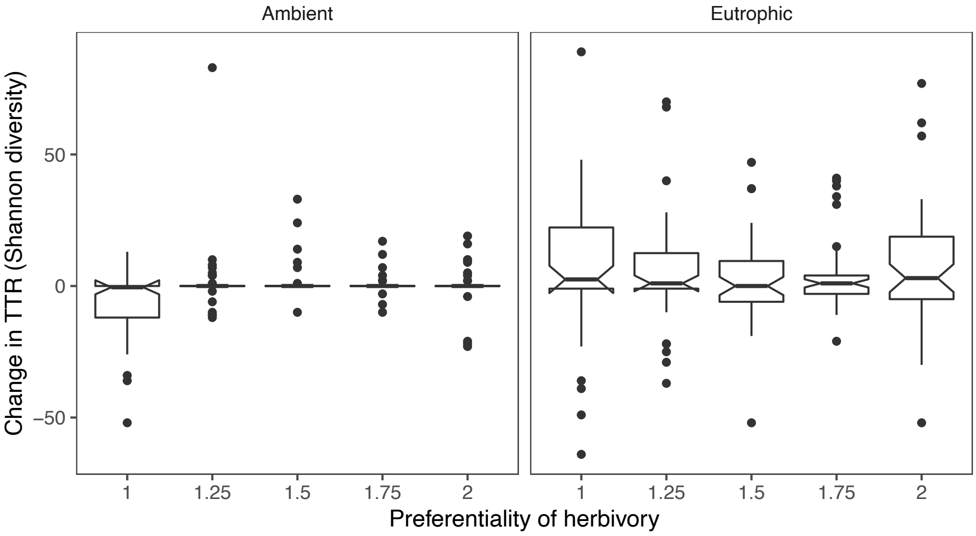


Figure B4: Change in time to return (measured in years; TTR) in Shannon diversity between simulations with belowground herbivores and those without. Aboveground herbivory is set to present; Notches reflect 95% confidence intervals of the median.