

Research article

Resource inequality limits transfer of nutrients from soils to plants in experimental grassland

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A system's functioning is influenced not only by resource availability but also, likely, by resource inequality. In ecological systems most experimental manipulations of resource availability typically focused on homogeneous resource addition, or spatial heterogeneity of resources in a qualitative sense. Here, we test whether resource inequality per se influences the diversity and functioning of model grassland communities in an Ecotron experiment. Specifically, we experimentally manipulated resource area and concentration (two quantitative components of heterogeneity) to create an inequality gradient quantified by the Gini coefficient. Moreover, we examine whether the association with mycorrhizal fungi can mediate the influence of resource inequality on nutrient dynamics between soils, plants and leachate. We show that resource inequality significantly increased phosphorus leaching and reduced plant phosphorus pools aboveground. Some plant species were more sensitive to inequality than others, as there were shifts in the relative dominance of the two species that produced the most biomass (*Plantago lanceolata* and *Holcus lanatus*). Taken together, shifts in plant community composition may provide cues that indicate changes in nutrient dynamics; even though overall plant biomass was not affected, and plant diversity showed a significant decline only during the first phase of the experiment. The enrichment with mycorrhiza did not significantly influence plant biomass and diversity or nutrient concentrations above- and belowground. These results demonstrate that inequality is an essential component in ecological systems determining nutrient availability for plants as well as nutrient use efficiency of plants. An important implication is that spatial



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inequality of resources in natural landscapes may alter community compositions and predictions of phosphorus uptake that are based on resource input alone.

Keywords: Ecosystem functioning, ecotone, Gini coefficient, grassland, nutrient dynamics, resource inequality

Introduction

Natural and managed ecosystems worldwide are characterized by spatially unequal distribution of resources which manifests itself in resource-poor to resource-rich patches, (Stein et al. 2014, Macdonald and Johnson 2015, Xue et al. 2019). Plant communities may respond to this resource variability in ways that fundamentally differ from homogeneous changes in resource supply, particularly concerning their ability to take up resources from water and soil into plant biomass. Spatial variability often has been assessed in the context of influences of heterogeneity or patchiness on plant diversity, plant biomass, or both (Maestre et al. 2006, Maestre and Reynolds 2006, Rajaniemi 2011, Gazol et al. 2013, Xue et al. 2019, 2021, 2023). Sometimes used synonymously, each term has positive and negative attributes with respect to quantifying variation in resources and environments across landscapes (Fig. 1). Resource inequality likely also influences plant diversity and ecosystem functioning, yet, in contrast to patchiness and heterogeneity, direct causal relationships between resource inequality and ecosystem responses have rarely been quantified in ecological systems. To fill this gap, we propose using the Gini coefficient, a well-established measure of inequality initially developed for assessing income disparity (Gini 1921), to calculate the deviation of equal resource distribution. In ecological systems, as demonstrated in economics, resource inequality may lead to polarization of growth strategies and low system productivity (Ostry et al. 2014, Berg et al. 2018), likely translating into impacts on nutrient cycling.

Decades of research have demonstrated that additional nutrient resource subsidies affect the diversity, stability and functioning of ecological systems (Tilman et al. 2006, Harpole et al. 2016, Xue et al. 2023). For example, over-fertilization leads to leaching of nitrates into groundwater or run-off of phosphates into surface waters, while burning of fossil fuels causes atmospheric deposition of nutrients (Peñuelas et al. 2013), affecting natural ecosystems and threatening their biological diversity and health (Isbell et al. 2013, Peñuelas et al. 2013, Köthe et al. 2023). In contrast, other areas have become depleted of nutrient resources. First observations of declines in resource availability (in particular nitrogen) have been reported in terrestrial ecosystems that are not subject to high levels of nitrogen deposition (e.g. parts of sub-Saharan Africa) caused by elevated atmospheric CO₂ or altered precipitation. Those might be driven by a rising demand for N of organisms (Mason et al. 2022). What we observe on global scales, may also be found on patch scale.

Macronutrients such as nitrogen (N), phosphorus (P), and potassium (K) are crucial for plant survival and development

(Elser et al. 2010), with plants having diverse nutrient acquisition strategies, e.g., physiological and morphological adaptation of their root system (Hodge 2004, Wang et al. 2022) or symbiotic associations with mycorrhizal fungi, for efficient foraging and uptake and transfer of these limiting nutrients from soils and soil water (van der Heijden et al. 1998, Phillips et al. 2013, Weigelt et al. 2021). Mycorrhizal fungi benefit plant growth through their extended mycelium network, which enables them to forage in nutrient-rich patches that plant roots cannot directly exploit, thus providing water and nutrients to their interaction partners (Tibbett 2000, Jakobsen and Hammer 2015, Chen et al. 2018, Martin and van der Heijden 2024). By doing so, arbuscular mycorrhizal fungi, a mycorrhizal type associated with a broad range of land plant species such as grasses and herbs (Smith and Read 2008), affect the response of plant coexistence to heterogeneity via responses in root and hyphal morphology (Farley and Fitter 1999, Chen et al. 2018). Further, the ability of arbuscular mycorrhiza to respond to resource inequality by transferring P from nutrient-rich to nutrient-poor patches was demonstrated using quantum-dot-tagged (fluorescence-labeled) P (Whiteside et al. 2019). These observations suggest that mycorrhizal fungi may mitigate the effects of resource inequality on plant communities.

Both nutrient deficiency and excess nutrients can lead to plant physiological stress and damage, as well as the inhibition of plant growth (Bobbink 1991, Barker and Pilbeam 2015, Malhotra et al. 2018). Consequently, most plants (and mycorrhizae) have ideal nutrient conditions or nutrient niches where they can thrive (Gerz et al. 2016, Harpole et al. 2016). It has often been argued that the addition of surplus resources into an ecosystem will cause above- and belowground species diversity to decline because increased dominance of a few well-suited species leads to a decrease in the number of coexisting species (Manning et al. 2008, Hautier et al. 2009, Harpole et al. 2016, Ben-Hur and Kadmon 2020). Here, plants may compete not only for nutrients, but also for light or space (Hautier et al. 2009, Harpole et al. 2016, Eskelinen et al. 2022). A decline in diversity can change community productivity and influence nutrient distribution between plants, soils and water, for example, by reduced exploitation of resource niches (Tilman et al. 2014). Insights into the consequences of lost nutrient niches have been demonstrated based on testing experimentally the response to homogenous nutrient additions (Harpole et al. 2016). Yet, this approach potentially overlooks the key roles of changes in heterogeneity (Eisenhauer et al. 2023), niche area (Ben-Hur and Kadmon 2020), and changes in resource concentration that likely play a key role determining the consequences of resource inequality for productivity, diversity and transfer

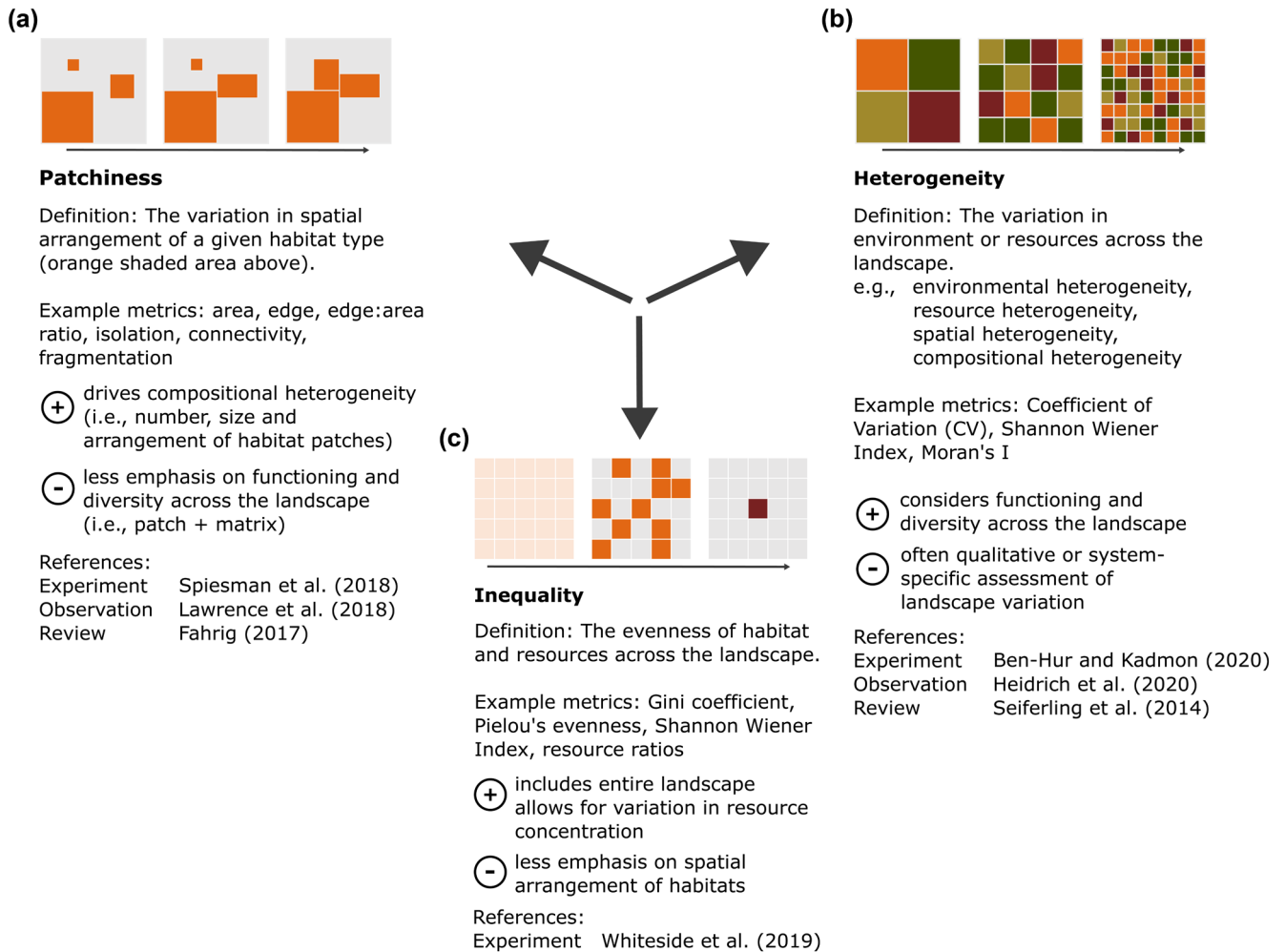


Figure 1. Characterization of three terms used to describe spatially variable environments: patchiness, heterogeneity and inequality. Sometimes used synonymously, these terms also have unique connotations that have strengths and weaknesses with respect to their ability to quantitatively describe variation in the spatial distribution of habitat and resources in the environment. Although spatial variation can be represented by continuous gradients in habitat configuration (see schematic drawings), landscape experiments often consist of a few levels (mostly two to three) of patchiness or heterogeneity (Maestre et al. 2006, Gazol et al. 2013, Xue et al. 2023), leaving open questions about the influence of intermediate levels. Here, we highlight examples of observational and experimental studies that examine spatial variability using gradient-based designs.

of nutrients between aboveground biomass, roots, soil and leachate (Fig. 2). Yet, the consequences of resource inequality (as a gradient in tradeoff between resource area and resource concentration, while the overall amount of resources per system remains the same) on plant community productivity and nutrient distribution has rarely been studied directly using spatially variable environments.

Here, we present the results of a novel experiment where we directly manipulated resource inequality and addition of mycorrhizal fungi to examine the consequences for grassland plant diversity and ecosystem function. Due to challenges controlling environmental variability at broader spatial scales, landscape experiments are often conducted in micro- or mesocosms (Jenerette and Shen 2012, Wiersma 2022). We used a set of mesocosms (EcoUnits) in an Ecotron facility and tested the following hypotheses:

H1) Highest resource inequality will result in the lowest diversity (Fig. 2g) and the lowest productivity as firstly, excess nutrients can lead to plant physiological stress and damage, or secondly, most plants growing in unfertilized plots cannot access nutrients (Fig. 2h). Accordingly, less plant biomass will lead to reduced storage of nutrients in aboveground biomass (Fig. 2h).

H2) In contrast, the highest concentrations of nutrients will be retained in soils (Fig. 2i) or lost via leachate when resource inequality is highest (Fig. 2j).

H3) Mycorrhiza will mitigate the hypothesized effects of resource inequality (H1, H2), by enhancing resource exploration.

H4) Variation observed in resource pools (e.g. leachate, soil, and plants) will explain changes in linked plant species productivity.

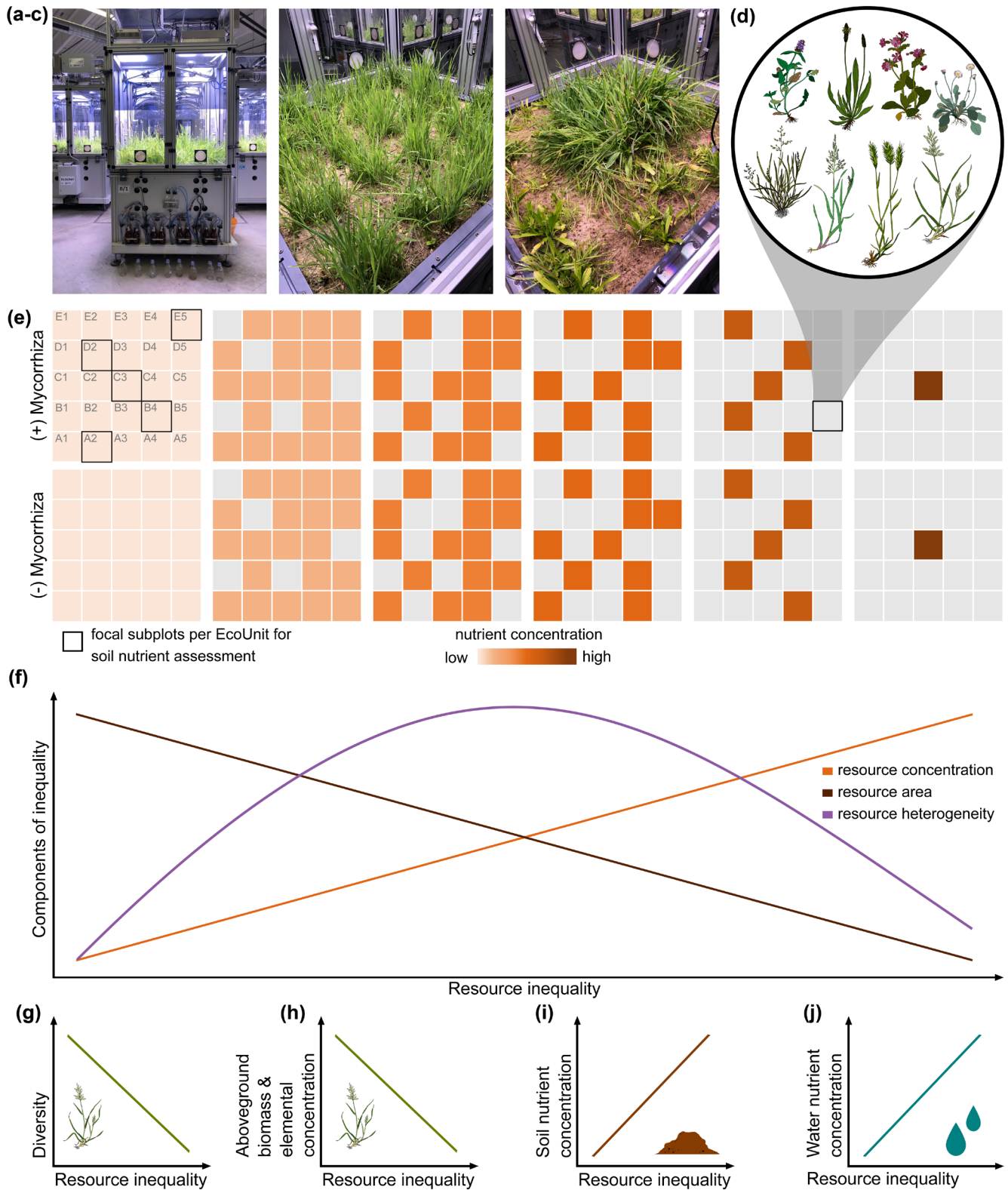


Figure 2. Overview of an experiment designed to directly quantify the relationship between resource inequality and ecosystem functioning. (a) an external view of an EcoUnit; (b) example picture showing plant community in low inequality (i.e. homogeneous environment); (c) example picture showing plant growth response in high inequality environment; (d) subset shows plant species sown into each of twenty-five subplots subjected to a gradient in resource inequality (four grasses: *Anthoxanthum odoratum*, *Bromus hordeaceus*, *Holcus lanatus*, *Poa annua* and four herbaceous species: *Bellis perennis*, *Plantago lanceolata*, *Prunella vulgaris*, *Silene dioica*); (e) a gradient of resource inequality

Figure 2. Continued

across six ecosystems consisting of 25 habitat patches (subplots) that either have nutrients withheld (depicted in gray) or nutrients added (depicted in orange). Each ecosystem receives the same total resource subsidy, but resource inequality differs according to variation in the area (depicted as the number of habitat patches subsidized) and the concentration of the subsidy (increased resource concentration is depicted by darker shades of orange) (Supporting information). Soil for assessment of soil nutrients was sampled in five focal subplots within each EcoUnit (depicted in the first EcoUnit). (f) At least three aspects of resource distribution (resource concentration, resource area and resource heterogeneity) vary across the hypothetical gradient in resource inequality. (g) Only few species may be able to cope with this strong inequality in nutrient availability. Therefore, a decrease in resource heterogeneity may be associated with community diversity loss. (h) Further, the highest resource inequality, with a heavy nutrient surplus in one subplot, while the other subplots receive no nutrients, might have a toxic effect on plant communities, strongly reducing the overall growth and biomass production. Further, low nutrient availability in unfertilized subplots might also contribute to reduced productivity of the plant community. (i) Subsequently, fewer nutrient niches in soils will be exploited, which enhances either storage of nutrients in the soil or (j) nutrient losses from the system with leachate.

Material and methods

Experimental facility. The experiment was set up in the iDiv Ecotron, a mesocosm facility located in Bad Lauchstädt, Germany (for more details on the experimental facility, see [Eisenhauer and Türke 2018](#), [Schmidt et al. 2021](#)). Briefly, EcoUnits consist of an upper compartment $1.46 \times 1.46 \times 1.50$ m (L $\times$ W $\times$ H) that contains LED lights and a precipitation system and a lower compartment $1.24 \times 1.24 \times 0.80$ m (L $\times$ W $\times$ H), 1.538 m², that can be filled with soil and is fitted with a soil cooling system to establish a near natural temperature gradient across the soil depth profile.

Experimental design. To test the influence of resource inequality on grassland plant diversity and ecosystem functioning (i.e. nutrients in water drained away from soil (hereafter: leachate), soil and plants, we established a six-level gradient-based design using 12 EcoUnits. This allowed us to increase prediction success by maximizing the number of levels of one factor (resource inequality) at the expense of replication at a limited number of levels ([Kreyling et al. 2018](#)). Although it was subsequently argued that such designs can lead to biased parameter estimates ([Chalcraft 2019](#)), several observational and experimental studies support the utility of such regression-based designs for hypothesis testing in general ([Somerfield et al. 2002](#), [Dunne et al. 2004](#), [Larios and Maron 2021](#)) and in landscape experiments in particular ([Fig. 1](#)).

Mycorrhizal treatment. The EcoUnits were filled with 1.23 m³ non-sterilized, low-nutrient soil ([Vetterlein et al. 2021](#)). The soil mainly consisted of a medium quartz sand fraction with a clay proportion of 5% and no carbonate content. On 20 May 2021, 500 g mycorrhizal inoculum (BioMycTM Vital – n.d., in total containing at least 100 000 infectious spores and parts of hyphae) was evenly distributed across the surface of six randomly selected EcoUnits. In the other six EcoUnits, no mycorrhizal inoculum was added. The inoculum contained spores and further organs of arbuscular fungi, mainly the species *Glomus intraradices* (Glomerales), which, as a generalist species, associates with many herbaceous and grass species ([Eisenhauer et al. 2009](#), [Sabais et al. 2012](#)). Subsequently, 0.76 m³ (i.e. 5 cm depth) soil was added to the surface of all EcoUnits. After allowing time for germination and growth of the plant community (26 August 2021), a second 500 g dose of mycorrhizal inoculum was added to the soil surface.

Nutrient inequality. To establish the resource inequality gradient, the EcoUnits were conceptually divided into 25 subplots (i.e. no physical barriers were imposed, [Fig. 2e](#)). The subplots were identified in an x-y coordinate system with letters ranging from A to E across the x-axis and numbers ranging from 1 to 5 across the y-axis, such that individual subplots were named A1 through E5. On 26 May 2021, a cocktail of NPK and micronutrient fertilizers was added by elemental mass as in the Nutrient Network protocol ([Borer et al. 2014](#)) (10 g m⁻² year⁻¹ by elemental mass at the EcoUnit level). Across the gradient of increasing resource inequality, nutrients were distributed into 25, 20, 15, 10, 5 or 1 subplot within EcoUnits (see experimental design in [Fig. 2e](#)). Because the overall nutrient allocation per EcoUnit was fixed, increasing inequality means that fewer fertilized subplots received an increasing amount of nutrients ([Fig. 2e](#)). Consequently, at highest inequality, a single subplot within the EcoUnit received 25×10 g m⁻² year⁻¹; at lowest inequality (i.e. complete equality), all subplots equally received $1/25$ of the dose (see the Supporting information for details).

Plant community. To establish plant communities, consistent combinations of seeds were sown evenly into each of the 25 subplots in all 12 EcoUnits on 27 May 2021. To enhance the potential of successful germination, seeds were also sown on a second date, 9 June 2021. Communities were chosen to include four grass species (*Anthoxanthum odoratum*, *Bromus hordeaceus*, *Holcus lanatus*, *Poa annua*) and four herbaceous species (*Bellis perennis*, *Plantago lanceolata*, *Prunella vulgaris*, *Silene dioica*), common to central Europe. These species were chosen to include species with varying growth forms from rosette to creeping lifestyle and different root strategies (e.g. tap roots to fibrous roots).

Environmental settings. Throughout the experiment, each EcoUnit received 700 ml daily precipitation distributed equally across all subplots. Day/night cycles of 12:8 h were established to be consistent with natural daylight conditions in the region.

Sampling regime. To assess the effects of resource inequality on plant diversity and nutrient transfer, samples from soil, leachate, and above- and belowground plant biomass were collected as described below. To provide an evaluation that was robust to potential temporal variations, multiple samples of each response variable were taken at time and spatial scales that provided a practical balance between expected

variation, experimental work-load, and destructiveness of the sampling method. For measurements, like aboveground plant biomass, it was possible to sample the entire EcoUnit. For other destructive or labor-intensive measurements, like soil chemistry, samples were taken randomly within the 'focal subplots' (i.e. subplots A2, B4, C3, D2, E5; Fig. 2e). These focal subplots were chosen to overcome potential bias in the number of fertilized subplots included. Specifically, they have an equal proportion of subplots with nutrients added, and withheld, as the whole EcoUnit inequality treatment. For example, when five of twenty-five subplots received fertilizer (20%), one of five focal subplots received fertilizer (20%). Additionally, to account for any potential spatial heterogeneity within the EcoUnits, the focal subplots include subplots in the center, middle, and edge of the EcoUnit.

Aboveground biomass. To assess plant community productivity, all aboveground plant biomass was clipped just above the soil surface in weeks 12 and 24 of the experiment, corresponding to the first and second harvest (August 16–25, 2021 and November 08–16, 2021). This cutting frequency is within the range of typical grassland management mowing regimes in the region (Roscher et al. 2004, Weisser et al. 2017, Schädler et al. 2019). Following clipping, all plant biomass was sorted into species, oven-dried at 50°C, and weighed. Plant biomass is reported as the sum of biomass across all subplots and scaled from EcoUnit surface area to m².

Aboveground plant elemental analysis (CNPK). Plants in the five focal subplots per EcoUnit were reserved for other analyses not presented here (i.e. species-specific elemental analyses). Therefore, for twenty out of the twenty-five subplots, dried biomass of the plant community was cut, homogenized, and ground with a ball mill (MM 400, Retsch, Haan, Germany) (20 subplots × 12 EcoUnits × 2 harvests = 480 samples). Chromatographic analyses of C and N were done by high-temperature combustion and subsequent thermal conductivity detection using an elemental analyzer vario EL cube (Elementar Analysensysteme GmbH, Langensfeld, Germany). The values were determined according to the response of an Acetanilide standard (10.35% N, 71.09% C) with a precision of the measurements of ± 0.1% for C and ± 0.03% for N.

Processing many samples for wet chemical analyses of phosphorus (P) and potassium (K) in aboveground biomass is labor-intensive. Therefore, we used near-infrared reflectance spectroscopy (NIRS) with Bagging-CARS-PLS models for nutrient prediction, a method proven reliable for a wide range of grassland species (Bassi et al. 2023). Spectral data were obtained for all samples using a Multi-Purpose FT-NIR-Analyzer (MPA, Bruker Corporation). Each sample was scanned three times in reflectance mode to retrieve the NIR spectra at 8 cm⁻¹ resolution. To increase the signal-to-noise ratio in the data, the three replicates were averaged and spectra were masked to 9090–4000 cm⁻¹ range. Standard normal variate transformation (SNV) was applied to the spectra to reduce scattering effects caused by e.g. varying sample particle size (Elle et al. 2019). Altogether, 120 samples (Supporting information) were available for the calibration

and validation of the Bagging-CARS-PLS models. Two samples were excluded as outliers from the calibration data set prior to prediction. The model repeatedly (100 times) creates new datasets via random sampling with replacement from the initial dataset, which were used to calibrate 100 CARS-PLS models. For each of the randomly drawn datasets, the leftover samples, out-of-bag (OOB) samples, constituting approximately one-third of the total, were used for model validation. In this process, each sample is predicted only by those models in which it was not already used for calibration. The resulting OOB predictions of all models were averaged by the median and used to calculate model accuracy metrics achieved in validation. To estimate P and K of the remaining 360 samples we used the median prediction of the 100 generated model for P and K. Prediction. Observed versus median out of bag predictions in internal model validation of predicted P and K concentration can be found in the Supporting information.

Aboveground biomass C, N and P pools (g m⁻²) are the product of aboveground plant biomass (g) and the respective elemental concentration (mg kg⁻¹).

Soil chemistry. In soil nitrate (NO₃⁻; mg kg⁻¹), ammonium (NH₄⁺; mg kg⁻¹), phosphate (PO₄³⁻; mg kg⁻¹), potassium (K⁺; mg kg⁻¹), pH, and soil moisture were assessed every six weeks for twenty-four weeks (four sample dates total: 6 July, 12 August, 27 September and 4 November 2021). On each sample date, five soil samples (2.5 cm diameter × 10 cm depth) were taken from each of the five focal subplots in each EcoUnit. Each sample was homogenized by sieving through a 2 mm mesh, and then divided into two parts that were either stored at -20°C until nutrient analyses or stored at 4°C for soil pH measurements. We are aware that freezing soil samples may introduce freeze-thaw effects, potentially altering absolute nutrient concentrations through microbial lysis or chemical changes. However, these effects are consistent across all samples and therefore do not affect the relative patterns of nutrient availability. Soil mineral nitrogen (nitrate and ammonium) was quantified using flow injection analysis (FIStar 5000, Foss GmbH). In brief, 5 g of fresh soil was mixed with 20 ml of 1 M KCl solution, shaken for 1 h on a horizontal shaker, and filtered through a 0.45 µm cellulose nitrate filter (Sartorius Biolab Products). Available phosphate and potassium were extracted from the soil using a double lactate solution (1:50 w/v) at pH 3.6. Phosphate concentrations were determined colorimetrically by the molybdenum blue method (Murphy and Riley 1962), while potassium levels were measured with a K⁺-selective electrode (perfection, Mettler Toledo). A halogen moisture analyzer (Mettler Toledo) was employed to ascertain the gravimetric soil water content, which was then used to calculate available nutrient concentrations per gram of dry soil. For measurements of soil pH, 10 g of air-dried soil from each sample were suspended in 25 ml CaCl₂-solution (0.01 mol l⁻¹), stirred, left for one hour, stirred again, and measured with a probe (Orion Star A211 pH-Benchtop Meter; Orion ROSS Ultra Triode pH/ATC-Kombinationselektrode).

Leachate chemistry. Leachate was collected from leachate collection bottles that store leachate exported from the bottom

of the lysimeters across 24 h every six weeks for 24 weeks (four sample dates total: 6 July, 12 August, 27 September and 4 November 2021). The leachate samples were stored at -20°C until analysis. Plant-available nutrients nitrate (NO_3^- ; mg l^{-1}), ammonium (NH_4^+ ; mg l^{-1}), phosphate (PO_4^{3-} ; mg l^{-1}), and potassium (K^+ ; mg l^{-1}) were measured simultaneously in a two channel on chromatography system (IC-930, Metrohm Deutschland). The frozen leachate samples were thawed overnight in the cooler, and 15 ml of the solution was filtered to $0.45\text{ }\mu\text{m}$. Twenty μl of the filtered solution was used for analysis. The linear range for the measurement of each ion was 0.1 to 10 mg ion l^{-1} ; higher concentrations were automatically diluted. Since ammonium concentrations in soil were below the detection threshold for most samples, we excluded the data from the analyses.

To allow for consistency of comparisons with plant biomass harvests, which were conducted in weeks 12 (harvest 1) and 24 (harvest 2), soil and leachate nutrient concentrations were averaged per EcoUnit and then also averaged across weeks 6 and 12 (considered as the first harvest), and across week 18 and 24 (considered as second harvest).

Root sampling. Plant roots were sampled using soil cores ($2.5\text{ cm diameter} \times 10\text{ cm depth}$) in the five focal subplots per EcoUnit, during the final harvest (week 24). The soil samples were stored in plastic bags at 5°C and processed within two weeks in the laboratory of the University of Göttingen. To determine root mass, the samples were cleaned from soil residues by washing the root material with a sieve and subsequently, used a stereomicroscope to remove remaining soil particles and remove dead roots. The roots were dried at 60°C and ground with a ball mill. C and N concentrations were determined chromatographically by high-temperature combustion and subsequent thermal conductivity detection using an elemental analyzer vario EL cube (Elementar Analysensysteme GmbH).

Assessment of mycorrhizal colonization. A subset of the roots sampled during the second harvest were examined for mycorrhizal colonization. For this the roots were first cleaned in a water bath at 80°C with 10% (w/v) KOH for approx. 45 min (depending on root thickness) and then rinsed well with tap water. The roots were then stained with ink (50 ml Black Parkers Quink mixed with 950 ml vinegar (5% acetic acid) (1:20)). For this, the roots were covered with the solution and heated in a water bath at 80°C for 10 min. Afterwards, the roots were rinsed with tap water mixed with a few drops of acetic acid (5%) until the water was clear. The roots were then stored in water with a few drops of acetic acid (5%) until the mycorrhizal colonization assessment. For this, ten small root pieces were cut from each sample (one sample per focal subplot per EcoUnit). The root pieces were examined under the microscope for fungal hyphae, vesicles or arbuscules using the gridline intersect method (McGonigle et al. 1990).

Statistical analyses

All statistical analyses were performed in R ver.4.3 (www.r-project.org). To test linear hypotheses (Fig. 2g–j) linear

mixed-effects models (type I sum of squares) were used to assess the influence of treatments on responses of plant biomass, elemental and nutrient concentrations, and elemental pools (R-package ‘nlme’ ver. 3.1-164; Pinheiro and Bates 2000). Fixed effects included resource inequality (continuous with 6 levels, indexed as Gini coefficient), mycorrhizal treatment (categorical, 2 levels: mycorrhizal fungi added (M), mycorrhizal fungi withheld (C)), harvest (categorical, two harvests: harvest 1 in week 12 and harvest 2 in week 24), and their interactive effects. To test for species identity effects an additional model was fitted, using the fixed effects mentioned above plus species as fixed effect. Further, species-wise testing of the treatment effects was conducted using species-specific aboveground biomasses as response variables. To account for repeated measures, EcoUnit (categorical, 12 levels) was included as a random effect. Samples taken on subplot level were summed (biomass) or averaged (elemental concentrations) per EcoUnit in order to maintain comparability of data (e.g. leachate assessed per EcoUnit versus soil sampled in focal subplots). To test species-specific aboveground biomass in fertilized relative to unfertilized subplots, the biomass was averaged per EcoUnit and harvest for both fertilizer treatments. The model was adapted by including fertilizer addition (Yes (Y), No (N)) as categorical factor in the model for testing species identity effects. To test for effects between groups (e.g. fertilized versus unfertilized), Tukey’s honestly significant difference (HSD) tests were conducted using the R-package ‘emmeans’ (Lenth et al. 2023). All models as well as information on variable transformation can be found in the Supporting information.

Inequality was calculated using the Gini coefficient of inequality (Eq. $\text{Gini} = A/(A+B)$, (Gini 1921), where A represents the area between the Lorenz curve and the perfect equality line, which is divided by the total area under the perfect equality line ($A+B$) (Sirihyot and Holasut 2020). The Gini coefficient ranges from 0 (a perfectly even distribution) to 1 (a perfectly uneven distribution). Here, a broad range of resource inequality as indexed by the Gini coefficient included the levels 0, 0.16, 0.4, 0.6, 0.8 and 0.96. The Gini coefficient was first introduced into ecology by Weiner and Solbrig (1984) as a measure of inequality in plant population structure. We tested for the effect of outliers using robust models (‘robustlmm’; Koller 2016) and compared the results with those from the original models (Supporting information). Instead of removing outliers, robust models assign them lower influence using robust weights.

To meet assumptions of normality of residuals, biomass data, elemental data from aboveground biomass, and nutrient data from soil and leachate were log-transformed prior to linear mixed effect model analysis (Supporting information). For this, model residuals were checked using the R-package ‘performance’, and log-transformed if necessary (Lüdecke et al. 2021). For figures, data of elemental concentrations in aboveground biomass and nutrient concentrations of soil and leachate were standardized between 0 and 1 to ease comparability. Data was visualized using ‘ggplot2’ ver. 3.5.0 (Wickham 2016), where regression lines were based on

mixed-effects models (predicted means, using *ggpredict* from package 'ggeffects'; (Lüdecke 2018).

Species diversity was calculated as Shannon diversity index (Shannon's H) using the function *diversity* of the R-package 'vegan' ver. 2.6-4 (Oksanen et al. 2024). Shannon's H was transformed to the effective number of common species, i.e. Hill number = 1 ($\exp(x)$), (Jost 2006), henceforth Shannon diversity.

We used Pearson correlations to test resource inequality driven shifts in nutrient concentrations among plant, soil and leachate on plant species-specific productivity (R-package 'corrplot' ver. 0.92 (Wei and Simko 2021). Variance partitioning of multivariate relationships between these groups was conducted using the function *varpart* of the package 'vegan'. For this, the variation in community dissimilarities was partitioned with respect to three explanatory tables (elemental or nutrient concentrations in aboveground biomass, soil, leachate), using adjusted R^2 (R-squared) in distance-based

redundancy analysis. For this, a Bray–Curtis dissimilarity matrix was set up for the abundance data (sum of species-specific biomass per EcoUnit). Significance testing of the variation partitioning was conducted using the function *test_vp3* (https://rdrr.io/github/jgmvc/comecol/man/test_vp3.html). Prior to correlation analysis and variance partitioning, data were not standardized between 0 and 1, but log transformed (elements and concentrations) or log + 1 transformed (total aboveground and species-specific biomass).

Results

Plant diversity, species-specific and total aboveground biomass

The effect of resource inequality on plant diversity (here reported as Hill numbers derived from Shannon H') varied depending on the harvest date ($F_{1,8} = 11.88$, $p = 0.009$; Fig. 3b).

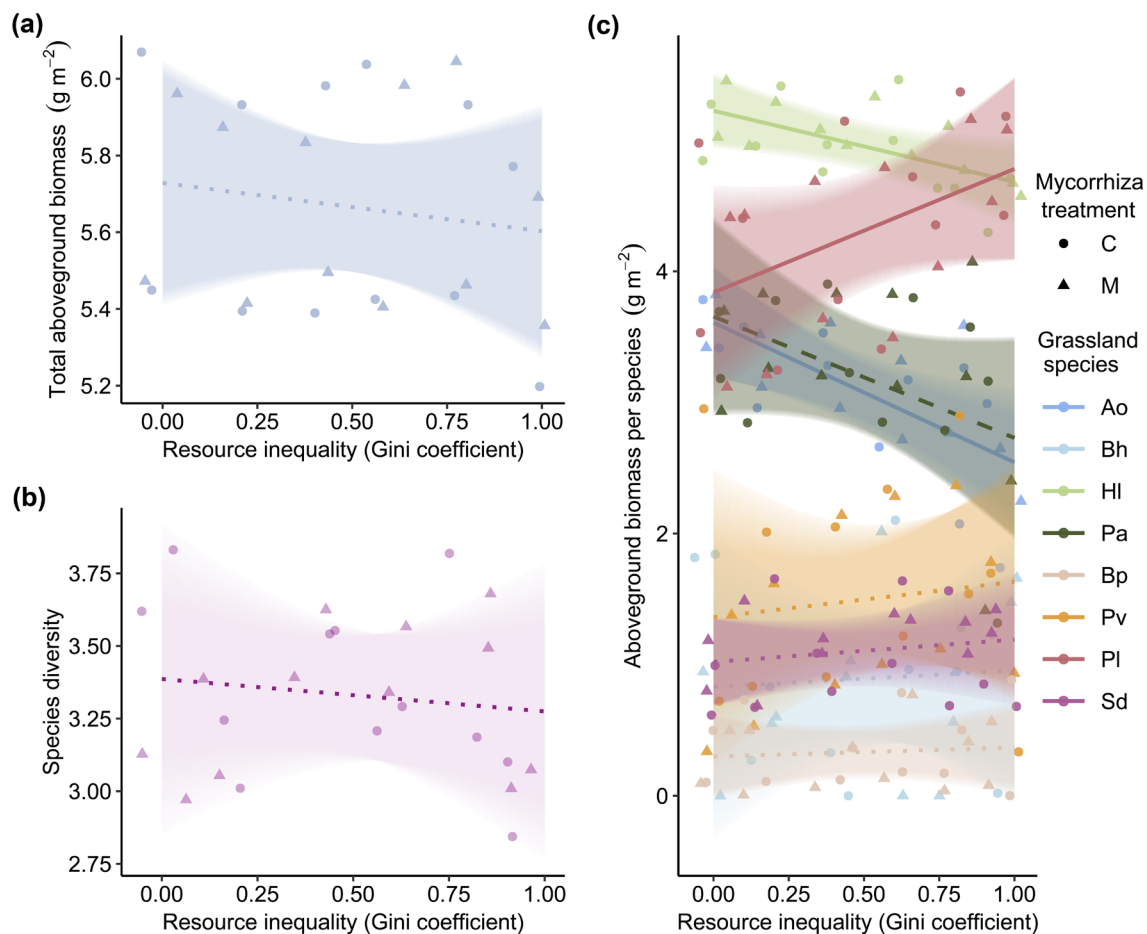


Figure 3. Effects of resource inequality as indexed by the Gini coefficient on (a) total aboveground biomass, (b) Shannon diversity and (c) aboveground biomass per species. Each symbol represents a grassland community (a and b) or species (c) sampled during each of the two harvests; shapes represent the different mycorrhiza treatments (C – no mycorrhiza addition, M – mycorrhiza addition). Regression lines are based on mixed-effects models (predicted means). Solid lines indicate significant relationships ($p < 0.05$), dashed lines marginally significant relationships ($0.1 > p > 0.05$), and dotted lines nonsignificant relationships ($p > 0.1$). Biomass data is presented as log+1-transformed values. Two letter abbreviations are used to indicate plant species names as follows: Ao – *Anthoxanthum odoratum*, Bh – *Bromus hordeaceus*, Hl – *Holcus lanatus*, Pa – *Poa annua*, Bp – *Bellis perennis*, Pv – *Prunella vulgaris*, Pl – *Plantago lanceolata*, Sd – *Silene dioica*.

Specifically, plant diversity decreased with resource inequality during the first sampling date, but this pattern was not observed during the second (Supporting information). The addition of mycorrhizal fungi had no effect on plant diversity.

Further, we found no significant effect of resource inequality on total aboveground plant biomass (Fig. 3a, Supporting information). Plant communities produced less biomass overall on the second compared to the first harvest date ($F_{1,8}=369.72$, $p < 0.001$; Supporting information). When plant species-specific responses were included in the linear mixed effect models, we observed significant interactions between resource inequality and species identity ($F_{7,150}=2.16$, $p=0.041$) and between harvest and species identity ($F_{7,150}=18.24$, $p < 0.001$) (Fig. 3c, Supporting information), with similar across both harvests for all species in the experimental communities, except *Plantago lanceolata* (Supporting information). While grass species were generally negatively affected (either significantly: *Anthoxanthum odoratum* $F_{1,8}=41.53$, $p < 0.001$; *Holcus lanatus* $F_{1,8}=12.07$, $p = 0.008$; or marginally: *Poa annua* $F_{1,8}=4.43$, $p=0.068$) or not affected (*Bromus hordeaceus*) by resource inequality, the herb, *Plantago lanceolata*, significantly increased its biomass

with resource inequality ($F_{1,8}=21.47$, $p=0.002$; Fig. 3c, Supporting information). Two of the four herb species (*Bellis perennis*, *Prunella vulgaris*) were not significantly affected by resource inequality. The remaining herb *Silene dioica* showed a significant response to resource inequality depending on the time of harvest, with a biomass decrease with resource inequality in the first harvest, and an increase in the second ($F_{1,8}=7.04$, $p=0.029$; Supporting information).

The addition of mycorrhizal fungi showed a marginal effect on total biomass depending on harvest ($F_{1,8}=4.08$, $p = 0.078$; Supporting information). Here, total biomass decreased in communities without added mycorrhiza during the first harvest. Species-specific biomasses were not significantly affected by the mycorrhizal treatment (Supporting information).

Total and species-specific aboveground biomass in fertilized and unfertilized subplots

Overall fertilizer addition significantly affected total aboveground biomass ($F_{1,290}=19.49$, $p < 0.001$, Supporting information) and species effects on total aboveground biomass ($F_{1,150}=271.31$, $p < 0.001$; Fig. 4a, Supporting information).

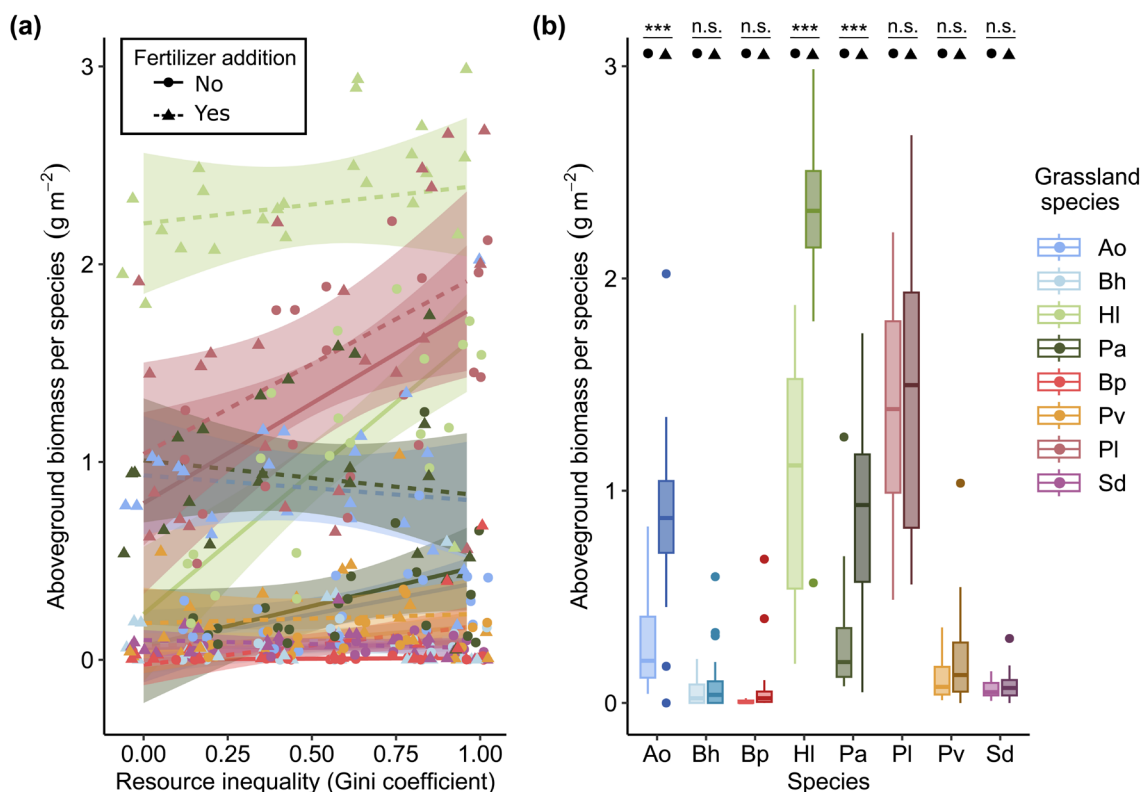


Figure 4. (a) Effects of resource inequality as indexed by the Gini coefficient on aboveground biomass of each plant species in unfertilized (●) and fertilized (▲) subplots. Solid lines indicate unfertilized and dashed lines fertilized subplots. Each symbol represents the averaged species biomass across either fertilized or unfertilized subplots, reflecting a balanced number of samples taken during each of the two harvests and for the two mycorrhiza treatments (visual differentiation of the mycorrhiza treatment was left out for clarity because no effects were detected). (b) Effects of fertilizer addition on aboveground biomass per species. Asterisks depict statistical significance of species biomasses in fertilized versus unfertilized subplots (not significant (n.s.), $p > 0.05$; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$). Two letter abbreviations are used to indicate plant species names as follows: Ao – *Anthoxanthum odoratum*, Bh – *Bromus hordeaceus*, Hl – *Holcus lanatus*, Pa – *Poa annua*, Bp – *Bellis perennis*, Pv – *Prunella vulgaris*, Pl – *Plantago lanceolata*, Sd – *Silene dioica*.

Here, resource inequality showed a significant interaction with fertilizer addition ($F_{4,150}=3.81$, $p=0.006$, Supporting information) which was also significant depending on species identity ($F_{28,150}=1.68$, $p=0.026$, Supporting information). *Poa annua*, *Bellis perennis* and *Silene dioica* were significantly and *Holcus lanatus* marginally affected by resource inequality depending on fertilizer addition. For example, *Bellis perennis* showed increased biomass production with resource inequality in fertilized subplots ($F_{4,15}=3.18$, $p=0.044$; Supporting information). Also, *Holcus lanatus* tended to benefit from resource inequality, in particular in fertilized subplots ($F_{4,15}=2.55$, $p=0.082$; Fig. 4a, Supporting information). In contrast, *Poa annua* and *Silene dioica* decrease their productivity in fertilized subplots under increasing resource inequality (respectively: $F_{4,15}=0.62$, $p=0.658$; $F_{4,15}=9.69$, $p<0.001$; Supporting information).

Comparing productivity of species biomasses in fertilized and unfertilized subplots, showed significantly enhanced productivity of the grass species *Anthoxanthum odoratum*, *Holcus lanatus* and *Poa annua* and well as a marginal difference for the herb species *Plantago lanceolata* in fertilized subplots (respectively: $p<0.001$, *Plantago lanceolata* $p=0.051$; Fig. 4b, Supporting information). The other four grassland species (*Bromus hordeaceus*, *Bellis perennis*, *Prunella vulgaris* and *Silene dioica*) performed equally under both conditions (no significant effect of fertilizer treatment). However, while most species in general showed only little growth in either fertilizer treatment or strongly enhanced growth under fertilizer addition, *Plantago lanceolata* showed high productivity under both treatments (Fig. 4b).

Elemental concentrations and pools

Temporal patterns and overall treatment effects. For all nutrients and elements, unless otherwise noted, concentrations and pools were reduced over time as the experiment proceeded (significant harvest effects; Supporting information). The influence of inequality on nutrient concentrations and pools was consistent across time for aboveground biomass (Supporting information) and leachate (Supporting information), but not soil (Supporting information), as described below (Supporting information). None of the nutrients in aboveground biomass, soil, or soil leachate were significantly affected by the addition of mycorrhizal fungi (Supporting information). Nonetheless, elemental and nutrient concentrations above- and belowground were differently affected by resource inequality (Supporting information, Fig. 5):

Aboveground biomass. In aboveground biomass, out of all four analyzed elements only P concentration was significantly negatively affected by resource inequality ($F_{1,8}=6.86$, $p=0.03$, Fig. 5b, Supporting information). C and K concentrations showed only marginal negative trends ($F_{1,8}=4$, $p=0.086$ and $F_{1,8}=4.66$, $p=0.063$), and N concentration a marginal positive trend with resource inequality ($F_{1,8}=4.08$, $p=0.078$). Over time, the aboveground biomass C concentration remained stable; it was the only elemental response that did not decline (no effect of harvest; Supporting information). When the nutrient concentrations were considered

in light of their distribution in plant biomass (i.e. aboveground elemental pools), we found similar patterns (Fig. 5a). That is, aboveground biomass elemental pools of N and C were not significantly influenced by resource inequality (Fig. 5a). In contrast, P and K pools significantly decreased with resource inequality ($F_{1,8}=13.13$, $p=0.007$ and $F_{1,8}=7.69$, $p=0.024$ Supporting information; for reference: plotted raw, non-standardized, data can be found in the Supporting information).

Further, stoichiometric analyses revealed mainly effects in ratios involving P (C:P, N:P) (Supporting information). Resource inequality showed a significant negative influence on the N:P ratio during both harvests which was expressed with increasing ratios, hence decreasing biomass quality ($F_{1,8}=35.57$, $p<0.001$; Supporting information). For C:P, resource inequality had the same effect but only during the second harvest ($F_{1,8}=5.93$, $p=0.041$; Supporting information). In general, the quality of plant biomass decreased (higher ratio) from the first to the second harvest considering C:N and C:P, but it increased for N:P (lower ratio).

Soil. Soil PO_4^{3-} and K^+ concentrations were not affected by resource inequality, and soil NO_3^- concentration was marginally increased ($F_{1,8}=5.07$, $p=0.054$, Fig. 5c). Further, depending on the time of assessment NH_4^+ ($F_{1,8}=7.26$, $p=0.027$) and $\text{N}_{\min}$ ($F_{1,8}=7.99$, $p=0.022$) were significantly increased by resource inequality (Supporting information).

Leachate. In leachate, only PO_4^{3-} was significantly affected by resource inequality, showing an increase ($F_{1,8}=7.51$, $p=0.026$, Supporting information, Fig. 5d). All nutrients in leachate were significantly affected by the time of harvest (Supporting information).

Influence of nutrient pools in plants, soil and leachate on species-specific productivity

Correlation analyses showed that the productivity of different grassland species varied strongly with nutrients in the soil, leachate, and aboveground biomass (Fig. 6a–c). For example, the biomass production of the grass species *Anthoxanthum odoratum* and *Bromus hordeaceus* were significantly negatively correlated with aboveground biomass concentrations of N and P, as well as N compounds ($\text{N}_{\min}$, NO_3^- , NH_4^+) and partly PO_4^{3-} in soil and leachate. In addition, the productivity of *Bromus hordeaceus* was significantly negatively correlated with K concentration in aboveground biomass, and with K^+ concentrations in soil and leachate. This contrasts with the other six species (*Holcus lanatus*, *Poa annua*, *Bellis perennis*, *Plantago lanceolata*, *Prunella vulgaris*, *Silene dioica*), which showed significant positive correlations between biomass production and either K or K^+ concentrations in aboveground biomass, soil, or leachate. Furthermore, the growth of *Holcus lanatus* and *Poa annua* was significantly negatively affected by PO_4^{3-} concentrations in leachate. Most species, however, were positively correlated with elements in aboveground biomass and nutrients in soil and leachate (Fig. 6a, b, c). For example, biomasses of *Poa annua*, *Bellis perennis*, *Plantago lanceolata* and *Prunella vulgaris* were significantly positively correlated with aboveground biomass N, P and K, as well as NO_3^- and K^+ in

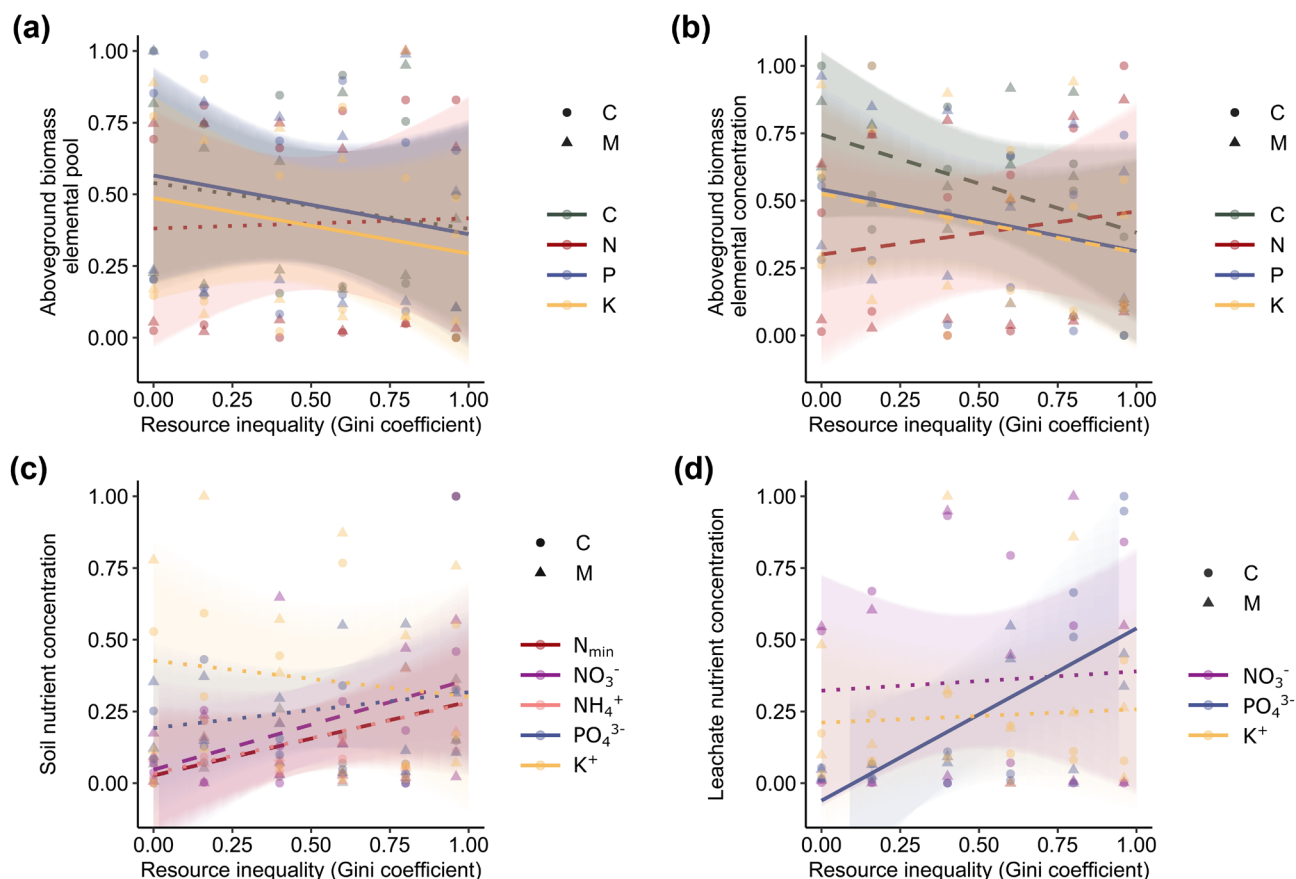


Figure 5. Effects of resource inequality as indexed by the Gini coefficient on elemental pools in (a) plant aboveground biomass, and elemental concentrations in (b) plant aboveground biomass (c) soil, and (d) leachate. Each symbol represents a grassland community, showing averaged results across the sampling period until harvest one and until harvest two; shapes represent the different mycorrhiza treatments (C – no mycorrhiza addition, M – mycorrhiza addition). Regression lines are based on mixed-effects models (predicted means), where solid lines indicate significant relationships ($p < 0.05$), dashed lines marginally significant relationships ($0.1 > p > 0.05$), and dotted lines non-significant relationships ($p > 0.1$). Data was standardized between 0 and 1 (results of actual (i.e. non-standardized) concentrations can be found in the Supporting information).

leachate. In addition, biomasses of *Anthoxanthum odroatum*, *Holcus lanatus* and *Poa annua* were positively correlated with aboveground biomass C concentration (Fig. 6a). The herb *Silene dioica* was not significantly correlated to nutrients and elements, with the exception of a significant negative correlation with K^+ in soil (Fig. 6b).

The variance partitioning analysis (Fig. 6d, Supporting information) indicated that together aboveground biomass elemental concentration, and nutrient concentrations in soil and leachate explained around 35% of the total variance of plant species-specific biomass. When considered in combination, the relative explanatory power of each pool varied substantially. Nutrients in leachate and elemental concentrations in aboveground biomass jointly explained 22% of the variation in plant biomass. In contrast, soil nutrient concentrations in combination with elemental concentrations in aboveground biomass explained 1% of the variation in species specific plant biomasses, and in combination with nutrient concentrations of leachate 1%. The three environmental variables individually explained 16% for aboveground biomass

and 2% for soil, respectively, whereas leachate did not explain any variance in plant biomass.

All observed results from linear mixed-effects models were also tested using robust models (Supporting information). When they were detected, outliers appeared across different experimental units or timepoints or were too minor to meaningfully influence model estimates (i.e. robustness weight close to 1; Supporting information), meaning that stochastic processes (e.g. potential differences in germination rates) in any given experimental unit did not consistently influence multiple response variables. The robust models provide the same or very similar estimates for treatment effects in 20 out of 32 response variables. Further, estimates of non-robust models with significant effects were not or only slightly different to the estimates of robust models. The only exception was P concentration in plant foliage, where the estimate suggested a decreased effect of resource inequality when using the robust model (Supporting information). Yet, the estimates for effect of resource inequality on P pools in foliage did not change between non-robust and robust models, despite

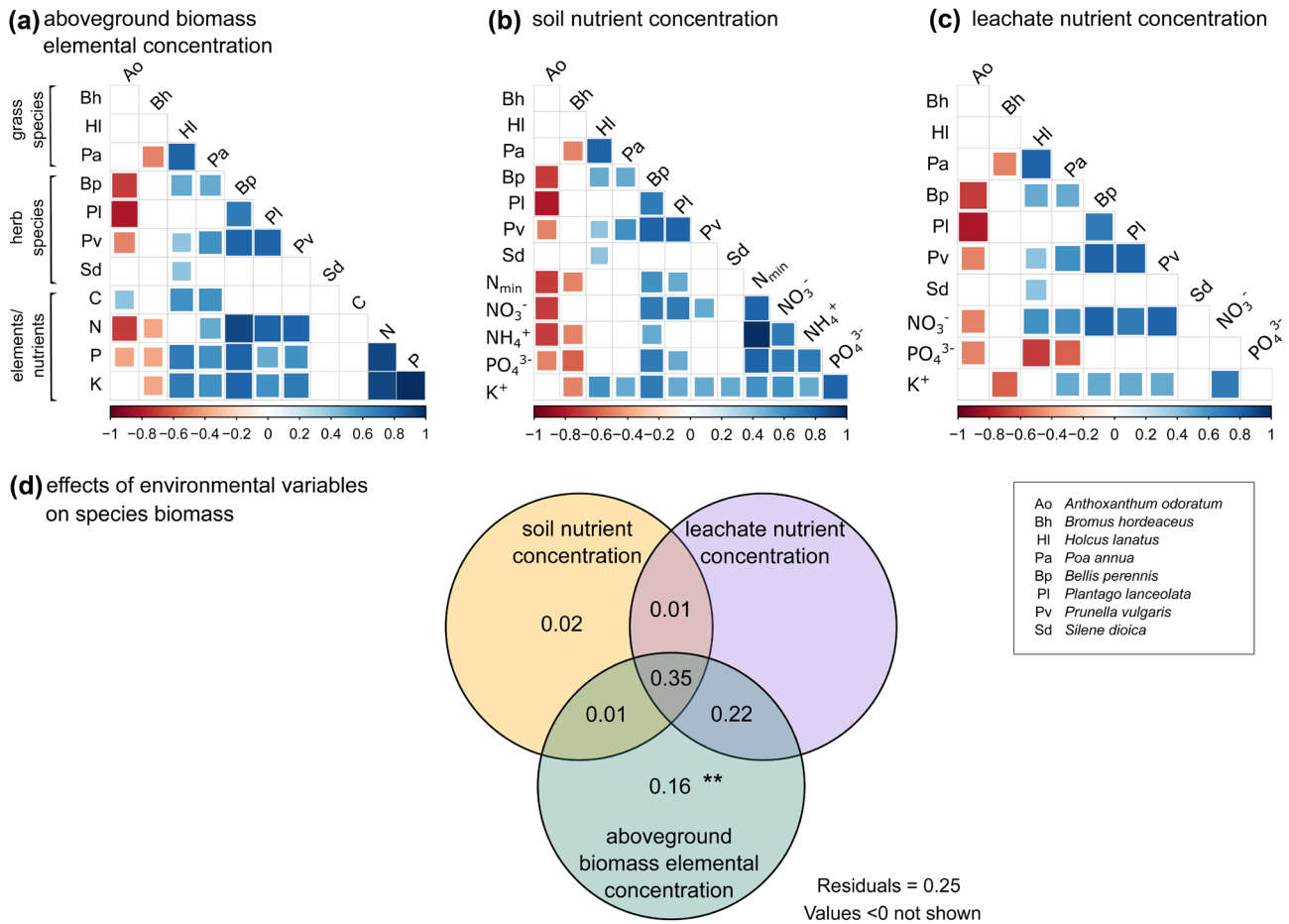


Figure 6. Heatmaps showing the Pearson correlations between abundance data of species-specific biomasses and environmental variables (a) aboveground biomass elemental concentrations, (c) soil nutrient concentrations, and (d) leachate nutrient concentrations. Only significant correlations ($p < 0.05$) are shown, represented by a color gradient ranging from dark red (negative correlation) to dark blue (positive correlation). Different square sizes denote the strength of correlation. Variation partitioning analysis (d) based on distance-based redundancy analysis (dbRDA) illustrates the effects of environmental variables on plant species-specific biomass. Reported are the adjusted R^2 values for each fraction, and statistical significance of testable functions are indicated by asterisks ($0.05 > p > 0.01$ **). The environmental group consisted of the aboveground biomass elemental concentrations (carbon (C), nitrogen (N), phosphorus (P), potassium (K)), and soil and leachate nutrients (N_{min}, NO₃⁻, and NH₄⁺, PO₄³⁻), and the abundance data consisted of the species-specific biomasses of grassland species.

missing significant treatment effects of total biomass, suggesting that inequality generally decreased P concentration.

When non-robust models failed to detect significant effects of treatments and their interactions, robust models of six response variables showed stronger changes in estimates for interaction effects, suggesting that there may be additional context dependency in the models that were not detected in the non-robust models. These could potentially lead to changes in the direction and/or strength of two- and three-way interactive effects. For example, the estimates of the robust models for K concentration in plant foliage showed a stronger interaction between inequality and mycorrhiza, as well as harvest, inequality, and mycorrhiza (Supporting information). Similar patterns were found for nitrate in soil and leachate, showing larger estimates for interaction effects. For five response variables (K pool of foliage, biomass of *Poa annua* and *Anthoxanthum odoratum*, NO₃⁻, PO₄³⁻ and K⁺ in

soil), the direction of interaction effects changed (e.g. PO₄³⁻ in soil: harvest × inequality, harvest × mycorrhiza) (Supporting information).

Discussion

Our novel experiment revealed that grassland plant communities maintained their overall productivity and diversity across levels of inequality, because gains in some species, in particular *Plantago lanceolata*, were balanced by declines in others (e.g. *Anthoxanthum odoratum* and *Holcus lanatus*). The increased success of *Plantago lanceolata*, a species known for its fast-growing characteristics, was associated with shifts in the concentrations of nutrients (e.g. P and K) retained in plant aboveground biomass and soils. These results suggest that inequality may influence multiple aspects of plant

physiology and ecosystem functioning through some generalizable processes that are discussed in more detail below.

Plant species-specific responses: *Plantago lanceolata* thrives under resource inequality

Each of our grassland communities were sown with standardized communities composed of eight plant species. Our experiment captures effects that could be due to advantages, or disadvantages, conveyed based on differences in germination, growth rate or ability to access resources. For example, one could expect that, with increasing inequality, there would be an advantage to species with ‘running’ compared to sedentary root traits, such as tap roots, because they would be able to access a broader spatial extent (Merrikkh-Bayat 2015). However, this is not what we observed. In contrast to H1, suggesting that diversity and productivity of the grassland communities will decline with resource inequality as a result of stress (either caused by nutrient deficiency and enhanced competition in unfertilized subplots or by nutrient excess in the fertilized subplot), we found no significant effects on the community level. Over the six-month experiment, we were able to see species-specific responses to resource inequality. In particular, the perennial herb species *Plantago lanceolata* (tap root; Sagar and Harper 1964) and the grass species *Holcus lanatus* (fibrous roots) exhibited strong responses that were opposite predictions of trait-based responses to resource inequality. Many studies have demonstrated the plasticity of *Plantago lanceolata* in adapting to extreme environmental conditions, such as drought and strong light exposure (Miszalski et al. 2023) or high abundance of heavy metals (Ahatović et al. 2020). We showed that *Plantago lanceolata* was capable of thriving and increasing its productivity under the severe conditions of resource inequality. This finding is further supported by the observation of high productivity of *Plantago lanceolata* that was not dependent upon fertilizer addition (Fig. 4). This outcome is surprising, as *Plantago lanceolata* possesses a tap root, which we initially assumed would make it less adaptable to resource inequality. Just as *Plantago lanceolata*, *Holcus lanatus* is present in a wide range of environmental conditions (Grime et al. 1988). *Holcus lanatus* is proven to be highly adaptable to harsh environments, for instance to soils contaminated with heavy metals (Rahman and Khan 2023) or highly acidic soils (Chen et al. 2013). However, despite being the most productive species within the communities, which is related to its fast-growing abilities (Poorter and Pothmann 1992), we observed a strong decline in abundance of *Holcus lanatus* with increased resource inequality, suggesting a coping-deficit of this species with nutrient imbalance. However, when examining the productivity of *Holcus lanatus* across fertilized and unfertilized subplots, it was evident that the grass maintains a constantly high biomass in fertilized subplots, while increasing its biomass in unfertilized subplots. Potentially, the fibrous roots of *Holcus lanatus* allow for mining of nutrients in further away subplots under some extent, when resource inequality is high. In addition, we observed a significant decline of *Anthoxanthum odoratum* with increased resource inequality.

This grass species naturally occurs in rather nutrient-poor habitats (Grime et al. 1988), suggesting it was also suffering within the nutrient-excess conditions given in the central subplot of the highest inequality level. Other species, such as the grass *Bromus hordeaceus*, or the herbs *Bellis perennis*, *Silene dioica* and *Prunella vulgaris* were very low in abundance and did not show any strong reactions to resource inequality.

Resource inequality alters nutrient dynamics, particularly phosphorus retention and leaching

In line with H2, resource inequality influenced the ability of the ecosystem to retain nutrients (especially significant for P) and transfer them between soils, leachate, and plants depending on the particular nutrient and pathway. Plants take up carbon from the atmosphere through photosynthesis, and plant community biomass is typically considered as predominantly carbon-based. Unsurprisingly, we found variation, but no significant declines, in total plant community C. However, we detected declines in the amount of phosphorus and potassium that were transferred from soil and leachate and retained in plant biomass. K is associated with enzyme activation and the movement of leachate, starch, and nutrients (Sardans and Peñuelas 2015, 2021, Dreyer et al. 2017); and P is important for plant development, because of its main role in construction of cell membranes, in energy conversion (ADP, ATP), regulation of protein activity or as an essential part of nucleic acids (Malhotra et al. 2018). Limitation of these processes due to insufficient P or K supply can lead to reductions in photosynthesis and capacity for growth and maintenance of the plant which may explain declines in plant biomass of certain species. Further, changes in the availability of nutrients N, P and K caused by turnover, leaching, or exudation, also lead to shifts in stoichiometric ratios (Güsewell 2004). In this study, in particular the N:P ratio was significantly increased by resource inequality during both harvests and the C:P ratio in harvest two. This is likely due to a slight increase of the N (and constant C concentration for C:P) in biomass simultaneous to the decrease in the P concentration, since it does not get built into biomass, but leaches out of the system.

While P and K concentrations and pools in aboveground biomass decreased with resource inequality, in soil the respective soluble forms (PO_4^{3-} and K^+) were not significantly affected. Here, N compounds, especially NO_3^- , increased with resource inequality. Uptake, translocation and distribution of NO_3^- between roots and shoots is heavily dependent on potassium availability in soil and plants (Wang and Wu 2013, Rubio et al. 2014, Nieves-Cordones et al. 2019). The reduced storage of potassium in plant aboveground biomass therefore could have led to decreased uptake of NO_3^- . NO_3^- is very mobile in soil and does not get bound to clay particles, which is why it is susceptible to leaching (Huang et al. 2017). However, despite slight increases of nitrate concentrations in leachate with resource inequality, this nutrient was not significantly affected. In leachate, only phosphate concentrations increased with the incline of the inequality gradient. Based on these results, we can partially confirm H2 (the highest concentrations of nutrients will be retained in soils or lost via

leachate when resource inequality is highest) – only P concentrations significantly decreased in aboveground biomass and significantly increased in leachate under high resource inequality. All other elements and nutrients were either marginally affected or showed no significant response.

Mycorrhizal fungi do not modulate effects of resource inequality

For this study, sandy, nutrient-poor soil was used, in order to capture stronger effects of resource inequality on ecosystem functioning. We therefore cannot rule out the possibility of different effects when using other soil types. Further, initially the experiment was set up with two treatments. The gradient of resource inequality crossed with half of the ecosystems being inoculated with arbuscular mycorrhizal fungi. Despite finding significant differences in the abundance of mycorrhizal structures (hyphae, arbuscules and vesicles; Supporting information), the mycorrhiza treatment did not show any significant effects on any of the assessed parameters above- or belowground (contrary to H3: mycorrhiza will mitigate the effects of resource inequality by enhancing resource exploration). Potentially, the high fertilizer additions hindered full establishment of symbioses between plants and mycorrhiza. A reason for this may have been the missing necessity to support plants in nutrient uptake. It is widely reported that nutrient surplus can inhibit the association of and mutualism between arbuscular mycorrhizal fungi and plants (Johnson et al. 1997, Nouri et al. 2014, 2015). However, considering the strongly reduced nutrient availability in soil in the second half of the experiment, we could have expected the formation of stronger mycorrhizal associations.

Relationships between species productivity and nutrients in aboveground biomass, soil and leachate

The productivity of an ecosystem is strongly determined by the availability and uptake of resources (Barry et al. 2019). Here we test the role of inequality in nutrient resources, although resources can also include other variables including water and light. Plants exhibit various mechanisms in order to compete with other species for nutrient resources: increased growth of roots, root formation in deeper soil layers, association with symbiotic partners (e.g. different species of N-fixing bacteria or mycorrhizal fungi), but also increased shoot and foliage growth (Wardle and Peltzer 2003, Poorter et al. 2012, Freschet et al. 2018). In diverse plant communities, this allows different species to coexist due to occupation of different resource niches (also: resource complementarity, Loreau and Hector 2001, Cardinale et al. 2007). However, it was also shown that nutrient enrichment in soils increases interspecific competition, leading to competitive exclusion of sub-dominant species (Xia and Wan 2008, Harpole et al. 2016). Here, we show that this is also true for increased resource inequality, confirming H4, that variation observed in resource pools (e.g. leachate, soil and plants) will explain changes in community functioning (e.g. plant species productivity). From all species in this study, the dominant species *Plantago lanceolata* increased its aboveground

biomass, while the productivity of other species (e.g. *Holcus lanatus*, *Anthoxanthum odoratum*) declined. Likely, *Plantago lanceolata* was the stronger competitor for nutrients, in particular for nitrate, from soil. In a study on adaptive changes of *Plantago lanceolata* to harsh environments, it was found that this herb species had increased nitrate uptake on sandy soils in a desert-like environment compared to a nearby forest ecosystem (Miszalski et al. 2023). This is also supported by our finding of stable aboveground biomass N concentrations and pools across resource inequality levels. Species-specific analyses of elemental pools in aboveground biomass could have further contributed to this observation. Further, root analysis of the species would have been advantageous. It was shown that *Plantago lanceolata* plants may have highly plastic root systems for improved nitrogen acquisition in both high and low nutrient conditions (Sagar and Harper 1964, Padilla et al. 2013). An analysis of species-specific root traits would have therefore potentially supported our findings, even if community level root traits paralleled non-significant effects observed for community shoot biomass. Indeed, on the plant community level, analyses of resource inequality on root C:N ratio showed no significant effects and only a marginal negative effect on root biomass (Supporting information). In future studies, more specifically quantifying species-specific root biomass and nutrient concentrations would likely reveal important insights as seen in aboveground plant shoots.

Plant community consequences of excessive inequality

We found a trend of plant community biomass decline, mostly driven by the grass species *Anthoxanthum odoratum*, *Holcus lanatus* and *Poa annua*, with highest resource inequality. The great discrepancy between the heavily fertilized area and unfertilized areas negatively affected most grassland species in this experiment. Excessive nutrient supply can lead to reduction of plant growth due to physiological stress, termed as nutrient toxicity (Lucassen et al. 2003, Güsewell 2004, Pandey et al. 2021), threatening essential ecosystem services (Sterner and Elser 2002, Elser et al. 2010, Fowler et al. 2013). Only one species, *Plantago lanceolata*, was able to benefit from the unequal conditions and increased its biomass. *Plantago lanceolata*, an ecologically important plant species in European grasslands (Sagar and Harper 1964), is known to grow under a wide range of environmental conditions. Similar to plant biomass, plant species diversity tended to decline with resource inequality, however trends were not significant. Nutrient surplus is known to reduce species and functional diversity (Chapin III et al. 2000, Tilman et al. 2001, Lambers et al. 2009) caused by the dominance of competitive species and altering plant community structure. However, the observed patterns may not only or not at all be attributed to nutrient competition, but to competition for light (Hautier et al. 2009). Patchy distribution of plant biomass within heterogeneous systems may result in more edge effects of light availability which might limit changes in plant diversity.

Next potential steps forward

Natural ecosystems are simultaneously confronted by multiple global change drivers (Isbell et al. 2023). Many experiments have aimed to elucidate the relative contribution of multiple drivers (e.g. resource availability) on ecosystem responses, thereby applying treatments in either homogeneous or heterogeneous way, or both (e.g. Nutrient Network, Hutchings et al. 2003, Rajaniemi 2011, Gazol et al. 2013, Xue et al. 2019, 2023). This novel ‘proof of concept’ experiment aims to show some of the potential effects of resource inequality, per se, not of resource patchiness or heterogeneity, on grassland ecosystem functioning. Yet, there are still many open issues with respect to how inequality in resource distribution will affect ecosystems, and it is useful to consider a few caveats. First, the factors contributing to inequality effects – concentration, heterogeneity, and area of resource application all co-varied with inequality in the present study. We have reason to believe that each of the factors influences communities (Isbell et al. 2013, Ben-Hur and Kadmon 2020), yet our experiment was not designed to tease apart the relative influence of these factors independently, which was beyond the scope of the current experiment, but could be addressed in future studies. Second, the conclusions drawn here are based on observations at fairly small spatial and temporal scales. These findings may be most relevant for spatial nutrient imbalances caused by nutrient inputs through plant litter (Berg and McClaugherty 2014), or animal feces (le Roux et al. 2020). The effects of resource inequalities on larger scale, such as over fertilization in some areas (e.g. agricultural fields; Isbell et al. 2013, Peñuelas et al. 2013, Köthe et al. 2023) and contrasting depletion of nutrient resources in others (e.g. declines of N in parts of sub-Saharan Africa or Australia; Mason et al. 2022) may impart an additional range of underlying mechanisms and processes that cannot be addressed here. Moreover, over the course of our experiment that spanned one growing season, we found a decline in plant biomass production between our harvests, which suggests that nutrients taken up by plants and removed during the first harvest led to overall nutrient declines in the experimental communities. In the long term, such effects could translate into generational effects realized from differences in seed set, particularly for annual versus perennial lifestyles. Indeed, many studies have shown that the plant compositional responses are strongly time dependent (Reich et al. 2012, Meyer et al. 2016, Guerrero-Ramírez et al. 2017). Therefore, it is probable that the changes in nutrients and species composition that we revealed after one growing season, may under-represent the longer-term consequences of resource inequality. A more detailed investigation of patch-dependent processes could provide further insights into how nutrient availability influences plant development and nutrient redistribution. To what extent patches are linked by abiotic processes (e.g. diffusion, leaching), or biotic processes (e.g. adventitious roots, mycorrhizae, and seed spread) will be important components for including inequality as a useful metric in landscape ecology. In future experiments longer gradients would help to better investigate the effects of

resource inequality and mycorrhiza addition on biodiversity and functioning, while reducing the risk of outliers influencing regression results. Using robust models, we tested and enhanced the strength of our model results across the six-level gradient. Our results were generally supported by the robust models). Although significant effects of resource inequality of foliar P concentration were decreased in robust models, we do not emphasize an outlier effect, since the effect for P pools in foliage remained consistent in both models. Further, total biomass was not significantly affected by resource inequality for the non-robust model in the first place, but P pools were, underlining the nevertheless strong effect of resource inequality on P concentration. Further significant effects detected by the non-robust linear models were not affected using robust models. For few response variables, some non-significant interactions (detected by non-robust linear models) directions of estimates changed using the robust model. This could have potentially led to stronger or weaker effects depending on time of harvest, mycorrhiza treatment, or inequality level. However, overall main effects, with the exception of P concentration in foliage, not or only weakly changed using robust models, indicating that the main conclusions or our study are supported by multiple ways of analyzing data and treating outliers.

Conclusions and broader significance

While the consequences of inequality are broadly addressed in other academic fields such as economics, in ecology the implications of resource inequality for ecosystem functioning had been less considered, even though parallels might exist. Here, single thriving species may have better growth, while overall productivity of the community is declining, because many subdominant species may recede. While we did not find any overall decline in productivity, indeed the most productive species *Plantago lanceolata* thrived under resource inequality, while other grassland species reduced their growth. Consequently, aboveground biomass elemental concentrations and leachate nutrient concentrations explained the most variation in productivity in the plant communities. Likely, this was caused because less P was taken up by plants and more P was lost in ecosystems with high resource inequality. This shows that, similar to shifts in resource uptake in economic systems, inequality in an ecological context may lead to shifts in resource distribution and uptake as well as changes in community composition. From an economic perspective, it has been argued that some degree of inequality may be beneficial for the efficient operation of a market-based economy (Chaudhuri and Ravallion 2006). This aligns with what we might expect for ecological systems, since some inequality simultaneously means more heterogeneity (Fig. 2f) (Eisenhauer et al. 2023). Many parallels can be found between ecological and economical concepts, which further highlight the potential benefits of adopting economic metrics, such as stability indicators (Loreau et al. 2021) and the Gini coefficient, to study ecological questions. We would

therefore like to motivate research to a broad line of future experiments that can address ecological questions related to mechanisms underlying ecosystem responses to inequality. With this study, we present first steps into plant community responses to nutrient heterogeneity through the lens of resource inequality. Small-scale (on patch level) as well as larger-scale studies (e.g. landscape ecology) may improve the broad understanding of resource inequality effects on ecosystem functioning.

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Data availability statement

Data and R-codes of analyses are available from the iDiv Data Repository: <https://doi.org/10.25829/ivid.3576-hskx59> (Bönisch et al. 2025).

Supporting information

The Supporting information associated with this article is available with the online version.

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