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Plant traits alone are poor predictors of ecosystem properties and long-term ecosystem functioning — Source link

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Abstract: Earth is home to over 350,000 vascular plant species that differ in their traits in innumerable ways. A key challenge is to predict how natural or anthropogenically driven changes in the identity, abundance and diversity of co-occurring plant species drive important ecosystem-level properties such as biomass production or carbon storage. Here, we analyse the extent to which 42 different ecosystem properties can be predicted by 41 plant traits in 78 experimentally manipulated grassland plots over 10 years. Despite the unprecedented number of traits analysed, the average percentage of variation in ecosystem properties jointly explained was only moderate (32.6%) within individual years, and even much lower (12.7%) across years. Most other studies linking ecosystem properties to plant traits analysed no more than six traits and, when including only six traits in our analysis, the average percentage of variation explained in across-year levels of ecosystem properties dropped to 4.8%. Furthermore, we found on average only 12.2% overlap in significant predictors among ecosystem properties, indicating that a small set of key traits able to explain multiple ecosystem properties does not exist. Our results therefore suggest that there are specific limits to the extent to which traits per se can predict the long-term functional consequences of biodiversity change, so that data on additional drivers, such as interacting abiotic factors, may be required to improve predictions of ecosystem property levels.

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PLANT TRAITS ALONE ARE POOR PREDICTORS OF ECOSYSTEM PROPERTIES AND LONG-TERM ECOSYSTEM FUNCTIONING

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ABSTRACT

Earth is home to over 350,000 vascular plant species that differ in their traits in innumerable ways. A key challenge is to predict how natural or anthropogenically driven changes in the identity, abundance and diversity of co-occurring plant species drive important ecosystem-level properties such as biomass production or carbon storage. Here, we analyze the extent to which 42 different ecosystem properties can be predicted by 41 plant traits in 78 experimentally manipulated grassland plots over 10 years. Despite the unprecedented number of traits analyzed, the average percentage of variation in ecosystem properties that they jointly explained was only moderate (32.6%) within individual years, and even much lower (12.7%) across years. Most other studies linking ecosystem properties to plant traits analyzed no more than six traits, and when including only six traits in our analysis, the average percentage of explained variation in across-year levels of ecosystem properties dropped to 4.8%. Furthermore, we found on average only 12.2% overlap in significant predictors among ecosystem properties, indicating that a small set of key traits able to explain multiple ecosystem properties does not exist. Our results therefore suggest that there are strong limits in the extent to which traits alone can predict the long-term functional consequences of biodiversity change, so that data on additional drivers, such as interacting abiotic factors, may be required to improve predictions of ecosystem property levels.

Worldwide, ecological communities are rapidly changing due to various anthropogenic activities[1-5]. This biodiversity change is non-random, and the functional traits of organisms driving their growth, survival and reproduction are key in determining which species thrive and which perish under global change[6-9]. This may have important implications, as traits not only affect individual plant performance, but they may also drive various ecosystem properties such as biomass production, and the services these properties provide to human well-being[7,8,10].

Predicting levels of ecosystem properties, such as biomass production or litter decomposition, from the composition or diversity of traits in plant communities is a main challenge in the field of functional ecology, and different perspectives exist on how this can be done. On the one hand, some authors emphasize the importance of environmental conditions, including soil factors, topography, climate, succession, disturbances and weather conditions, in addition to traits as direct drivers of ecosystem processes[11,12]. On the other hand, in the "Holy Grail" framework developed by Lavorel and Garnier[7], environmental conditions are primarily emphasized as indirect drivers of ecosystem processes, through their effects on plant communities in their traits. Thus, in their framework plant traits are emphasized as the only direct drivers of ecosystem properties. Even through Lavorel and Garnier[7] mention the importance of environmental contexts[7], the practice of using traits alone as direct predictors of ecosystem properties is widely embraced in ecological studies[13-15]. In this study, we aim to test the general hypothesis that plant traits alone can be sufficient for predicting levels of ecosystem-level properties within and across years. Importantly, in this study we focus on the general capacity of plant trait data to *predict* levels of ecosystem properties. Hence, we are not primarily interested in relationships between particular traits and ecosystem properties or in the

mechanisms underlying relationships, but rather in the overall ability of multiple traits in explaining a large proportion of variance in levels of ecosystem properties.

Various previous studies have shown links between plant traits and *species-level* variation in photosynthetic rate, growth, and reproductive output present in the plant kingdom[16-18]. In natural communities, plants interact with individuals from other species, so that both the identity, abundance and diversity of traits may matter for *ecosystem-level* properties. Despite this, so far some field studies only found relatively weak links between the identity and diversity of plant traits and ecosystem-level properties[8,19]. Furthermore, while many other studies did find strong links between traits and ecosystem properties[12-14,20,21], these were typically carried out within a single year. However, as links between traits and ecosystem properties are often highly context-dependent[11,22,23], the capacity of traits to predict the long-term consequences of global change, may be much more limited than studies based on single years suggest. Alternatively, strong and consistent links between plant traits and ecosystem properties may exist, but higher numbers and more appropriate traits than assessed in previous studies may be needed to demonstrate strong links with long-term levels of ecosystem properties.

Results and Discussion

To test these ideas, we first performed a systematic literature review to investigate which and how many traits 100 recent studies measured when attempting to link the diversity or composition of traits within terrestrial plant communities to ecosystem properties. We found that most studies analyzed six traits, and only two studies[24,25] assessed more than 15 traits (Fig. 1B). Nine of the ten most frequently studied traits (Fig. 1A) described aboveground plant parts, of which six described leaf characteristics. Only one frequently measured trait was related to plant

roots, even though roots provide important plant functions (e.g. anchoring, resource uptake, interface to symbionts) and represent approximately 50% of total plant biomass[26]. Thus, most previous studies assessed a sparse set of traits, with a strong bias towards leaf traits.

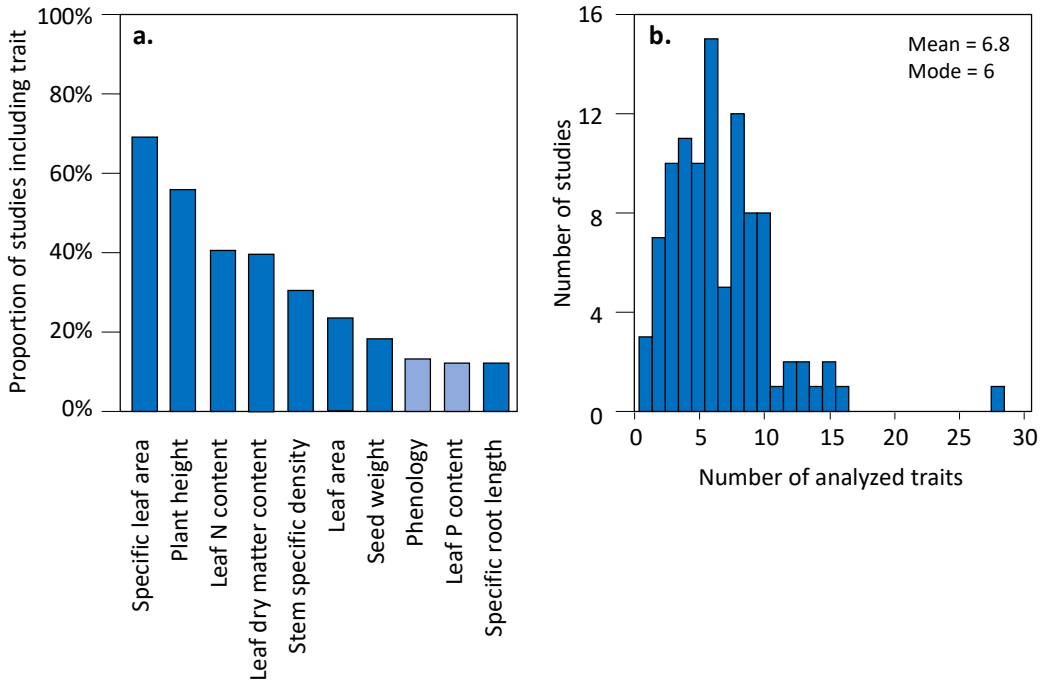


Figure 1. *Overview of which and how many traits are typically analyzed in other ecosystem functioning-related studies. A: Percentage of studies in which the 10 most frequently measured traits were investigated, according to the review of 100 recently published articles. The lighter blue bar shows the only two functions not measured in this study. B: Number of measured traits among studies.*

We then investigated to what extent a much higher number of traits can explain variation in ecosystem properties. We did this using a dataset containing 10 years of measurements of 42 ecosystem properties, assessed in 78 experimentally established grassland communities in Germany. The 42 ecosystem properties described various above- and belowground stocks and rates of plant, faunal, and abiotic properties including e.g. above- and belowground plant

biomass, pollination and herbivory rates, soil respiration and soil moisture content and carbon stocks (see Supplementary Methods for a full list). Both the diversity and composition of the studied plant communities were experimentally manipulated, by sowing different combinations of species[27,28]. At the same time, as all plots were in close proximity within the same experimental field, spatial variation in environmental conditions was relatively minor, making this study particularly suitable for testing the effects of plant communities (and their traits) on levels of ecosystem properties. For each plant species, we measured 41 traits (more than any of the studies assessed in our review) related to structural, morphological, chemical and physiological properties of all main plant parts, including leaves, stems, flowers, seeds, and roots. Traits included e.g. specific leaf area, leaf and root nutrient concentrations, plant height, seed mass, flowering duration and nutrient uptake efficiency. For a complete list of the traits, we refer to the Supplementary Methods. By combining these trait data with plant community data, we quantified both the Functional Identity and the Functional Diversity for each plot in each year. Functional Identity was calculated as the abundance-weighted mean of a trait within a community, and drives ecosystem properties if the contributions of species to ecosystem properties are proportional to their relative abundance[10,12,29]. Functional Diversity was calculated as Rao's Quadratic Entropy[30], and can drive ecosystem properties if species contribute differently to functioning when co-occurring with plant species with different traits, e.g. due to trait-driven resource complementarity[20,28,30,31].

We used linear mixed models to analyze how much of the variation of each of the 42 ecosystem properties was explained by Functional Identity and Functional Diversity metrics of all 41 traits, as well as by random year and plot differences. We used a forward model selection procedure in which during each step a trait was added, if it significantly improved model fit and

did not strongly correlate with the traits already present in the model. We chose for a forward model selection procedure to overcome problems related to multicollinearity, as many FI and FD metrics were correlated (see Table S2.2). Despite the high number of traits included in our analysis, and even though each ecosystem property was on average driven by the FI and/or FD of 4.8 traits (Fig. 2B), the average marginal R^2 of final models was 0.127, indicating that traits explained on average only 12.7% (ranging from 0.0% to 40.0%) of the variation in ecosystem properties (Fig. 2C). Marginal R^2 values were even lower (mean of 0.078) when we used a more conservative model selection procedure, correcting for False Discovery Rates. Conditional R^2 values, which also account for the variance explained by random factors, i.e. plot and year differences, were much higher, with an average value of 0.632. Our finding that traits alone explained a very low proportion of variance of ecosystem properties may seem surprising, as various other studies explained more variance with fewer predictors[8,12-14,20,21,32]. However, these other studies typically used data for single years only, and it is possible that links between traits and ecosystem functions are only strong within years. To test this, we also analyzed links between ecosystem functions and traits for each year separately. This showed that within years marginal R^2 values were much higher, with an average value of 0.326. Thus, while traits alone were poorly linked to ecosystem properties across years, they explained much more variation within years, indicating that links between traits and ecosystem properties are strongly context-dependent.

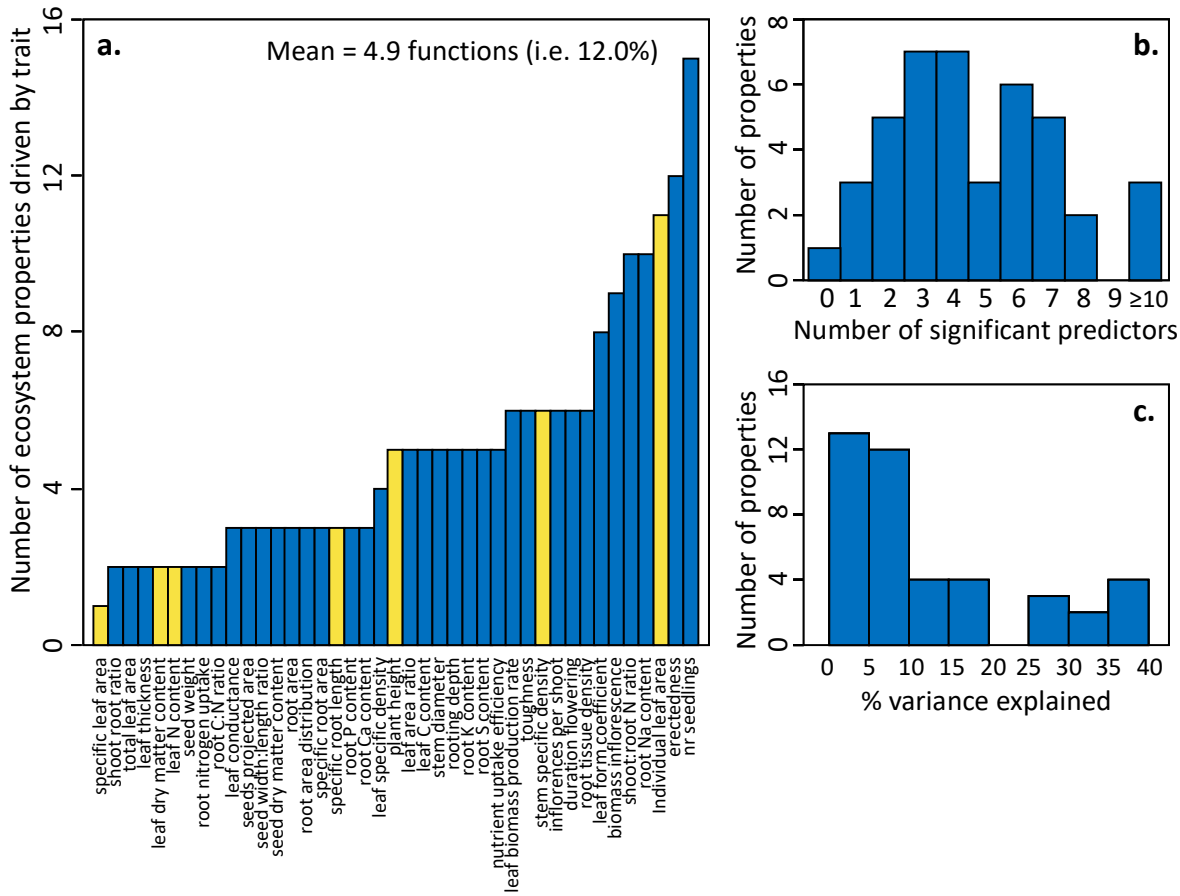
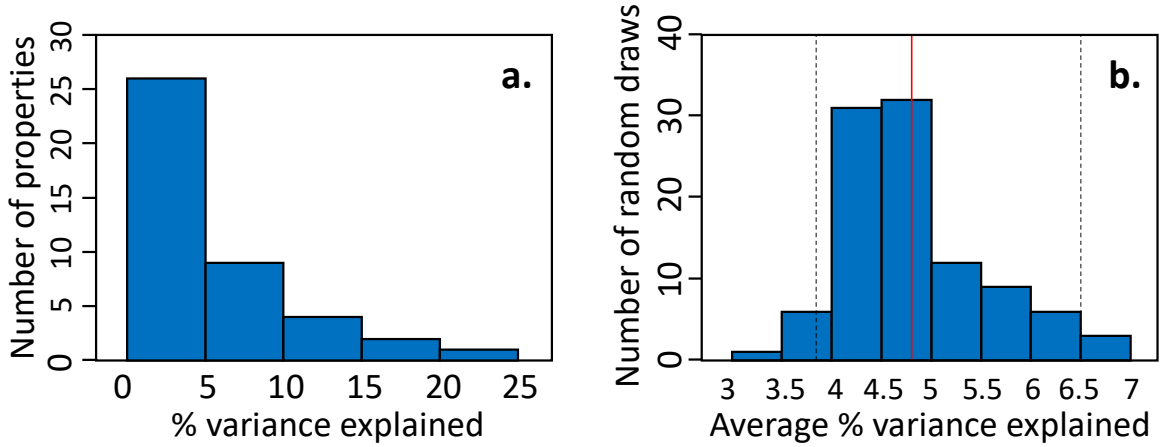


Figure 2. *The relative importance of different and multiple traits for ecosystem properties across years. A: the number of analyzed properties that was significantly driven by each trait, according to final models. The traits analyzed in over 10% of the papers included in the review are shown in yellow. B: Number of significant predictors in final models for each ecosystem property. C: Marginal* R^2 *values for final models for each ecosystem property.*



176

177 ***Figure 3.*** *R^2 values of models in which only six traits were analyzed to explain ecosystem properties*
178 *across years. A: Distribution of marginal R^2 values of final models for each trait, when only the six most*
179 *frequently investigated traits (see review) were included in the analysis. B: Distribution of mean marginal*
180 *R^2 values (across final models for each trait), when based on 100 random draws, six randomly selected*
181 *investigated traits were included in the analysis. The vertical dashed line show the 95% confidence*
182 *interval, while the vertical red line shows the mean marginal R^2 across all ecosystem properties when*
183 *only the six most frequently investigated traits were included in the analysis.*

184

185 We then assessed how our ability to explain levels of ecosystem properties across years
186 depends on how many and which traits are included in analyses. We found that those traits most
187 frequently assessed in other studies did not drive more ecosystem properties than traits less
188 frequently studied (Fig. 2A). One trait (specific leaf area) only significantly drove a single
189 ecosystem property (evapotranspiration from the upper soil layer), while others (e.g. individual
190 leaf area) drove many more ecosystem properties (e.g. drought resilience and abundance of soil
191 layer fauna), but an overall pattern was not detectable (Fig. 2A). We investigated more formally
192 how our ability to explain variation in ecosystem properties would change, if we had measured

either *a*) a random subset of six (corresponding to the number of traits assessed in most other studies) out of the 41 traits (based on 100 random draws), or *b*) only the six traits most frequently assessed in other studies, or if *c*) we analysed species richness (the most commonly used biodiversity indicator) instead as a predictor of ecosystem properties. Irrespective of whether six random traits or those most frequently investigated in other studies were analyzed, on average only 4.8% (95 percentile: 3.8-6.5%) of variation in ecosystem properties could be explained (Fig. 3A,B), while species richness could explain only 1.7% of variation in levels of ecosystem properties. This represents a strong decrease compared to the 12.7% of variation explained when all 41 traits were assessed (Fig. 2B). We also assessed to which extent analyzing subsets of fewer or more than six traits influenced the proportion of explained variance in ecosystem properties. This showed that there was an asymptotic relationship between the number of traits analyzed and the average proportion of explained variation in ecosystem properties. While such an asymptotic relationship is statistically inevitable, it was a surprise that as many as 9 and 24 traits were required to explain 5% and 10% of the variation in ecosystem properties, respectively (Fig. 4A).

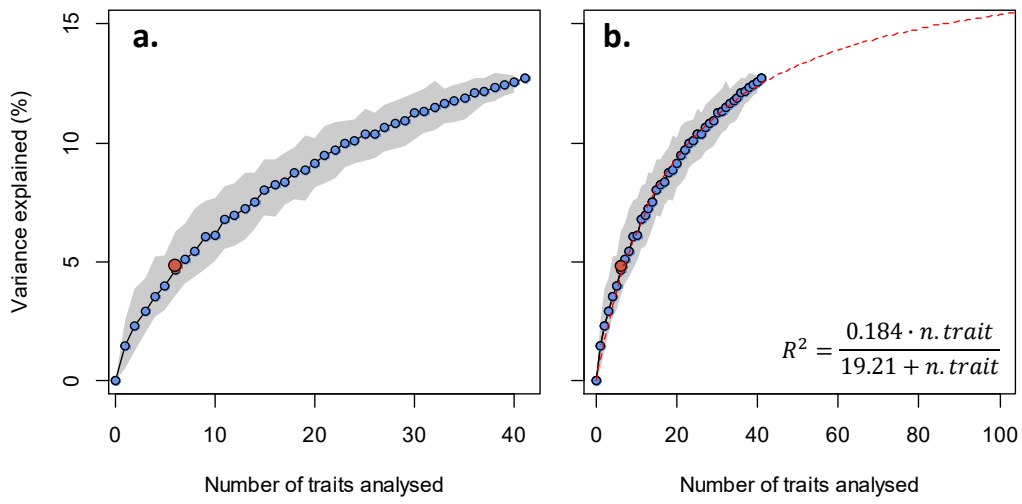


Figure 4. *The average proportion of variation in levels of ecosystem properties across years explained by plant traits increases asymptotically with the number of traits included in the analysis. The*

red dot shows the proportion of explained variation when only the six traits most commonly assessed in other studies are included. The grey area shows the middle 95% of values. A: the marginal R^2 – number of traits relationship based on analysis of actual data. B: an additional extrapolated (based on a fitted Michaelis–Menten equation) marginal R^2 – number of traits relationship (red, dashed line).

Thus, while each ecosystem property alone was on average explained by fewer than five traits (Fig. 2B), many more traits were needed to explain multiple ecosystem properties (Fig. 4). While seemingly a paradox, this happens if different ecosystem properties are driven by different traits. We demonstrated this by calculating the overlap (o) in the traits significantly driving each pair of ecosystem functions, using Sørenson's index[33]. The average overlap indicated that pairs of ecosystem properties had on average only 12.2% significant trait drivers in common. Thus, while traits are commonly advertised as conveying more general information than a species identity does[9,10,12,31], a small set of key traits able to explain variation in multiple ecosystem properties does not exist in Central European grasslands, just like 'superspecies' providing multiple ecosystem functions don't exist[34].

While across-year levels of *many* ecosystem properties were relatively poorly explained by traits, strong links between plant traits and *some* ecosystem properties did exist, as the proportion of explained variance of some ecosystem properties (e.g. aboveground plant biomass and the cover of invasive species) exceeded 30%. This begs the question whether generalities exist between the type of ecosystem property and the extent by which its variation can be explained by plant traits. We hypothesized that *i*) plant traits should be more strongly linked to plant-based ecosystem properties than those related to higher trophic levels or abiotic conditions, and that *ii*) above- and belowground ecosystem properties should have equally strong links with plant traits, as both above- and belowground plant traits were well represented in our study. Partly in line

234 with our first hypothesis, we found that vegetation-based ecosystem properties were most
235 strongly predicted by plant traits (average marginal R^2 = 0.23), while variation explained of
236 heterotroph-related ecosystem properties was on average slightly, albeit non-significantly lower
237 (average marginal R^2 = 0.17) and the proportion of explained variation of abiotic ecosystem
238 properties was substantially and significantly lower (average marginal R^2 = 0.04). Regarding our
239 second hypothesis, we found that ecosystem properties related to aboveground stocks or
240 processes were on average much better predicted (average marginal R^2 = 0.21) than those related
241 to belowground stocks or processes (average marginal R^2 = 0.07). However, this difference was
242 non-significant, and caused by the fact that aboveground, a higher fraction of plant-related
243 ecosystem properties and a lower fraction of abiotic ecosystem properties were studied than
244 belowground (Table S1.1). Despite the finding that variation in some ecosystem properties could
245 be better explained than variation in other ecosystem properties, it is important to note that even
246 the proportion of explained variance in plant-related ecosystem properties was with 21% still
247 relatively moderate.

248 We highlight five possible, and not mutually exclusive, explanations for our overall finding
249 that plant traits alone were generally rather poorly linked to ecosystem properties. First, the plots
250 of our study were rather large (10 × 10m), so that even within plots, variation in plant community
251 composition and levels of ecosystem properties exist. Therefore, spatial mismatches between
252 within-plot locations of ecosystem property measurements and vegetation surveys could have
253 weakened links between traits and ecosystem properties.

254 Second, traits can vary substantially among individuals within species[35]. While in this study,
255 we did not take intraspecific trait variation into account (which would have rrquired to measure
256 41 traits of 60 species in 78 plots, over a 10 year period), other studies have shown that including

intraspecific variation can improve links with ecosystem properties[36,37]. On the other hand, in our own system, interspecific trait variation is much more important than intraspecific trait variation for community-wide trait variation[38], and therefore it is likely that the interspecific trait variation that we focused on is also most important for levels of ecosystem properties.

Third, there is always the possibility that important traits are being overlooked when trying to understand drivers of ecosystem properties. For example, unmeasured traits related to litter quality or mycorrhizal associations could have links to functions such as soil respiration or carbon cycling[39]. Our analysis supports the idea that with more trait data, links between traits and ecosystem properties become stronger (Fig. 4). While this is likely a major issue for the many studies that study comparatively few traits (e.g. the inclusion of six traits only, which is the median of other studies, would have decreased our explanatory variance by a factor of over 2.5), our analyses, which were based on more traits than any other study we are aware of, show that this is not a major issue in our study. Extrapolation of the observed relationships between model R^2 and the number of analyzed traits suggests that 87 traits are needed to increase the proportion of variance explained to 15%, and that there is an (surprisingly low) upper limit of around 18% in the proportion of variance that can be explained by traits alone, even if an unlimited number of traits is analyzed (Fig. 4B). Hence, the inclusion of more trait data would only yield limited gains in our ability to explain ecosystem functioning.

Fourth, it is important to note that while our study focused on temperate, Central European grasslands, it is possible that links between traits and levels of ecosystem properties are stronger across systems. For example, there are major differences in carbon stocks and fluxes between grasslands and forests[40], and these differences in ecosystem properties likely coincide with major differences in the traits (e.g. plant height and seed mass) of the dominant plant species[41].

Last, if the effects of traits on ecosystem properties are context dependent, then the inclusion of interaction effects in statistical models between plant traits and other factors, such as soil factors, topography, weather conditions or disturbances, should improve our predictive capacity of ecosystem properties. For example, while we found that specific leaf area (SLA) was only linked to the across-year levels of one ecosystem property, it is well established that this trait reflects a trade-off between photosynthetic capacity and leaf longevity[42,43]. Due to this trade-off, both positive and negative relationships between SLA and biomass production could be expected, depending on whether high photosynthetic rates (e.g. in productive environments) or conservative strategies (e.g. in dry environments) are most adaptive. In line with this, observed relationships between community-weighted mean SLA values and biomass production are highly variable among other studies, with both positive[13,44-45] and negative[46-49] relationships. In our study, it is possible that in wet years, species with high SLA became more abundant and promoted biomass production in these years, while in dry years the opposite happened. While explicitly testing for context dependency (which would require annual data on e.g. various soil and weather conditions) was outside the scope of our study, our finding that links between traits and ecosystem properties were much stronger within years than across years does point in the direction that taking spatial or temporal environmental contexts into account may be essential to improve our understanding on how traits drive ecosystem properties.

Using one of the most comprehensive studies so far, we showed that while traits can be strongly linked to ecosystem properties within years, our capacity to predict levels of multiple ecosystem properties across years (differing in e.g. weather conditions) is strongly limited. Thus, when using traits only, finding ecology's Holy Grail is extremely challenging at best, or even a 'mission impossible'. This indicates that additional data, such as information on abiotic

conditions (e.g. soil factors, topography, climate/weather and disturbances) and their interactions with plant traits, may be necessary to improve links with ecosystem properties. This may have strong implications. The functional composition and diversity of plant communities are rapidly changing[1-4], and researchers are employing increasingly complex models to predict the consequences of these changes for worldwide biogeochemical and hydrological cycles[50,51]. While we encourage the use of such models and their inclusion of increasingly accurate trait information, our work also highlights that as long as we do not understand the context dependency of links between plant traits and ecosystem properties, and that as long as these context dependencies are not taken into account, there are strong limitations in our predictive capacity of the ecosystem-level consequences of ongoing biodiversity change. Human well-being relies on ecosystem services that are underpinned by various ecosystem properties[52,53], and insuring that these properties are provided at desirable levels is extremely challenging if future environments are dominated by plant communities differing from those observed today. Hence, policies halting the current-day, rapid changes in biodiversity are the safest bet to guarantee nature's contributions to future generations of people.

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AUTHOR CONTRIBUTIONS

F.v.d.P., T.S-G., A.W., K.B. and C.W. conceived the ideas and designed the study. F.v.d.P., T.S-G., S.M. and A.A. performed the analyses. All authors, except for F.v.d.P., K.B. and A.A., contributed to the data collection. F.v.d.P wrote a first draft of the paper, and all other authors contributed to editing several manuscript versions.

COMPETING INTERESTS

The authors declare no competing interests for this study.

DATA AVAILABILITY STATEMENT

The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request. After acceptance, all data will be deposited on a publicly available repository.

METHODS

Review

We performed a review to investigate which traits were most often analyzed as predictors of ecosystem properties in recent years. We did this on the Clarivate Analytics Web of Science website in July 2018, using the search terms (functional-diversity *or* community-weighted-mean *or* CWM *or* trait-diversit*) *and* ecosystem function* *and* (plant *or* vegetation). This initially yielded 654 results. Among these, we searched for papers that analyzed an ecosystem property (broadly defined as energy or trophic fluxes and biomass stocks, measured at the ecosystem or community level) as the response of the Functional Diversity or Functional Identity (e.g. (abundance-weighted) trait mean values) of one or more terrestrial plant traits. We only focused on the 100 most recently published articles that met these criteria. The main objective of this mini-review was to get an overview of a representative sample of recent studies linking terrestrial plant traits to ecosystem properties, rather than to get an exhaustive overview of all published literature.

Among the 100 selected papers (see Appendix A), we screened which plant traits were analyzed as predictors of ecosystem properties. Some traits had different labels among different publications (e.g. specific leaf area versus leaf mass per area[54,55]. In those cases, we used our expert judgement and a plant trait thesaurus (http://www.top-thesaurus.org/home)[56] to relabel traits in order to obtain a common terminology. We then counted and ranked the frequencies (number of papers) by which each trait was analyzed as a predictor of ecosystem properties, and we identified the top ten of traits analyzed in most papers, and the five most commonly analyzed traits.

Experimental design

We studied relationships between various ecosystem properties and plant traits using data from the Jena Main Biodiversity Experiment[27,28], which is one of the biggest and longest running biodiversity experiments worldwide. This grassland biodiversity experiment was set up in spring 2002 in the floodplain of the Saale river close to the city of Jena (Germany, 50°55`N, 11°35`E, 130 m a.s.l.), at a field that was previously managed as a fertilized agricultural field for at least four decades. The experiment was designed to study the effects of species and functional group richness on various ecosystem properties.

In short, 78 plots were established, each measuring 20×20 m. In these plots, different subsets of a species pool of 60 species were sown in spring 2002. The different species were selected to be representative of a Molinio-Arrhenatheretea grasslands[57] and were classified in four functional groups as 'grass' (including Poaceae and one Juncaceae species), small herb, tall herb or legume, with 16, 12, 20 and 12 species in the species pool, respectively. In each plot, 1, 2, 4, 8 or 16 species were sown, with each richness level replicated 16 times. The 16 species mixture plots formed an exception, and were replicated only 14 times. Total sowing density was 1000 seeds per m^2, irrespective of the richness level. Each plot contained a unique species composition. In addition to a species richness gradient, a functional group richness gradient was established, in such a way that sown species and functional group richness were as orthogonal as possible. Functional group richness ranged from 1, 2, 3 and 4, with 34, 20, 12 and 12 replicates, respectively. Due to this experimental design, variation in plant diversity and composition across plots was much larger than in equivalent, non-manipulated grasslands[58], making this experiment particularly useful for linking traits to ecosystem properties. Plots were assigned to four blocks in parallel to the riverside to account for differences in soil properties with increasing distance from

383 the river (with e.g. sand content being higher in plots closer to the Saale river). Each block had a
384 similar number of plots, and each block had all levels of species and functional group richness
385 approximately equally represented.
386 Twice per growing season, plots were weeded in order to avoid species that were not
387 sown in the plots upon establishment. We refer to two other publications[27,28] for more details on
388 the design of the Jena main experiment.
389
390 *Plant community assessments*
391 During the period between 2003 and 2012, twice per year, during spring (May) and
392 summer (August), cover of all target plant species was estimated in each plot, within a 3×3 m
393 subplot. For more details, we refer to Roscher et al. (2013)[38].
394
395 *Ecosystem property measurements*
396 During the years 2003 till 2012, 42 different ecosystem variables ('ecosystem properties'
397 hereafter) were measured, describing plant, faunal and abiotic pools and process rates, some of
398 which were measured aboveground, and some of which were measured belowground. We
399 focused on ecosystem properties that met the criteria of being 'ecosystem functions' according to
400 the definition by de Groot et al (2002)[59]: "the capacity of natural processes and components to
401 provide goods and services that satisfy human needs, directly or indirectly". This definition
402 includes regulatory functions (e.g. those related to biogeochemical cycles, such as soil
403 respiration and nutrient leaching), production functions (e.g. plant above- or belowground
404 biomass, abundances of heterotrophic groups), and habitat functions (i.e. the properties that
405 indicate the capacity of ecosystems to provide habitat, such as diversity levels of invertebrate

406 taxa)[59]. All ecosystem properties were measured in multiple seasons or years, always using
407 standardized protocols. The ecosystem properties measured were: plant biomass consumed by
408 herbivores, herbivory rate, frequency of pollinator visits, abundance of soil surface fauna,
409 richness of soil surface fauna, abundance of vegetation layer fauna, richness of vegetation layer
410 fauna, number of pollinator species, drought resilience, drought resistance, leaf area index, bare
411 ground cover, aboveground plant biomass, dead plant biomass, cover of invasive plant species,
412 richness of invasive plant species, rain throughfall, basal soil respiration, soil respiratory
413 quotient, earthworm biomass, soil larvae abundance, soil mesofauna abundance, soil macrofauna
414 abundance, biomass of soil microbes, biomass of plant roots, downward flux water in upper soil,
415 downward flux water in deeper soil, upward flux water in upper soil, upward flux water in
416 deeper soil, evapotranspiration in upper soil, evapotranspiration in deeper soil, upper soil water
417 content, deep soil water content, inorganic carbon content, organic carbon content, soil bulk
418 density, soil nitrogen content, soil $\delta^{15}N$ values, soil NH_4 content, soil NO_3 content, nitrate
419 leaching and soil phosphorus content (see Table S1.1 for a more detailed overview). Some of the
420 ecosystem properties were directly related to those mentioned in the original paper of the "Holy
421 Grail framework"[7] (e.g. target plant biomass in grasslands that are mown at the end of each
422 growing season represents Net Primary Production), while others were more indirectly related.
423 For example, soil microbial biomass and soil respiration are often linked to decomposition
424 rates[60,61] and soil NH_4 content results from, and is often related to, N mineralization[62]. When
425 ecosystem properties were measured multiple times within a year (e.g. both in spring and
426 summer) within the same plot, we used averages of those repeated measurements in further
427 analyses. For detailed descriptions on the methodology of all ecosystem property measurements,
428 we refer to the Supplementary Materials.

Trait measurements

In total, 41 plant traits were measured. These traits described whole plant, leaf, stem, flower, seed, (fine) root characteristics, and were structural, morphological, chemical, physiological, phenological. The measured traits included all terrestrial plant traits identified as 'most commonly assessed' in our mini-review, except for leaf phosphorus content. For a complete overview of all measured traits, we refer to Table S1.2. The majority of the traits, including most leaf and root traits, were measured in mesocosms filled with Jena field soil mixed with sand in the Botanical Garden of Leipzig (Saxony, Germany), in 2011 and 2012. Mass fraction and number of inflorescences and seedling density were measured in monocultures at the Jena Experiment. Rooting depth and flower duration could not be reliably estimated in the 80 cm high mesocosms and was therefore derived from earlier published measurements[27]. Detailed information on the individual trait measurements is provided in Supplementary Material.

Quantifying Functional Diversity and Functional Identity

We combined the species-level abundance assessments for each plot with the trait measurements to quantify Functional Diversity and Identity in each plot, separately for each combination of year and season. Functional Diversity was calculated for each trait (thus yielding 42 Functional Diversity measures in total) separately using Rao's Quadratic Entropy metric[30] (or Q), which measures the sum of pairwise trait distances of co-occurring species, whereby pairwise distances are weighted by the relative abundance of the species: $\mathrm{Q} = \sum_{i=1}^{S-1} \sum_{j=i+1}^{S} d_{ij}\, p_i p_j$, where i and j are the two species forming a species pair, S is the species richness within a community, d_{ij} is the Euclidean trait distance and p_i and p_j are the relative

abundance of species *i* and *j*, respectively. Here, relative abundances are measured as the species' cover (estimated in subplots of 3 x 3 m, see above) within a plot divided by the total community cover. Functional Identity was measured for each trait (thus also yielding 41 measures in total) using the Community Weighted Mean (CWM) metric[10], which measures the abundance-weighted average of trait values among species within a community as: $CWM = \sum_{i=1}^{S} p_i T_i$, where T_i indicates the trait value of species *i*. We also recalculated FD and CWMs based on presence-absence data (thus ignoring differences in relative abundance of species present in a plot) for sensitivity analyses.

In addition to calculating CWM and FD values, we also calculated the realized species richness for each plot and each year, based on the species-level abundance assessments.

Statistical analyses

We first analyzed how each ecosystem property was related to all 41 measured traits. This was done using a separate Linear Mixed Model (LMM) for each ecosystem property, in which the CWM and Rao's Q values for each trait were treated as fixed factors (thus yielding 2 × 41 = 82 fixed factors), and year and plot were treated as random factors. We used a forward model selection procedure, in which first 'empty' models only containing random factors were fitted, and then significant fixed factors were added step-by-step. We chose a forward model selection procedure to overcome problems related to multicollinearity (many traits, and hence FD and FI metrics, were correlated, see Table S2.2). During each step in our selection procedure, we first tested for the significance of all *n* fixed factors (where *n* = the total number of 82 fixed factors minus the number of fixed factors already included at earlier steps of the model selection procedure) that could be added to the previous, less complex model, using log-likelihood tests.

We then investigated which factor was most significant, and added this factor to the previous model if it did not lead to any Variance Inflation Factor (VIF) exceeding 5. In case the most significant fixed factor did cause multicollinearity (maximum VIF > 5), we investigated if the next-most significant factor could be added. This procedure was repeated until we ended up with a model only containing significant fixed factors with VIF values ≤ 5, to which no significant (P ≤ 0.05) fixed factors could be added. LMM fitting was done using a Restricted Maximum Likelihood procedure, using the lmer function of the lme4 package[63] in R-3.5.1[64]. We calculated the marginal (proportion of variance exclusively explained by fixed factors, i.e. traits) and conditional (proportion of variance explained by fixed factors and random factors combined) R^2 values[65] using the r.squaredGLMM function of the MuMIn package[66] in R-3.5.1[64]. We also performed some sensitivity analyses, in which we repeated the above analyses, with *i*) as the only difference that we corrected for False Discovery Rates[67], to reduce the risk of type I errors, *ii*) as the only difference that FD and CWM values based on presence-absence data were used as predictors and *iii*) where we replaced FD and CWM predictor variables by realized species richness.

We then investigated to which extent the proportion of variance explained by traits only (marginal R^2 values) depended on *i*) whether the ecosystem property was vegetation based, animal based or abiotic, and *ii*) whether it described an above- or belowground ecosystem stock or process. For this we categorized ecosystem properties (see Table S1.1) and we used a linear model to investigate how marginal R^2 values from the final models described above depended on *i*) the 'trophic level' of the ecosystem property (i.e. primarily vegetation-based, heterotroph-based or an abiotic property) and on *ii*) 'stratum' (above- vs. belowground).

We also investigated to which extent links between the Functional Diversity and Identity of traits and ecosystem properties changed, if we analysed ecosystem properties for each year in which they were measured separately. We did this by running the same models and model selection procedure as described above, except that the random factor 'year' was omitted from the models (as ecosystem properties were analyzed for each year separately, this random factor had become obsolete). In addition, the random factor 'plot' was omitted from the models, as we only had one measurement per plot within each year.

To quantify the overlap in significant predictors among different ecosystem properties, we created a 42 (number of ecosystem properties) × 41 (number of traits) binary matrix, with cells containing values of 1 when either the FD and/or the FI of the corresponding trait significantly drove the ecosystem property, and a value of 0 when neither the FD nor the FI significantly drove the ecosystem property. We then calculated the overlap (o) in the sets of traits significantly driving each pair of ecosystem properties, using Sørenson's index[33] as: $o = \frac{|T_i \cap T_j|}{0.5(|T_i| + |T_j|)}$ where $|T_i|$ and $|T_i|$ are the numbers of traits significantly driving respectively ecosystem property *i* and *j*, and $|T_i \cap T_j|$ is the number of traits significantly driving both ecosystem property *i* and *j* and we then calculated the average overlap. Importantly, these overlap estimates could be conservative (i.e. underestimated) due to strong correlations between traits. Therefore, we repeated the above described linear mixed models (originally with 82 fixed factors, corresponding to the FD and FI values of 41 traits), but then using Principal Component Analysis (PCA) axis values based on the FD and FI values as explanatory variables. To this end, we first performed a PCA, and we selected the 15 PCA axes that explained more than 100/82 (the number of input variables) = 1.22% of all FD and FI variation. Together, these 15 PCA axes explained 92% of all FD and FI variation. The selection procedure of models linking ecosystem

520 properties with PCA axes was the same as for the main analyses linking ecosystem properties
521 with FD and FI variables. We then repeated the overlap analysis in the same way as described
522 above, and found that for FD and FI metrics based on PCA variables, the average overlap of
523 13.4% was somewhat, but not much, higher than the overlap based on FD and FI metrics of raw
524 traits.

525 We then analyzed to what extent a subset of the six traits most commonly assessed in
526 other studies, i.e. specific leaf area, plant height, leaf N concentration, leaf dry matter content,
527 stem tissue density and leaf area, could explain variance in ecosystem properties. To this end, we
528 repeated the modeling procedure described above, except that only the above mentioned six traits
529 were assessed in the model selection procedure, rather than the full set of 41 traits. In addition,
530 we also assessed how random subsets of *n* traits, with n ranging from 1 to 40, could explain
531 ecosystem properties. To this end, we ran 100 simulations for each level of *n*. In each of these
532 simulations, we first randomly selected a subset of *n* traits out of the total of 41 traits. For these
533 random subsets of *n* traits, we again ran the same model selection procedure as described above
534 for each ecosystem property, to assess which of the traits significantly drove the levels of each
535 property, and in order to assess the marginal R^2 values of final models. For each simulation, we
536 then calculated the mean (across all ecosystem properties) marginal R^2 value, and for each *n*, we
537 calculated the mode and 95% percentiles for the mean marginal R^2 value across the 100
538 simulations (as reported in Fig. 4). Only for $n = 1$ and $n = 40$ traits this procedure was slightly
539 different, as for both of these levels of *n*, there were only 41 traits or trait combinations possible.
540 Thus, in those cases, we did not take 100 random draws of traits, but instead systematically
541 analysed at all possible combinations. Based on the resulting relationship between the number of
542 traits analyzed and the marginal R^2 values, we fitted a non-linear model using the nls function in

R3.5.3, of the form: $R^2 = \frac{R^2_{max} \cdot n.trait}{K + n.trait}$ in which R^2 is the marginal R^2 value, R^2_{max} is the asymptote in marginal R^2 value, n.trait the number of traits analysed, and K describes the slope by which the R^2_{max} is reached. The resulting R^2_{max} and K values were 0.184 and 19.21 respectively, and these were used to extrapolate the observed relationship between the number of traits analyzed and the marginal R^2 values, in order to calculate how many traits were required to obtain marginal R^2 values of 0.150 and higher.

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SUPPLEMENTARY MATERIALS

S1. SUPPLEMENTARY METHODS

S1.1. Ecosystem property measurements

During the years 2002 until 2012, 42 different ecosystem properties were measured. Some ecosystem properties were measured in multiple seasons or years, although always using standardized protocols. An overview of the different ecosystem properties can be seen in Table S1.1.

Table S1.1. List of all ecosystem properties analyzed in this study. The information in brackets after ecosystem property names indicate whether the ecosystem property was primarily related to heterotrophs (HE), vegetation (VE), or abiotic conditions (AB), and whether it described an aboveground (A) or belowground (B) property.

Ecosystem property	unit	Summary description	Years measured
Consumed plant biomass (HE, A)	g m^{-2}	Biomass consumed by herbivores	2010-2012
Herbivory rate (HE, A)	%	% of leaves damaged	2003-2005, 2010-2012
Frequency pollinator visits (HE, A)	nr	Number of observed pollinator visits	2005, 2006, 2008
Abundance soil surface fauna (HE, A)	nr	Abundance of invertebrates caught in pitfall traps	2003, 2005, 2010
Richness soil surface fauna (HE, A)	nr	Species richness of invertebrates caught in pitfall traps	2003, 2005, 2010
Abundance vegetation layer fauna (HE, A)	nr	Abundance of invertebrates caught via suction sampling	2003, 2005, 2010
Richness vegetation layer fauna (HE, A)	nr	Species richness of invertebrates caught via suction sampling	2003, 2005, 2010
Number of pollinator species (HE, A)	nr	Number of observed pollinator species	2005, 2006, 2008
Drought resilience (VE, A)	g m^{-2}	Resistance biomass production after drought	2009-2012
Drought resistance (VE, A)	g m^{-2}	Resistance biomass production to drought	2008-2012
Leaf Area Index (VE, A)	unitless	Leaf area index (measure of light interception)	2003-2012
Bare ground cover (VE, A)	%	Cover of bare ground	2002-2011
Target plant biomass (VE, A)	g m^{-2}	Aboveground dry mass of target species	2002-2012
Dead plant biomass (VE, A)	g m^{-2}	Aboveground dry mass of dead target species	2003-2008
Cover invasive species (VE, A)	%	Cover of non-target plant species	2003-2007
Richness invasive species (VE, A)	nr	Number of non-target plant species	2003-2007
Rain throughfall (AB, A)	mm	Amount of rainwater reaching lower vegetation layers	2008-2012
Basal soil respiration (HE, B)	µL g^{-1} h^{-1}	Basal soil respiration (proxy of decomposition)	2003-2008, 2010-2012
Soil respiratory quotient (HE, B)	µL g^{-1} h^{-1}	Respiration per biomass soil microbes	2008, 2010-2012
Earthworm biomass (HE, B)	g	Biomass of earthworms	2003-2008
Soil larvae abundance (HE, B)	nr	Number of larvae in soil	2004, 2006, 2008
Soil mesofauna abundance (HE, B)	nr	Count of mesofauna individuals in soil	2004, 2006, 2008
Soil macrofauna abundance (HE, B)	nr	Count of macrofauna individuals in soil	2004, 2006, 2008
Biomass soil microbes (HE, B)	µg C g^{-1}	Biomass of microbes in soil	2003, 2004, 2006-2008, 2010-2012
Biomass plant roots (VE, B)	g	Belowground plant biomass in soil	2003, 2004, 2006-2008, 2011
Downward flux water upper soil (AB, B)	L m^{-2}	Downward flux of water in upper soil	2003-2007
Downward flux water deep soil (AB, B)	L m^{-2}	Downward flux of water in deeper soil	2003-2007
Upward flux water upper soil (AB, B)	L m^{-2}	Upward flux of water in upper soil	2003-2007
Upward flux water deep soil (AB, B)	L m^{-2}	Upward flux of water in deeper soil	2003-2007
Evapotranspiration upper soil (AB, B)	L m^{-2}	Evapotranspiration in upper soil	2003-2007

Evapotranspiration deep soil (AB, B)	L m^{-2}	Evapotranspiration in deeper soil	2003-2007
Upper soil water content (AB, B)	L m^{-2}	Water content in upper soil	2003-2007
Deep soil water content (AB, B)	L m^{-2}	Water content in deeper soil	2003-2007
Inorganic soil carbon (AB, B)	%	Concentration of inorganic carbon in soil	2002, 2004, 2006
Organic soil carbon (AB, B)	%	Concentration of organic carbon in soil	2002, 2004, 2006
Bulk density soil (AB, B)	g m^{-3}	Bulk density soil (proxy for compaction)	2002, 2004, 2006
Nitrogen content soil (AB, B)	%	Soil total nitrogen content	2002, 2004, 2006
Soil 15N (AB, B)	‰	Soil nitrogen isotope ratios	2002, 2004, 2006
Soil NH4 content (AB, B)	µg g^{-1}	Soil ammonium concentration	2002-2008
Soil NO3 content (AB, B)	µg g^{-1}	Soil nitrate concentration	2002-2008
Nitrate leaching (AB, B)	mg m^{-2}	Nitrate leaching	2002-2006
Soil phosphate content (AB, B)	mg L^{-1}	Soil phosphate content	2003-2007, 2009, 2011, 2012

S1.1.1. Consumed plant biomass

Herbivory rates were converted into estimates of consumed plant biomass in three steps. First, the total leaf biomass of a species in a plot was estimated from the species-specific aboveground biomass that included the biomass of leaves, stems, and inflorescences, using the ratio of leaf biomass to total aboveground biomass. Second, the leaf biomass of each species in each mixture was multiplied by the respective herbivory rate to obtain the leaf biomass consumed from this species in gram dry weight per square meter. Third, the total biomass removed from a particular plant community was calculated by summing the consumed leaf biomass over all plant species in the community[68,69].

S1.1.2. Herbivory rate

Large vertebrates were excluded from the experimental site by a fence such that herbivory was only caused by invertebrates (though there was occasional grazing by voles). Herbivory was measured during the biomass harvest twice a year – typically at the end of May and the end of August. Herbivory was measured in five years (2012 to 2014)[68,69]. For each target species present in the sorted biomass samples, usually, 30 fully developed leaves (only 20 in

2012 and 2013) were sampled randomly for herbivory measurements. For species with fewer than the target number of leaves in the sample, all available leaves were measured. The leaf area of all sampled leaves (i.e. the area left after feeding of the herbivores including petioles) was measured with a leaf area meter (LI-3000C Area Meter, LI-COR Biosciences, Lincoln (NE), USA). Herbivore damage (i.e., the leaf area damaged by herbivores in mm^2) was estimated visually by comparing the damaged leaf area to a series of circular and square templates ranging in size from 1 mm^2 to 500 mm^2. Herbivory damage included four different herbivory damage types: chewing, sap sucking, leaf mining and rasping damage. For each leaf, a single value of the total area damaged by all types of herbivory was estimated. Herbivory rates (the proportion of leaf area damage) for each plant species in a mixture was calculated by dividing the estimated area damaged by herbivores by the original leaf area without damage. To obtain the total leaf area before herbivore feeding, we summed the leaf area remaining after feeding by herbivores that was measured with a leaf-area meter and the leaf area removed by chewing herbivores using plant species-specific ratios of herbivory damage types. A community level herbivory rate was calculated by summing the species-specific herbivory rates weighted by their respective relative leaf biomass for each biomass sample. For a detailed description of the methodology used see Meyer et al. 2017[69].

S1.1.3. Frequency of pollinator visits

We observed flower-pollinator interactions within a quadrat of 80x80cm three times during the vegetation period in 2005, 2006 and 2008[70,71]. During the six-minute observation period every interaction was counted as a flower visitation. Observations were only conducted on sunny days between 09:00 and 17:00 h.

835

836 *S1.1.4. Fauna soil surface abundance*

837 For recording the activity abundance of ground-dwelling arthropods, we installed two pitfall
838 traps of 4.5 cm diameter per plot in 2003, 2005, and 2010[72,73]. Traps were replaced six times in
839 2003 and 2005 between May and October, and every two weeks between May and September in
840 2010. In the field we filled traps with 3% formalin, and stored them later in 70% ethanol.

841

842 *S1.1.5. Fauna soil surface species richness*

843 For recording the activity abundance of ground-dwelling arthropods, we installed two pitfall
844 traps of 4.5 cm diameter per plot in 2003, 2005, and 2010[72,73]. Traps were replaced six times in
845 2003 and 2005 between May and October, and every two weeks between May and September in
846 2010. In the field we filled traps with 3% formalin, and stored them later in 70% ethanol.

847

848 *S1.1.6. Fauna vegetation abundance*

849 For recording the abundance of vegetation-associated arthropods we used suction sampling in
850 2003, 2005, 2010[72,73]. Five (2003 and 2005) and nine (2010) times during the vegetation period
851 we randomly placed cages of 0.75 m^3, cleared them from arthropods, and stored all sampled
852 animals in 70% ethanol.

853

854 *S1.1.7. Fauna vegetation species richness*

855 For recording the species richness of vegetation-associated arthropods we used suction sampling
856 in 2003, 2005, 2010[72,73]. Five (2003 and 2005) and nine (2010) times during the vegetation
857 period, we randomly placed cages of 0.75 m3 and cleared them from arthropods. We stored all

858 sampled animals in 70% ethanol and sent them to external taxonomists for species-level
859 identification.
860
861 *S1.1.8. Pollinator species richness*
862 We observed flower-pollinator interactions within a quadrat of 80x80cm three times per year in
863 2005, 2006 and 2008[70,71]. During the six-minute observation period we identified every flower-
864 visiting insects to species or morphospecies. Unknown species were captured for later
865 identification. Observations were only conducted on sunny days between 09:00 and 17:00 h.
866
867 *S1.1.9. Drought resilience*
868 We used data from the drought experiment established as 1x1 m subplots on 76 plots of the Jena
869 Main Experiment in 2008. The two subplots per plot were designated as either drought or
870 ambient control using rainout shelters constructed using wooden frames and transparent PVC
871 roofs[74] (see Vogel et al. 2013 for details). Rainwater was collected in rain barrels and used to
872 water ambient subplots following rainfall events[74,75]. Shelters were set up mid-summer and
873 excluded natural rainfall from mid-July to the end of August (six weeks). Standing biomass was
874 harvested in May and August (before removal of the shelters) as described for standing
875 aboveground biomass.
876 We calculated resilience from our biomass data according to van Ruijven and Berendse[76].
877 Resilience determines the change in biomass production after perturbation and was calculated as
878 difference of post-drought biomass and the corresponding ambient treatment from the first
879 harvest after drought (May the following year).
880

S1.1.10. Drought resistance

Drought resistance was calculated based on the same data as drought resilience (S1.1.9). We calculated resistance from our biomass data according to van Ruijven and Berendse[76] as the difference of biomass under perturbed and unperturbed conditions (drought - ambient) at the end of the drought period in August.

S1.1.11. Leaf area index

Community leaf area index (LAI) was measured twice a year just before biomass harvest (see S1.1.13) with a LAI-2000 plant canopy analyzer (LI-COR) using high resolution and a view cap masking 45° of the azimuth towards the operator. In 2003 and 2004, 10 randomly allocated measurements were taken at 5 cm height within an area of 3 x 3 m in the center of the core area. From 2005 onwards all measurements were taken along a 10 m transect in the core area of each experimental plot. One above reading was taken at the first transect point, followed by 10 below readings taken with 1 m distance from each other. We used the mean over the 10 calculated LAI values from the below readings as mean community LAI per plot.

S1.1.12. Bare ground cover

Bare ground cover was visually estimated together with sown species cover in September 2002 and twice a year just before biomass harvest. Bare ground cover was estimated directly as percentage of area. From 2002 to 2004, measurements were taken in two extra carefully weeded sub-areas of 2 x 2.25 m. We report the average value based on these two estimates for community cover. From 2005 onwards all measurements were taken in one 3 x 3 m area in the core area of each experimental plot.

904

905 *S1.1.13. Target aboveground plant biomass*

906 Aboveground community biomass was harvested twice a year just prior to mowing (during peak
907 standing biomass in late May and in late August) on all experimental plots. This was done by
908 clipping the vegetation at 3 cm above ground in two to four randomly selected rectangles of 0.2 x
909 0.5 m per plot. The harvested biomass was sorted into sown species, total weeds and detached
910 dead organic material and dried to constant weight (70°C, ≥ 48 h). Target aboveground plant
911 biomass was calculated as the sum of biomass for all sown species from all rectangles per plot.

912

913 *S1.1.14. Dead plant biomass*

914 Sum of biomass of detached dead organic material from all rectangles per plot as described in
915 target aboveground plant biomass.

916

917 *S1.1.15. Cover invasive species*

918 Cover of invader species was visually estimated to the nearest percentage before weeding (spring
919 = April, summer = July) on the same subplot size as used for the quantification of invader species
920 richness (S1.1.16) in each large plot from 2003 to 2007. In the field, invader species cover was
921 separately recorded for internal invader species (i.e. species belonging to the experimental species
922 pool, but not to the sown species composition of the respective plot) and external invader species
923 (i.e. species not belonging to the experimental species pool). Cover of internal and external invader
924 species was summed to get the total cover of invader species[77].

925

926 *S1.1.16. Richness invasive species*

927 Within each large plot one subplot of 2.00 × 2.25 m was permanently marked to quantify invasion
928 resistance from 2003 to 2007. All invader species present in this subplot were recorded before
929 weeding (spring = April, summer = July) to assess invader species richness[77].
930
931 *S1.1.17. Rain throughfall*
932 In biweekly intervals from 2008 to 2012, throughfall volume was collected with rain collectors
933 (2-L sampling bottles connected to funnels [diameter of 0.12 m], both polyethylene). The
934 sampling bottles were protected against larger particles and small animals with a polyethylene
935 net (0.005 m mesh width). The collectors were cleaned with deionized water before installation
936 and replaced by clean collectors in 2- to 3-month intervals.
937
938 *S1.1.19. Basal soil respiration*
939 In each year, five randomly located soil samples were taken per plot with a soil corer (5 cm
940 diameter, 5 cm deep) and pooled plot-wise. Before measuring, all samples were homogenized,
941 sieved (2 mm), larger roots and soil animals were picked by hand, and samples were stored in
942 plastic bags at 5°C. Microbial respiration was measured using an electrolytic O_2-
943 microcompensation apparatus[78]. O_2 consumption of soil microorganisms in ~5 g of fresh soil
944 (equivalent to c. 3.5 g soil dry weight) was measured at 22°C over a period of 24 h. Basal
945 respiration [μL O_2 g^{-1} dry soil h^{-1}] was calculated as mean of the O_2 consumption rates of hours
946 14 to 24 after the start of the measurements.
947
948 *S1.1.19. Soil respiratory quotient*

In each year, five randomly located soil samples were taken per plot with a soil corer (5 cm diameter, 5 cm deep) and pooled plot-wise. Before measuring, all samples were homogenized, sieved (2 mm), larger roots and soil animals were picked by hand, and samples were stored in plastic bags at 5°C. Microbial respiration was measured using an electrolytic O_2-microcompensation apparatus[78]. O_2 consumption of soil microorganisms in ~5 g of fresh soil (equivalent to c. 3.5 g soil dry weight) was measured at 22°C over a period of 24 h. Basal respiration [µL O_2 g^{-1} dry soil h^{-1}] was calculated as mean of the O_2 consumption rates of hours 14 to 24 after the start of the measurements. Substrate-induced respiration (SIR) was determined by adding D-glucose to saturate catabolic enzymes of the microorganisms according to preliminary studies (4 mg D-glucose g^{-1} dry soil solved in 400 µL deionized water[79]. The maximum initial respiratory response (MIRR; [µL O_2 g^{-1} dry soil h^{-1}]) was calculated as mean of the lowest three O_2-consumption values within the first 10 h after glucose addition. Microbial biomass carbon [µg C g^{-1} dry soil] was calculated as 38 × MIRR[80]. The soil respiratory quotient was calculated by dividing basal respiration by microbial biomass[81].

S1.1.20. Earthworm biomass

Earthworm extractions were performed on one subplot of 1 x 1 m per plot that was established to extract earthworms repeatedly. Subplots were enclosed with PVC shields aboveground (20 cm) and belowground (15 cm). Two earthworm extraction campaigns were performed twice per year in spring and autumn of 2005, 2006, and 2008 by electro-shocking[82]. Therefore, a combination of four octet devices (DEKA 4000, Deka Gera¨ tebau, Marsberg, Germany; Thielemann[83]) was used which were powered by two 12 V car batteries. Eight steel rods (length 60 cm) were

971 inserted into the soil (to a depth of w55 cm) per octet device forming four circles of six rods
972 (each 50 cm in diameter) with two rods in the center of each
973 circle. An electrical voltage was applied in pulses to the moist soil (earthworm extractions were
974 always performed during humid and mild weather conditions) sequentially to pairs of rods in
975 the circle (negative pole) and in the center of the circle (positive pole). In each subplot
976 earthworm extraction was performed for 35 min, increasing the voltage from 250 V (10 min) to
977 300 V (5 min), 400 V (5 min), 500 V (5 min), and 600 V (10 min). Despite the PVC shields,
978 earthworms re-colonized earthworm subplots until the next extraction campaign[82]. Extracted
979 earthworms were identified, counted and weighed in the laboratory.
980
981 *S1.1.21. Soil larvae abundance*
982 Soil macrofauna was collected from soil cores taken to a depth of 10 cm in autumn 2004
983 (October), 2006 (November) and 2008 (October). Soil cores were taken using a steel corer (22
984 cm diameter). One soil core per plot was taken, and soil animals were extracted by heat[84],
985 collected in diluted glycerol, and transferred into ethanol (70%) for storage. Soil animals were
986 identified[85-87] and counted. A detailed list of soil animal taxa and their trophic assignment is
987 given in Eisenhauer et al. (2011)[88].
988
989 *S1.1.22. Soil mesofauna abundance*
990 Soil mesofauna was collected from soil cores taken to a depth of 10 cm in autumn 2004
991 (October), 2006 (November) and 2008 (October). Soil cores were taken using a steel corer (5 cm
992 diameter). One soil core per plot was taken, and soil animals were extracted by heat[84], collected
993 in diluted glycerol, and transferred into ethanol (70%) for storage. Soil animals were identified[85-

994 [87] and counted. A detailed list of soil animal taxa and their trophic assignment is given in
995 Eisenhauer et al. (2011)[88].
996
997 *S1.1.23. Soil macrofauna abundance*
998 Soil macrofauna was collected from soil cores taken to a depth of 10 cm in autumn 2004
999 (October), 2006 (November) and 2008 (October). Soil cores were taken using a steel corer (22
1000 cm diameter). One soil core per plot was taken, and soil animals were extracted by heat[84],
1001 collected in diluted glycerol, and transferred into ethanol (70%) for storage. Soil animals were
1002 identified[89-91] and counted. A detailed list of soil animal taxa and their trophic assignment is
1003 given in Eisenhauer et al. (2011)[88].
1004
1005 *S1.1.24. Soil microbial biomass*
1006 In each year, five randomly located soil samples were taken per plot with a soil corer (5 cm
1007 diameter, 5 cm deep) and pooled plot-wise. Before measuring, all samples were homogenized,
1008 sieved (2 mm), larger roots and soil animals were picked by hand, and samples were stored in
1009 plastic bags at 5°C. Soil microbial biomass respiration was measured using an electrolytic O_2-
1010 microcompensation apparatus[78]. O_2 consumption of soil microorganisms in ~5 g of fresh soil
1011 (equivalent to c. 3.5 g soil dry weight) was measured at 22°C over a period of 24 h. Substrate-
1012 induced respiration (SIR) was determined by adding D-glucose to saturate catabolic enzymes of
1013 the microorganisms according to preliminary studies (4 mg D-glucose g^{-1} dry soil solved in 400
1014 µL deionized water[55]). The maximum initial respiratory response (MIRR; [µL O_2 g^{-1} dry soil h^{-1}])
1015 was calculated as mean of the lowest three O_2-consumption values within the first 10 h after

glucose addition. Microbial biomass carbon [µg C g^{-1} dry soil] was calculated as 38 × MIRR[80]. The soil respiratory quotient was calculated by dividing basal respiration by microbial biomass[81].

S1.1.25. Plant root biomass

Standing root biomass was sampled down to 30 cm depth in all plots in June 2003, September 2004, and June 2006, 2008 and 2011. Two monoculture plots were excluded because of poor establishment. In all years we took several soil cores per plot and processed the pooled samples (2003: 5 cores with 4.8 cm diameter; 2004: 3 cores with 4.8 cm diameter; 2006: 5 cores with 8.7 cm diameter; 2008: 3 cores with 4.8 cm diameter; 2011: 3 cores with 3.5 cm diameter). The cores were cooled (4 °C; frozen in 2006) until further handling. The bulk material of the pooled cores was weighed and cut to 1 cm pieces before subsampling. For root washing, a 50 g subsample was soaked in water and then repeatedly rinsed with tap water over a 0.5 mm sieve. In 2011, the full bulk sample was washed for root material. Roots were dried at 60 – 70 °C and weighed subsequently.

S1.1.26. Upper (0-30 cm) and deep (0-70 cm) soil water content

Volumetric soil water contents were measured with frequency domain reflectometry (FDR) using a mobile manual FDR probe (PR1/6 and PR2/6, Delta-T-Devices, Cambridge, UK) on all plots in 1–2 weekly resolution in the 0.1, 0.2, 0.3, 0.4, and 0.6 m soil depths[92,93].
Soil water contents per plot were aggregated to depth-weighted means for the 0-0.3 m ("upper soil") and 0.3-0.7 m ("deep soil") soil layers. At a central automatic meteorological station on the field site, soil water contents in the 0.08, 0.16, 0.32, and 0.64 m soil depths were measured with Theta Probe soil moisture sensors – ML2x (Delta-T Devices, Cambridge, UK) in 10-min

resolution between 1 July 2002 and 31 December 2007 and aggregated to daily depth-weighted means for the 0.0-0.3 and 0.3-0.7 m soil layers. To obtain a complete soil water contents data set for the 0.0-0.3 and 0.3-0.7 m soil layer per plot for the years 2003-2007, data gaps were filled with Bayesian hierarchical models using the soil water contents from the central meteorological station as explanatory variable[72].

S1.1.27. Downward and upward flux and evapotranspiration of soil water, in upper and deep soil

A water balance model was used to simulate downward and upward water fluxes and actual evapotranspiration from the 0-0.3 m ("upper soil") and the 0.3-0.7 m ("deep soil") soil layers per plot for the years 2003-2007 in weekly resolution[93]. The model uses the input variables precipitation (measured at the central meteorological station in 10-min resolution), potential evapotranspiration (calculated from meteorological data from the central station using the Penman-Wendling equation), and volumetric soil water contents (see S1.1.26). The model is based on the water balance equation: precipitation + upward flux = downward flux + actual evapotranspiration - change in volumetric soil water content between two subsequent observation dates. The percentage of roots in each soil layer was used as a proxy for the percentage of potential evapotranspiration that could be evaporated from the respective soil layer. Together with using the net flux (downward flux - upward flux) from the upper soil layer as input into the deep soil layer, this allowed for modeling of the water fluxes for the two soil layers 0-0.3 m and 0.3-0.7 m separately[94].

S1.1.28. Inorganic and organic soil carbon

Total carbon concentration was analyzed biannually on ball-milled sub-samples by an elemental analyzer at 1150 °C (Elementaranalysator vario Max CN, Elementar Analysensysteme GmbH, Hanau, Germany). To determine the organic carbon concentration we measured inorganic carbon concentration by elemental analysis at 1150 °C after removal of organic carbon for 16 h at 450 °C in a muffle furnace. Organic carbon concentration was then calculated from the difference between both measurements[95,96].

S1.1.29. Soil bulk density

In 2002, soil bulk density in the plough horizon was determined on 27 plots from undisturbed soil samples with a depth resolution of 10 cm. The respective samples were taken with a metal bulk density ring of 10 cm height, passed through a sieve with 2 mm mesh size, dried to constant weight at 105 °C and were subsequently weighed to calculate the density. The chosen plots represented a spatial gradient across the field site and resulted in average soil bulk density estimations at the beginning of the experiment. Starting in 2004 all bi-annually soil samples were taken with the split tube sampler, dried and weighed to detect changes in the bulk density. The inner diameter of the soil corer was used for volume calculation[95].

S1.1.30. Total soil nitrogen

Total nitrogen concentration was analyzed bi annually on ball-milled sub-samples by an elemental analyzer at 1150 °C (Elementaranalysator vario Max CN, Elementar Analysensysteme GmbH, Hanau, Germany)[95,96].

S1.1.31 Soil $\delta^{15}N$ values

Soil nitrogen isotope ratios (i.e. bulk soil $\delta^{15}N$ values) were measured every two years from 50 mg of dried soil (after grinding with a ball-mill) with an IRMS (Delta C prototype IRMS, Finnigan MAT)[97].

S1.1.32. Soil NH_4 and soil NO_3

Each autumn from 2002 to 2008, five soil cores (diameter 0.01 m) were taken at a depth of 0 to 0.15 m of the mineral soil from each of the experimental plots and pooled. As an estimate of plant-available N, NO_3-N and NH_4-N concentrations were determined by extraction of soil samples with 1 M KCl solution[95]. Nitrate-N and NH_4-N concentrations were measured in the soil extract with a Continuous Flow Analyzer (CFA, 2003–2005: Skalar, Breda, Netherlands; 2006–2008: AutoAnalyzer, Seal, Burgess Hill, United Kingdom).

S1.1.33. Nitrate leaching

Nitrate leaching was calculated by multiplying soil NO3 concentrations (see S1.1.32) with downward fluxes of soil water (0-30 cm depth) (S1.1.27).

S1.1.34. Soil Phosphate

Concentrations of soil phosphate were determined in soil solution, which was collected every two weeks (cumulative sample) between 2003 and 2007, 2009, 2011 and 2012 using suction plates with permanent vacuum at 30cm soil depth. Soil solution samples were then analysed photometrically with Continuous Flow Analysis (CFA; see 1.1.32). From these biweekly measurements, an annual average was calculated for each plot.

S1.2. Trait measurements

Table S1.2: Overview of traits

Trait	Unit	Description
shoot:root ratio	g g^{-1}	Shoot mass per root mass
shoot:root N ratio	unitless	Leaf nitrogen uptake / root nitrogen uptake
plant height	cm	Standing height of the shoot
leaf biomass production rate	g day^{-1}	Maximum daily leaf dry mass production
total leaf area	cm^2	Total area of all leaves of plant
leaf area	mm^2	Average area of a single leaf
leaf thickness	mm	Leaf thickness
specific leaf area	mm^2 g-^{1}	Fresh leaf area per leaf dry mass
leaf specific density	g cm^{-3}	Leaf dry weight per leaf fresh volume
leaf area ratio	cm^2 g^{-1}	Leaf area per shoot mass
leaf form coefficient	mm^2 mm	Leaf area divided by leaf perimeter
leaf dry matter content	g g^{-1}	Leaf dry weight per leaf fresh weight
leaf C content	%	Leaf carbon content
leaf N content	%	Leaf nitrogen Content
leaf conductance	µM s^{-1} A^{-1}	Stomatal conductance per leaf area
leaf toughness	N	Leaf resistance to penetration
stem diameter	mm	Diameter of stem
stem specific density	g cm^{-3}	Stem dry weight per stem fresh volume
erectness	cm cm^{-1}	Stretched height per standing height
biomass fraction inflorescence	mg mg^{-1}	Inflorescence:shoot biomass fraction
inflorescences per shoot	nr	Number of inflorescences per shoot
duration flowering	ordinal	Duration of flowering period
seeds projected area	mm^2	Total area of individual seed
nr seedlings	nr	Number of plant seedlings within subplot
seed weight	g	Weight of 1000 seeds
seed width length ratio	mm mm^{-1}	Ratio of seed width to seed length
seed dry matter content	g g^{-1}	Seed dry weight per seed fresh weight
root area	cm^2	Root area
rooting depth	ordinal	Depth of the root system
root area distribution	unitless	Evenness of vertical root area distribution
specific root area	cm^2 g^{-1}	Root surface area per root mass
specific root length	cm g^{-1}	Root length per root mass
root tissue density	g cm^{-3}	Root dry weight per root volume
root nitrogen uptake	mg day^{-1}	Nitrogen uptake into roots
root CN ratio	unitless	Root total carbon:nitrogen content
root P content	‰	P content per root dry biomass
root K content	‰	K content per root dry biomass
root S content	‰	S content per root dry biomass
root Ca content	‰	Ca content per root dry biomass
root Na content	‰	Na content per root dry biomass
nutrient uptake efficiency	mg g^{-1}	Root nitrogen uptake:root biomass

Most of the functional traits listed in Table S1.2 (except for the seed traits and biomass fraction of inflorescences, number of inflorescences per shoot and number of seedlings) were measured in mesocosms. To this end, we obtained seeds of all 60 plant species used in the Jena Biodiversity Experiment from a seed supplier (Rieger Hoffmann GmbH, Blaufelden-Raboldshausen, Germany and Saaten Zeller e.K., Riedern, Germany). In April 2011 and 2012 we germinated the seeds in petri dishes and we planted seedlings of 1-3 weeks old into mesocosms, with for each species five replicates. Seedlings that dead within 4 weeks after transplanting were replaced. Mesocosms were made of PVC pipes (height = 60 cm, diameter = 15 cm). Mesocosms were placed outside in the Botanical Garden of Leipzig (Germany), in randomized blocks. Traits were measured after 12 weeks. For more details of the mesocosm design, we refer to Schroeder-Georgi *et al.*[6].

For detailed methods on the trait measurements of shoot:root ratio, plant height, leaf biomass production rate, total leaf area, leaf area, leaf thickness, specific leaf area, leaf specific density, leaf area ratio, leaf dry matter content, leaf C content, leaf N content, leaf conductance, leaf toughness, stem specific density, erectness, root area distribution, specific root area, specific root length, root tissue density, root nitrogen uptake, root C:N ratio, we refer to Schroeder-Georgi *et al.*[6]. Shoot:root N ratio was calculated as the leaf nitrogen uptake divided by the root nitrogen uptake, based on measurements of Schroeder-Georgi *et al.*[6]. Leaf form coefficient was calculated as the leaf area (see above) divided by the leaf perimeter. Leaf perimeter was measured on the same picture from samples as leaf area, using the software WinFolia (Regent Instruments Inc., Canada). Stem diameter was measured on the same stems as those used for stem specific density[6] and defined as the diameter of a stem in mm. Nitrogen uptake efficiency was calculated as the root nitrogen uptake divided by the root dry biomass (measurements from Schroeder-Georgi *et*

al.[6]). Root area was based on the root area measurements of Schroeder-Georgi *et al.*[6]. Duration of flowering was defined as the duration of the flowering period, and expressed using an ordinal scale: 1 (1 month), 2 (2 months), 3 (3 months) and 4 (more than three months). Root element contents (P, K, S, Ca, Na) were analyzed using a subsample of dried fine root material of each mesocosm. A microwave digestion system (Berghof Speedwave SW-2) was used to digest 0.2 g ground material for 50 min at 190° using 8ml HNO3, 3ml H2O2. The method was tested using standard reference material. Samples were analyzed using ICP-OES (Spectro Acros, Spectro Analytical Instrument). Seed traits were measured on a subsample of the seeds purchased for the mesocosm experiment (see above). Seeds were cleaned from all attached tissue (e.g. bracts from grass spikelets), placed in batches of 30 - 200 well apart in glass petri dishes and scanned using a flatbad scanner (resolution 800 dpi) and analyzed using WinSeedle (Reg. 2009a, Regent Instruments Inc., Canada). WinSeedle output provided data on seed length, seed width and seed projected area for individual seeds from each image. Seed projected area and seed width to length ratio were calculated as mean over individual seed measures per species. Seed batches were weighed fresh, dried (70°, 48 h), and weight again to calculate seed dry matter content as dry weight per fresh weight for the total seed batch and the weight of 1000 seeds per species using the seed number measured with WinSeedle and seed dry weight. Data on duration of flowering was obtained from Roscher et al. 2004[27]. Rooting depth was also obtained from Roscher et al. 2014[27]. It was measured on an ordinal scale: 1 (up to 20 cm), 2 (up to 40 cm), 3 (up to 60 cm), 4 (up to 100 cm) and 5 (> 100 cm). Biomass fraction of inflorescence ($mg_{inflorescence}$ mg^{-1}_{shoot}) and number of inflorescences per shoot were recorded in the small-area monocultures of the field experiment (between 2006 and 2009) or in a low-diversity mixture for three species not abundant enough in the monocultures. Five to seven shoot per species were

sampled. In the laboratory, the number of inflorescences per shoot was counted. Afterwards shoots were separated into compartments (stems, leaves and reproductive parts), the compartments were dried (48 h, 70°C) and weighed. The mass of reproductive parts was divided by summed biomass of all compartments per shoot to derive inflorescence mass fraction[77].

The number of seedlings (i.e. plant individuals with cotyledons) was counted in all small-area monocultures three times (April, July, October) in 2007 to account for species-specific differences of seedling emergence. Three quadrats of 0.3 × 0.3 m size per subplot were randomly placed for each census. Total numbers of emerged seedlings per m^2 were calculated for each monoculture based on pooled data from all census dates[98].

Table S1.3. Pearson correlation coefficients between traits.

	shoot root ratio	shoot:root N ratio	plant height	leaf biomass production rate	total leaf area	leaf area	leaf thickness	specific leaf area	leaf specific density	leaf area ratio	leaf form coefficient	leaf dry matter content	leaf C content	leaf N content	conductance	toughness	stem diameter	stem specific density	erectedness	biomass inflorescence	inflorenes per shoot	duration flowering	seeds projected area	nr seedlings	seed weight	seed width length ratio	seed dry matter content	root area	rooting depth	root area distribution	specific root area	specific root length	root tissue density	root nitrogen uptake	root CN ratio	root P content	root K content	root S content	root Ca content	root Na content	nutrient uptake efficiency
shoot root ratio		0.17	0.07	-0.3	0.01	-0.3	0.09	0.33	-0.2	-0.3	0.36	-0.2	-0	0.32	0.04	-0.3	-0.3	0.28	-0.3	-0.2	-0.1	0.25	-0.2	-0	-0.2	0.15	0.21	-0.3	-0.2	-0.2	0.2	0.14	-0.2	-0.5	-0.4	0.24	-0	0.39	0.03	0.43	0.38
shoot:root N ratio	0.17		-0.1	-0.2	-0.3	-0	0.24	0.15	0.21	0.24	0.03	-0.2	-0.5	-0.1	-0.1	0.14	-0.1	-0	0.34	0.18	-0.3	-0.1	0	-0.1	-0.4	-0.3	-0.2	-0.3	-0.3	-0.2	0.54	0.55	-0.3	-0.3	0.19	-0.2	0.41	-0.1	-0	-0.1	0.42
plant height	0.07	-0.1		0.37	0.27	-0.1	-0.2	-0.2	-0	-0.5	-0.3	0.47	0.2	-0.2	0.07	0.27	-0.1	0.3	0.46	-0.1	-0.1	-0.1	-0.1	-0.1	-0.1	-0.1	0.45	0.27	0.4	0.25	-0.2	-0.2	0.09	0.04	0.39	-0.4	-0.3	-0.4	-0.1	-0.2	-0.2
leaf biomass production rate	-0.3	-0.2	0.37		0.53	0.03	-0.1	-0.2	0.12	-0.3	-0.3	0.38	0.03	-0.5	-0.1	0.46	0.07	0.21	0.18	-0	-0.1	-0.2	-0.1	-0	-0.1	-0.4	0.27	0.63	0.34	0.23	-0.2	-0.1	0.22	0.46	0.58	-0.6	-0.3	-0.5	-0.1	-0.3	-0.4
total leaf area	0.01	-0.1	0.27	0.53		-0.1	-0.2	0.03	-0.1	-0	0.25	0.17	0.32	-0.1	0.04	0.16	0	0.02	-0	-0	-0.1	0.12	-0.1	0.08	-0.2	-0.2	0.14	0.29	0.21	0.23	-0.1	-0.1	0.09	0.42	0.19	-0.2	-0.3	-0	-0.1	-0	-0.2
leaf area	-0.3	-0	-0.1	0.03	-0.1		0.15	-0.4	0.19	0.15	-0.1	-0.2	-0.4	-0.3	0.1	-0.3	0.72	-0.4	0.03	0.36	0.23	0.15	0.45	0.03	0.09	-0.1	-0.4	0	0.4	0.31	-0.4	-0.4	0.4	0.16	0.27	-0	0.02	-0.2	0.09	-0.2	-0.2
leaf thickness	0.09	0.24	-0.2	-0.1	-0.2	0.15		-0.2	0.23	0.06	0.18	-0.4	-0.4	-0.1	-0.1	-0.1	0.22	-0.2	0	0.25	-0.1	0.05	-0.1	-0.1	-0.1	0.03	-0.2	-0.1	-0.1	-0.4	-0	-0	0.14	-0.3	-0.1	0.11	0.25	0.08	0.04	0.16	0.04
specific leaf area	0.33	0.15	-0.2	-0.2	0.03	-0.4	-0.2		-0.2	0.31	0.27	-0	0.15	0.32	0.07	-0.2	-0.5	0.2	-0.1	-0.3	-0	-0	-0.2	0.14	-0.2	0.06	0.14	-0.2	-0.6	-0.4	0.44	0.42	-0.3	-0.4	-0.3	0.06	0.05	0.25	-0.2	0.14	0.3
leaf specific density	-0.2	0.21	-0	0.12	-0.1	0.19	0.23	-0.2		0.1	-0.2	0	-0.4	-0.1	-0.2	0.46	0.15	-0.2	0.19	0.23	0.06	-0.1	0.19	-0.1	-0.1	-0	-0.3	0.29	0.02	0.02	0.12	-0	-0.1	0.36	0.2	-0.2	0.09	-0.2	-0.1	-0.2	-0.1
leaf area ratio	-0.3	0.24	-0.5	-0.3	-0	0.15	0.06	0.31	0.1		0.17	-0.3	-0.1	0.21	-0.1	-0.2	0.13	-0.4	0.12	0.18	0.26	0.09	0.1	0.25	0.1	0.04	-0.5	-0.2	-0.3	-0.2	0.17	0.07	-0	0.1	-0.2	0.28	0.35	0.23	0.01	-0.1	0.31
leaf form coefficient	0.36	0.03	-0.3	-0.3	0.25	-0.1	0.18	0.27	-0.2	0.17		-0.3	0.12	0.38	0.1	-0.4	-0.1	-0	-0.3	-0.1	0.04	0.37	-0.2	0.09	-0.3	0.28	-0	-0.3	-0.3	-0.1	0.08	-0	-0.1	-0.3	-0.4	0.5	0.21	0.48	-0	0.37	0.18
leaf dry matter content	-0.2	-0.2	0.47	0.38	0.17	-0.2	-0.4	-0	0	-0.3	-0.3		0.39	-0.1	-0	0.56	-0.4	0.28	0.08	0.04	-0.1	-0.4	0.03	-0.1	0.08	-0.1	0.32	0.42	0.16	0.05	-0	0.12	0.05	0.18	0.35	-0.5	-0.2	-0.4	-0.1	-0.6	-0.3
leaf C content	-0	-0.5	0.2	0.03	0.32	-0.4	-0.4	0.15	-0.4	-0.1	0.12	0.39		0.47	0.18	-0.1	-0.4	0.15	-0.1	-0.3	-0	-0.1	0.1	0.06	0.4	0.3	0.3	-0.1	0.12	-0	-0.2	-0.2	-0.1	-0	-0.3	0.25	-0.2	0.31	0.14	0.11	-0.1
leaf N content	0.32	-0.1	-0.2	-0.5	-0.1	-0.3	-0.1	0.37	-0.1	0.21	0.38	-0.1	0.47		0.18	-0.3	-0.3	-0.1	-0.2	-0.2	0.12	0.15	0.03	-0	0.23	0.49	-0	-0.4	-0.1	-0.2	0.06	-0	-0.2	-0.2	-0.8	0.6	-0.2	0.58	0.1	0.36	0.28
conductance	0.04	-0.1	0.07	-0.1	0.04	0.1	-0.1	0.07	-0.2	-0.1	0.1	-0	0.18	0.18		-0.3	-0	0.06	-0.2	-0.1	0.32	0.11	0.05	0.02	0.01	0.27	0.08	-0.3	0.15	0.13	-0.3	-0.3	0.14	-0.3	-0	0.13	-0.1	0.04	-0.1	0.06	-0
toughness	-0.3	0.14	0.27	0.46	0.16	-0.3	-0.1	-0.2	0.46	-0.2	-0.4	0.56	-0.1	-0.3	-0.3		-0.2	0.06	0.21	0.06	-0.3	-0.4	-0.1	-0.1	-0.2	-0.4	0.06	0.58	0.04	0.01	0.28	0.28	-0.2	0.32	0.48	-0.6	-0.1	-0.5	-0.2	-0.4	-0.2
stem diameter	-0.3	-0.1	-0.1	0.07	-0	0.72	0.22	-0.5	0.15	0.13	-0.1	-0.4	-0.4	-0.3	-0	-0.2		-0.4	0.08	0.24	0.4	0.28	0.18	0.11	0.11	-0.1	-0.3	0.02	0.37	0.25	-0.4	-0.4	0.32	0.32	0.23	-0	-0.1	-0.1	0.12	-0	-0.3
stem specific density	0.28	-0	0.3	0.21	0.02	-0.4	-0.2	0.2	-0.2	-0.4	-0	0.28	0.15	-0.1	0.06	0.06	-0.4		-0.1	-0.3	-0.2	-0.3	-0.3	0	-0.2	-0.1	0.78	0.03	0.05	-0.1	0.05	0.19	-0	-0.1	0.16	-0.3	-0.1	-0.1	-0.1	-0.2	0.13
erectedness	-0.3	0.34	0.46	0.18	-0	0.03	-0	-0.1	0.19	0.12	-0.3	0.08	-0.1	-0.2	-0.2	0.21	0.08	-0.1		0.08	-0.2	-0.1	0.07	0.09	-0.1	-0.4	-0.1	0.19	0.09	0.07	0.07	0	-0	0.09	0.38	-0.4	-0	-0.3	-0	-0.1	-0.1
biomass inflorescence	-0.2	0.18	-0.1	-0	-0	0.36	0.25	-0.3	0.23	0.18	-0.1	0.04	-0.3	-0.2	-0.1	0.06	0.24	-0.3	0.08		-0.1	-0	0.23	-0.2	-0.1	-0.2	-0.3	-0.1	-0.1	-0	0.05	0.16	0.29	0.19	0.12	0.05	0.26	-0	-0.1	-0.3	-0.1
inflorences per shoot	-0.1	-0.3	-0.1	-0.1	-0.1	0.23	-0.1	-0	0.06	0.26	0.04	-0.1	-0	0.12	0.32	-0.3	0.4	-0.2	-0.2	-0.1		0.28	0.05	0.23	0.19	0.26	-0.1	-0.1	0.16	0.11	-0.3	-0.4	0.18	0.2	-0.1	0.21	-0.1	0.13	0.09	0.06	-0.1
duration flowering	0.25	-0.1	-0.1	-0.2	0.12	0.15	0.05	-0	-0.1	0.09	0.37	-0.4	-0.1	0.15	0.11	-0.4	0.28	-0.3	-0.1	-0	0.28		0.03	0.23	-0.1	0.12	-0.2	-0.3	-0.1	0.25	-0.2	-0.4	-0.1	-0.3	-0.3	0.34	-0.1	0.39	0.07	0.42	0.18
seeds projected area	-0.2	0	-0.1	-0.1	-0.1	0.45	-0.1	-0.2	0.19	0.1	-0.2	0.03	0.1	0.03	0.05	-0.1	0.18	-0.3	0.07	0.23	0.05	0.03		-0	0.58	0.02	-0.3	-0.1	0.19	0.15	-0.3	-0.3	0.15	0.08	-0	0.13	0	0.16	0.47	0.06	0.07
nr seedlings	-0	-0.1	-0.1	-0	0.08	0.03	-0.1	0.14	-0.1	0.25	0.09	-0.1	0.06	-0	0.02	-0.1	0.11	0	0.09	-0.2	0.23	0.23	-0		-0.1	-0.1	0	0.11	-0.2	0.05	-0	-0.1	-0.1	0.03	0.03	-0	-0.1	0.15	-0.1	-0	-0.1
seed weight	-0.2	-0.4	-0.1	-0.1	-0.2	0.09	-0.1	-0.2	-0.1	0.1	-0.3	0.08	0.4	0.23	0.01	-0.2	0.11	-0.2	-0.1	-0.1	0.19	-0.1	0.58	-0.1		0.34	-0.1	-0.2	0.23	-0.1	-0.4	-0.3	0.05	0.09	-0.3	0.33	-0.1	0.18	0.64	0.2	-0.1
seed width length ratio	0.15	-0.3	-0.1	-0.4	-0.2	-0.1	0.03	0.06	-0	0.04	0.28	-0.1	0.3	0.49	0.27	-0.4	-0.1	-0.1	-0.4	-0.2	0.26	0.12	0.02	-0.1	0.34		0	-0.3	0.05	-0.1	-0.1	-0.2	0.02	-0.3	-0.5	0.58	0.1	0.25	0.21	0.21	0.1
seed dry matter content	0.21	-0.2	0.45	0.27	0.14	-0.4	-0.2	0.14	-0.3	-0.5	-0	0.32	0.3	-0	0.08	0.06	-0.3	0.78	-0.1	-0.3	-0.1	-0.2	-0.3	0	-0.1	0		0.09	0.09	-0.1	-0.1	0.12	0.11	0	0.14	-0.3	-0.3	-0.1	-0.3	-0.2	-0.1
root area	-0.3	-0.3	0.27	0.63	0.29	0	-0.1	-0.2	0.29	-0.2	-0.3	0.42	-0.1	-0.4	-0.3	0.58	0.02	0.03	0.19	-0.1	-0.1	-0.3	-0.1	0.11	-0.2	-0.3	0.09		0.19	0.2	0.04	0.04	-0	0.53	0.56	-0.6	-0.2	-0.5	-0.2	-0.4	-0.3
rooting depth	-0.2	-0.3	0.4	0.34	0.21	0.4	-0.1	-0.4	0.02	-0.3	-0.3	0.16	0.12	-0.1	0.15	0.04	0.37	0.05	0.09	-0.1	0.16	-0.1	0.19	-0.2	0.23	0.05	0.09	0.19		0.47	-0.4	-0.5	0.43	0.27	0.3	-0.2	-0.4	-0.4	0.11	-0.2	-0.2
root area distribution	-0.2	-0.2	0.25	0.23	0.23	0.31	-0.4	-0.4	0.02	-0.2	-0.1	0.05	-0	-0.2	0.13	0.01	0.25	-0.1	0.07	-0	0.11	0.25	0.15	0.05	-0.1	-0.1	-0.1	0.2	0.47		-0.3	-0.4	0.11	0.16	0.21	-0.1	-0.2	-0.1	-0.2	-0.1	-0.2
specific root area	0.2	0.51	-0.2	-0.2	-0.1	-0.4	-0	0.44	0.12	0.17	0.08	-0	-0.2	0.06	-0.3	0.28	-0.4	0.05	0.07	0.05	-0.3	-0.2	-0.3	-0	-0.4	-0.1	-0.1	0.04	-0.6	-0.3		0.88	-0.6	-0.3	-0.1	-0.1	0.35	0.08	-0.1	0.06	0.24
specific root length	0.14	0.57	-0.2	-0.1	-0.1	-0.4	-0	0.42	-0	0.07	-0	0.12	-0.2	-0	-0.3	0.28	-0.4	0.19	0	0.16	-0.4	-0.4	-0.3	-0.1	-0.3	-0.2	0.12	0.04	-0.2	-0.4	0.88		-0.4	-0.2	0.06	-0.2	0.32	-0	-0.1	-0.2	0.22
root tissue density	-0.2	-0.3	0.09	0.22	0.09	0.4	0.14	-0.3	-0.1	-0	-0.1	0.05	-0.1	-0.2	0.14	-0.2	0.32	-0	-0	0.29	0.18	-0.1	0.15	-0.1	0.05	0.02	0.11	-0	0.43	0.11	-0.6	-0.4	1	0.35	0.22	-0.1	-0.2	-0.3	-0.2	-0.4	-0.2
root nitrogen uptake	-0.5	-0.3	0.04	0.46	0.42	0.16	-0.1	-0.4	0.36	0.1	-0.1	0.18	-0	-0.2	-0.3	0.32	0.32	-0.1	0.09	0.19	0.2	-0.1	0.08	0.03	0.09	-0.1	0	0.53	0.27	0.16	-0.3	-0.2	0.35	1	0.27	-0.2	-0.2	-0.3	0.06	-0.3	-0.3
root CN ratio	-0.4	0.19	0.39	0.58	0.19	0.27	-0.1	-0.3	0.2	-0.2	-0.4	0.35	-0.3	-0.5	0	0.48	0.23	0.16	0.38	0.12	-0.1	-0.3	-0	0.03	-0.3	-0.5	0.14	0.54	0.3	0.21	-0.1	0.06	0.22	0.27	1	-0.8	-0.1	-0.2	-0.3	-0.6	-0.4
root P content	0.24	-0.2	-0.4	-0.6	-0.2	-0	0.11	0.06	-0.2	0.28	0.5	-0.5	0.25	0.6	0.13	-0.6	0	-0.3	-0.4	0.05	0.21	0.34	0.13	-0	0.33	0.58	-0.3	-0.6	-0.2	-0.1	-0.1	-0.2	-0.1	-0.2	-0.8	1	0.28	0.65	0.28	0.57	0.28
root K content	-0	0.41	-0.3	-0.3	-0.3	0.02	0.25	0.05	0.09	0.35	0.21	-0.2	-0.2	-0.2	-0.1	-0.1	-0.1	-0.1	-0	0.24	-0.1	-0.1	-0	0	-0.1	-0.1	0.1	-0.3	-0.2	-0.4	-0.2	0.35	0.32	-0.2	-0.2	-0.1	0.28	1	0.06	0.04	-0.1	0.34
root S content	0.39	-0.1	-0.4	-0.5	-0	-0.2	0.08	0.25	-0.2	0.23	0.48	-0.4	0.31	0.58	0.04	-0.5	-0.1	-0.1	-0.3	-0	0.13	0.39	0.16	0.15	0.18	0.25	-0.1	-0.5	-0.4	-0.1	0.08	-0	-0.3	-0.3	-0.7	0.65	0.06	1	0.27	0.58	0.37
root Ca content	0.03	-0	-0.1	-0.1	-0.1	0.09	0.04	-0.2	-0.1	0.01	-0	-0.1	0.14	0.1	-0.1	-0.2	0.12	-0.1	-0	-0.1	0.09	0.07	0.47	-0.1	0.64	0.21	-0.1	-0.2	0.11	-0.2	-0.1	-0.1	-0.2	0.06	-0.3	0.28	0.04	0.27	1	0.37	0.11
root Na content	0.43	-0.1	-0.2	-0.3	-0	-0.2	0.16	0.14	-0.2	-0.1	0.37	-0.6	0.11	0.36	0.06	-0.4	-0	-0.2	-0.1	-0.3	0.06	0.42	0.06	-0	0.2	0.21	-0.2	-0.4	-0.2	-0.1	0.06	-0.2	-0.4	-0.3	-0.6	0.57	-0.1	0.58	0.37	1	0.08
nutrient uptake efficiency	0.38	0.42	-0.2	-0.4	-0.2	-0.2	0.04	0.3	-0.1	0.31	0.18	-0.3	-0.1	0.28	0	-0.2	-0.3	0.13	-0.1	-0.1	-0.1	0.18	0.07	-0.1	-0.1	0.1	-0.1	-0.3	-0.2	-0.2	0.24	0.22	-0.2	-0.3	-0.4	0.28	0.34	0.37	0.11	0.08	

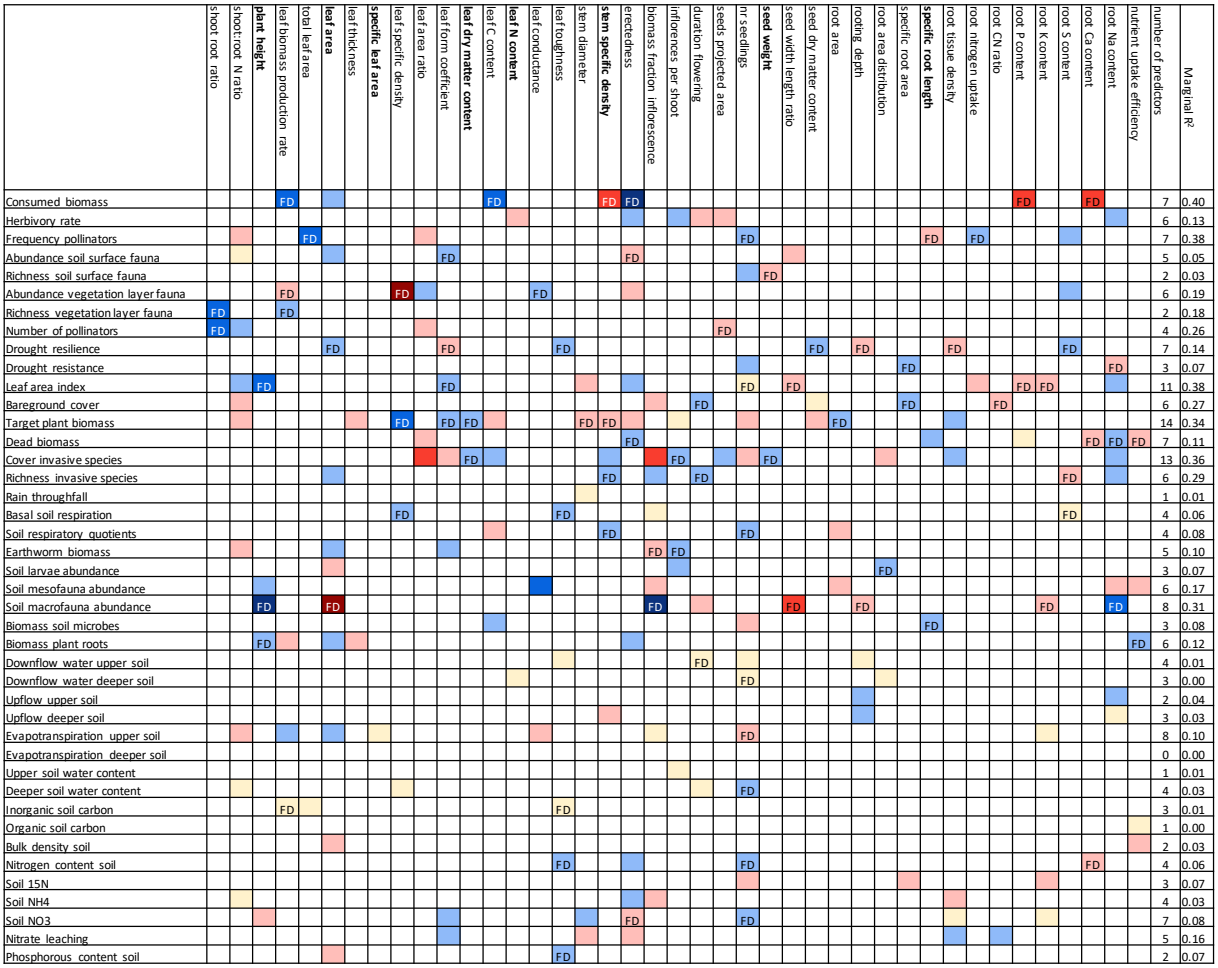
S2. SUPPLEMENTARY RESULTS

S2.2. Overview of final model outcomes

On average, each trait significantly affected 4.9 out of the 42 ecosystem functions in the final models, and each ecosystem function was driven by 4.8 different traits. However, traits varied in the identity and number of ecosystem functions they drove, and vice versa, ecosystem functions varied in the identity and number of traits by which they were driven. Table S.2.1 gives an overview of which traits (their functional identity and/or their functional diversity) were significantly driving which functions in final models. Average marginal R^2 values of models were 0.127. This was slightly lower (0.121) when FI and FD metrics based on presence-absence data (instead of abundance data) were used as predictors.

Table S2.1 Ecosystem functions and their relationships with plant traits. Colored squares indicate whether the Functional Diversity and/or Community Weighted Mean of a given trait was present in the final model explaining the corresponding ecosystem function, and whether the effect was strongly negative (dark red, $r < -0.5$), moderately negative (normal red, $-0.5 \leq r < -0.3$), weakly negative (light red, $-0.3 \leq r < -0.1$), neutral (yellowish, $-0.1 \leq r < 0.1$), weakly positive (light blue, $0.1 \leq r < 0.3$), moderately positive (normal blue, $0.3 \leq r < 0.5$) or strongly positive (dark blue, $r < 0.5$). When the Functional Diversity of the trait was the strongest predictor, FD is written in the cell; in all other cases, Functional Identity of the trait was the strongest predictor. The ecosystem functions analyzed in over 10% of the papers included in the mini-review are shown in bold. At the end of each row, a number is given indicating how many traits were significantly related to the corresponding ecosystem function. Similarly, at the bottom

of each column, a number is given indicating how ecosystem functions were significantly related to the corresponding trait.



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