



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

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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.

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, because 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, pollination, litter decomposition or nutrient leaching from the composition or diversity of traits in plant communities, is a key challenge in the field of functional ecology, and different perspectives exist on how this can be done. On the one hand, some papers

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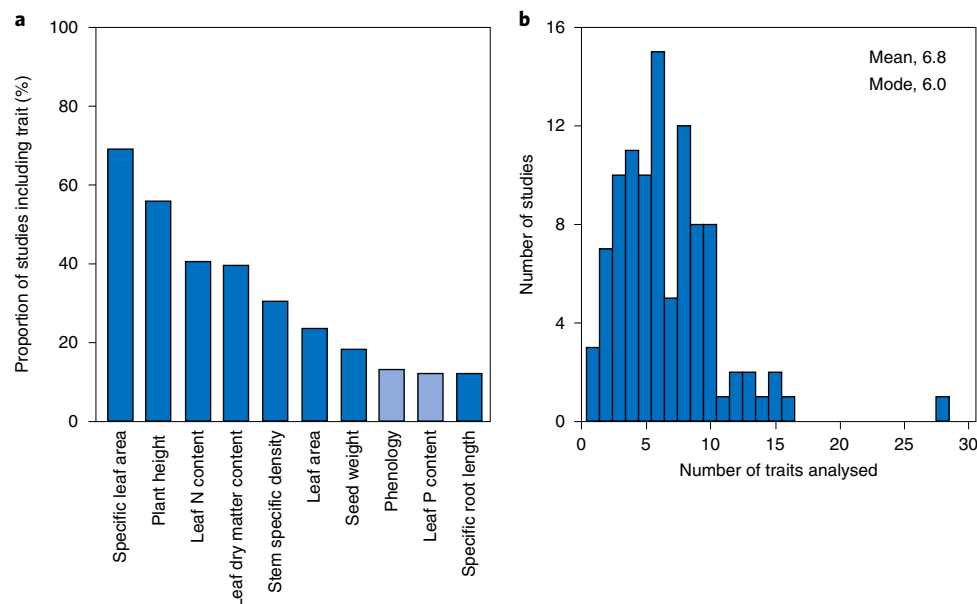


Fig. 1 | Overview of which and how many traits were typically analysed in other ecosystem functioning-related studies. a, Percentage of studies in which the ten most frequently measured traits were investigated, according to a review of 100 recently published articles. The two lighter blue bars show the only functions not measured in this study. **b,** Number of measured traits among studies.

primarily emphasize traits as direct drivers of ecosystem processes, with the influence of environmental conditions being less emphasized or mostly discussed as indirect drivers through their effects on plant traits⁷. On the other hand, others emphasize the simultaneous 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}. While none of the above studies denies the importance of environmental factors in influencing ecosystem properties, the practice of using traits per se (thus ignoring environmental drivers) as 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 per se can be sufficient for predicting levels of ecosystem-level properties within and across years, using a field experiment in which the diversity and composition of plant communities were manipulated but in which spatial variation in environmental conditions is minimal. 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 to explain a large proportion of variance in levels of ecosystem properties.

Various 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 the identity, abundance and diversity of traits may be of importance for ecosystem-level properties. Despite this, some field studies found only 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, because 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 that suggested by studies based on single years. Alternatively, strong and consistent links between plant traits

and ecosystem properties may exist, but higher numbers and more appropriate traits than those 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 literature review to investigate which and how many traits were measured by 100 recent studies^{13–15,21,24–119} when attempting to link the diversity or composition of traits within terrestrial plant communities to ecosystem properties. We found that most studies analysed six traits, and only two studies^{88,90} assessed more than 15 (Fig. 1b). Nine of the ten most frequently studied traits (Fig. 1a) described above-ground plant parts, with six describing leaf characteristics. Only one frequently measured trait was related to plant roots, even though these provide important plant functions (for example, anchoring, resource uptake and interface with symbionts) and represent approximately 50% of total plant biomass¹²⁰. Thus, most previous studies assessed a sparse set of traits with a strong bias towards leaf traits. We also found that a large fraction (44%) of the studies assessed linked traits or other biotic predictors only to ecosystem properties, without additionally testing for the independent effects of environmental conditions or their interactive effects with traits. This fraction was somewhat lower, although still substantial (24%), among those 55 studies with a non-experimental design, which typically have strong gradients in environmental conditions.

We then investigated to what extent a much higher number of traits could 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 below-ground stocks and rates of plant, faunal and abiotic properties including, for example, above- and below-ground plant biomass, pollination and herbivory rates, soil respiration and moisture content and carbon stocks (Supplementary Information provides a full list). Both the diversity and functional composition of the plant communities studied were experimentally manipulated, by sowing different combinations of a pool of 60 species^{121,122}.

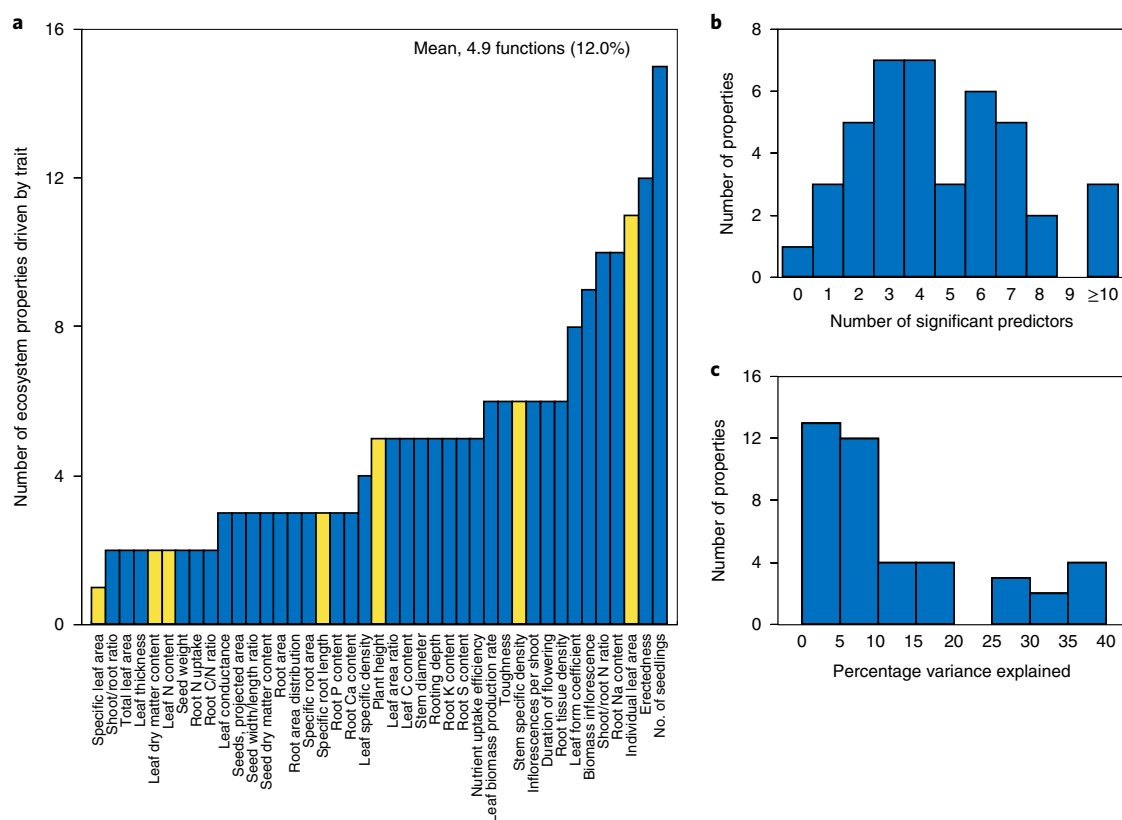


Fig. 2 | The relative importance of different and multiple traits regarding ecosystem properties across years. a, Number of analysed properties significantly driven by each trait, according to final models. Traits analysed in >10% of the papers included in the review are shown in yellow. **b**, Number of significant predictors in final models for each ecosystem property. **c**, Marginal R^2 values in final models for each ecosystem property.

At the same time, because 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 59 of the 60 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, for example, specific leaf area (SLA), leaf and root nutrient concentrations, plant height, seed mass, flowering duration and nutrient uptake efficiency. For a complete list of the traits refer to Supplementary Methods. By combining these trait data with plant community data, we quantified both the functional identity (FI) and functional diversity (FD) 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^{10,12,123}. Functional diversity was calculated as Rao's quadratic entropy¹²⁴, and can drive ecosystem properties if species contribute differently to functioning when co-occurring with plant species with different traits—for example, due to trait-driven resource complementarity or facilitation^{20,122,124,125}.

We used linear mixed models (LMMs) to analyse how much of the variation of each of the 42 ecosystem properties was explained by FI and FD 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 a forward model selection procedure to overcome problems related to multicollinearity,

because many FI and FD metrics were correlated (Supplementary Table 2.2). 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 the final models was 0.127, indicating that traits explained on average only 12.7% (0–40.0%) of the variation in ecosystem properties (Fig. 2c). Marginal R^2 values were even lower (mean, 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 (plot and year differences) were much higher, with an average value of 0.632. Our finding that traits per se explained a very low proportion of variance in ecosystem properties may seem surprising, as various other studies explained more variance with fewer predictors^{8,12–14,21,126}. However, it is possible that there has been a publication bias against studies showing no or only weak links between traits and ecosystem properties, which may have increased the perceived strength of the relationship between traits and ecosystem properties. In addition, these studies typically used data for single years only and it is possible that links between traits and 'ecosystem functions' are strong only within years. To test this, we also analysed 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 per se 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.

We then assessed the dependence of our ability to explain levels of ecosystem properties across years on how many and which traits are included in analyses. We found that those traits most frequently assessed in other studies did not drive more ecosystem properties

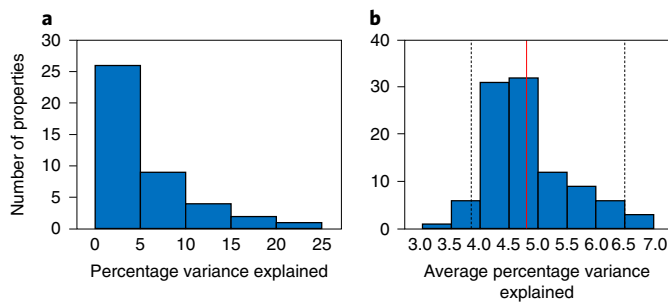


Fig. 3 | R^2 values of models in which only six traits were analysed to explain ecosystem properties across years. **a**, Distribution of marginal R^2 values of final models for each trait when only the six most frequently investigated traits in the studies included in the literature review described above were included in the analysis. **b**, Distribution of mean marginal R^2 values (across final models for each trait) when based on 100 random draws; six randomly selected investigated traits were included in the analysis. Vertical dashed lines denote the 95% confidence interval while the vertical red line denotes mean marginal R^2 across all ecosystem properties when only the six most frequently investigated traits were included in the analysis.

than traits less frequently studied (Fig. 2a). One trait (SLA) significantly drove only a single ecosystem property (evapotranspiration from the upper soil layer) while others (for example, individual leaf area) drove many more ecosystem properties (for example, drought resilience and abundance of soil layer fauna), but no overall pattern was detectable (Fig. 2a). We investigated more formally how our ability to explain variation in ecosystem properties would change if we had (1) measured either a random subset of six (corresponding to the number of traits assessed in most other studies) of the 41 traits (based on 100 random draws), (2) measured only the six traits most frequently assessed in other studies or (3) 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 analysed, on average only 4.8% (95th 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 what extent analysis of 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 analysed 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).

Thus, while each ecosystem property per se 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 (ϕ) in the traits significantly driving each pair of ecosystem functions, using Sørensen's index¹²⁷. 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 does a species' identity^{9,10,12,125}, a small set of key traits able to explain variation in multiple ecosystem properties does not exist in Central European grasslands, just as 'superspecies' providing multiple ecosystem functions do not exist¹²⁸.

While across-year levels of many ecosystem properties were relatively poorly explained by traits, strong links between plant traits and certain ecosystem properties did exist, because the proportion of explained variance of certain ecosystem properties (for example, above-ground plant biomass and the cover of invasive species) exceeded 30%. This begs the question as to whether generalities exist between the type of ecosystem property and the extent to which its variation can be explained by plant traits. We hypothesized that (1) plant traits should be more strongly linked to plant-based ecosystem properties than those related to higher trophic levels or abiotic conditions, and that (2) above- and below-ground ecosystem properties should have equally strong links with plant traits, as both above- and below-ground plant traits were well represented in our study. Partly in line with our first hypothesis, we found that vegetation-based ecosystem properties were most strongly predicted by plant traits (average marginal $R^2=0.23$), while the variation explained in heterotroph-related ecosystem properties was on average slightly, but non-significantly, lower (average marginal $R^2=0.17$) and the proportion of explained variation in abiotic ecosystem properties was substantially and significantly lower (average marginal $R^2=0.04$). Regarding our second hypothesis, we found that ecosystem properties related to above-ground stocks or processes were, on average, much better predicted (average marginal $R^2=0.21$) than those related to below-ground stocks or processes (average marginal $R^2=0.07$). However, this difference was non-significant and resulted from the fact that, above ground a higher fraction of plant-related ecosystem properties and a lower fraction of abiotic ecosystem properties were studied than those below ground (Supplementary Table 1). Despite the finding that variation in some ecosystem properties could be better explained than variation in other ecosystem properties, it is important to note that even the proportion of explained variance in plant-related ecosystem properties was, at 21%, still relatively moderate.

We highlight five possible, and not mutually exclusive, explanations for our overall finding that plant traits per se are generally rather poorly linked to ecosystem properties. First, the plots in our study were relatively large ($10 \times 10 \text{ m}^2$) so that, even within plots, variation in plant community composition and levels of ecosystem properties exist. Therefore, spatial mismatches between within-plot locations of ecosystem property measurements and vegetation surveys could have weakened links between traits and ecosystem properties.

Second, traits can vary substantially among individuals within species¹²⁹. While in this study, we did not take intraspecific trait variation into account (which would have required the repeated measurement of 41 traits of 60 species in 78 plots over a 10-year period), other studies have shown that the inclusion of intraspecific variation can improve links with ecosystem properties^{130,131}. On the other hand, in our own system, interspecific trait variation is much more important than intraspecific trait variation for community-wide trait variation¹³², and therefore it is likely that the interspecific trait variation on which we focused is also key regarding 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 cycling¹³³. Our analysis supports the idea that, with more trait data, links between traits and ecosystem properties become stronger (Fig. 4). While this is probably a major issue for the many studies that investigate comparatively few traits (for example, the inclusion of six traits only, which is the median of other studies, would have decreased our explanatory variance by a factor of >2.5), our analyses, which were based on a large number of traits, show that this is not a major issue in our study. Extrapolation of the observed relationships between model R^2 and the number of

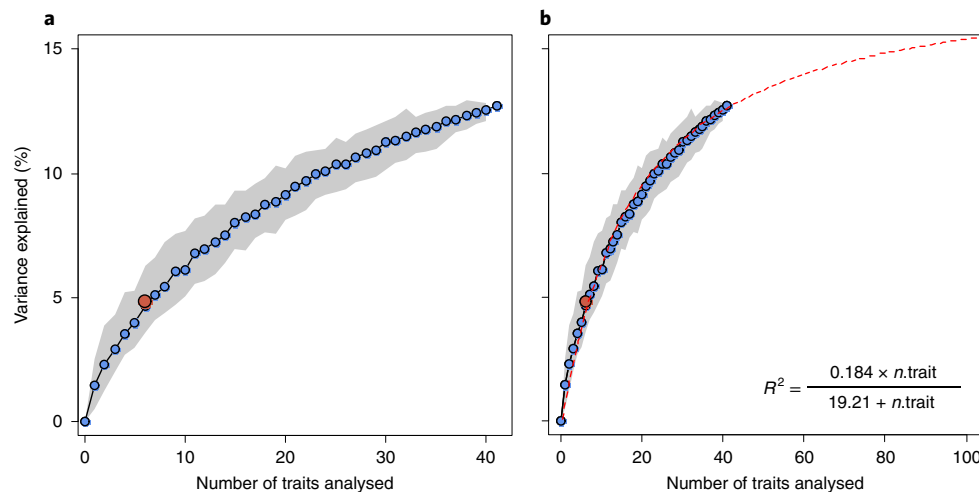


Fig. 4 | The average proportion of variation in levels of ecosystem properties across years explained by plant traits increases asymptotically with the number of traits included in the analysis. a,b, Percentage of variance explained according to number of traits analysed. The red dot indicates the proportion 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 relationship between variance explained (marginal R^2 , on the y axis) and the number of traits used as predictors, based on actual data analyses. **b,** The extrapolated (based on a fitted Michaelis-Menten equation) relationship between variance explained (marginal R^2 , on the y axis) and the number of traits used as predictors, indicated by the red, dashed line. Blue dots and the grey area show the actually observed relationship (also seen in **a**).

traits analysed suggests that 87 traits are needed to increase the proportion of variance explained to 15%, and that there is a (surprisingly low) upper limit of around 18% in the proportion of variance that can be explained by traits per se, even if an unlimited number of traits is analysed (Fig. 4b). Hence, the inclusion of more trait data would have yielded only 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 forests¹³⁴, and these differences in ecosystem properties probably coincide with major differences in the traits (for example, plant height and seed mass) of the dominant plant species¹³⁵.

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 SLA was linked only to across-year levels of one ecosystem property, it is well established that this trait reflects a trade-off between photosynthetic capacity and leaf longevity¹³⁶. Due to this trade-off, both positive and negative relationships between SLA and biomass production could be expected, depending on whether high photosynthetic rates (for example, in productive environments) or conservative strategies (for example, 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^{13,26,49} and negative^{40,64,68,80} 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 explicit testing for context dependency (which would require annual data on, for example, 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 indicate that taking into account spatial or temporal environmental contexts may be essential to improving our understanding of how traits drive ecosystem properties.

Using one of the most comprehensive studies to date, 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, for example, weather conditions) is strongly limited. This indicates that additional data, such as information on abiotic conditions (for example, soil factors, topography, climate/weather and disturbances) and their interactions with plant traits, should be considered to improve links with ecosystem properties. While consideration of environmental contexts has previously been emphasized as being important to understanding drivers of ecosystem properties^{7,11}, we also found that many studies did not follow this recommendation. This may have strong implications. The functional composition and diversity of plant communities are rapidly changing¹⁻⁴, and researchers are employing increasingly complex models to predict the consequences of these changes for worldwide biogeochemical and hydrological cycles^{137,138}. While we encourage the use of such models and their inclusion of increasingly accurate trait information, our work also highlights that, providing we do not understand the context dependency of links between plant traits and ecosystem properties and that, providing 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^{139,140}, and ensuring 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 rapid current-day changes in biodiversity are the safest bet to guarantee nature's contributions to future generations of people.

Methods

Review. We performed a review to investigate which traits were most often analysed in recent years as predictors of ecosystem properties. 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-diversity*) and (ecosystem-function*) and (plant or vegetation). This initially yielded 654 results. Among these, we searched for papers that analysed 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 FD or FI (for example, mean values of the abundance-weighted trait) of one or more terrestrial plant traits. We focused on only 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 acquire an exhaustive overview of all published literature. For a PRISMA flowchart of our literature search, refer to Extended Data Fig. 1.

Among the 100 selected papers (Supplementary Data 1), we screened which plant traits were analysed as predictors of ecosystem properties. Some traits had different labels among different publications—for example, SLA versus leaf mass per area^{61,117}. In those cases, we used our expert judgement and a plant trait thesaurus¹⁴¹ to relabel traits to obtain a common terminology. We then counted and ranked the frequencies (number of papers) by which each trait was analysed as a predictor of ecosystem properties and then identified the top ten traits analysed in most papers and the five most commonly analysed. In addition, for each paper we assessed whether its design corresponded to a 'biodiversity experiment' (that is, an experiment in which the biodiversity or community composition of plant communities was directly manipulated) and whether only biotic predictors (including plant traits), or also abiotic environmental conditions, were analysed as predictors of ecosystem properties.

Experimental design. We studied relationships between various ecosystem properties and plant traits using data from the Jena Main Biodiversity Experiment^{121,122}, 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 above sea level), 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 m². 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 Molinio-Arrhenatheretea grasslands¹⁴² 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 1,000 seeds m⁻², irrespective of 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 grasslands¹⁴³, 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 the river (with, for example, sand content being higher in plots closer to the Saale river). Each block had a similar number of plots, and each block had all levels of species and functional group richness approximately equally represented.

Twice per growing season, plots were weeded to avoid species that were not sown in the plots following establishment. We refer to two other publications^{121,122} for more details on the design of the Jena Main Biodiversity Experiment.

Plant community assessments. During the period 2003–2012, twice per year, during spring (May) and summer (August), cover of all target plant species was estimated in each plot within a 3 × 3-m² subplot. For more details, we refer to Roscher et al.¹³².

Ecosystem property measurement. During the period 2003–2012, 42 different ecosystem variables ('ecosystem properties' hereafter) were measured, describing plant, faunal and abiotic pools and process rates, some of which were measured above ground and some below. We focused on ecosystem properties that met the criteria of being ecosystem functions according to the definition of de Groot et al.¹⁴⁴: "the capacity of natural processes and components to provide goods and services that satisfy human needs, directly or indirectly". This definition includes regulatory functions (for example, those related to biogeochemical cycles such as soil respiration and nutrient leaching), production functions (for example, plant above- or below-ground biomass, abundances of heterotrophic groups) and habitat functions (that is, the properties that indicate the capacity of ecosystems to provide habitat, such as diversity levels of invertebrate taxa)¹⁴⁴. All ecosystem properties were measured in multiple seasons or years, always using standardized protocols. The ecosystem properties measured were: plant biomass consumed by herbivores, herbivory rate, frequency of pollinator visits, abundance of soil surface fauna, richness of soil surface fauna, abundance of vegetation layer fauna, richness of vegetation layer fauna, number of pollinator species, drought resilience, drought resistance, leaf area index, bare ground cover, above-ground plant biomass, dead plant biomass, cover of invasive plant species, richness of invasive plant species, rain throughfall, basal soil respiration, soil respiratory quotient, earthworm biomass, soil larvae abundance, soil mesofauna abundance, soil macrofauna abundance, biomass of soil microbes, biomass of plant roots,

downward flux water in upper soil, downward flux water in deeper soil, upward flux water in upper soil, upward flux water in deeper soil, evapotranspiration in upper soil, evapotranspiration in deeper soil, upper soil water content, deep soil water content, inorganic carbon content, organic carbon content, soil bulk density, soil nitrogen content, soil δ¹⁵N values, soil NH₄ content, soil NO₃ content, nitrate leaching and soil phosphorus content (Supplementary Table 1 provides a more detailed overview). Some of the ecosystem properties were directly related to those mentioned in key papers on traits and ecosystem properties⁷ (for example, target plant biomass in grasslands that are mown at the end of each growing season represents net primary production), while others were more indirectly related. For example, soil microbial biomass and soil respiration are often linked to decomposition rates^{145,146} while soil NH₄ content results from, and is often related to, N mineralization¹⁴⁷. When ecosystem properties were measured multiple times within a year (for example, in both spring and summer) within the same plot, we used averages of those repeated measurements in further analyses. All ecosystem properties were Z-transformed before analyses. For detailed descriptions on the methodology of all ecosystem property measurements, please refer to Supplementary Information.

Trait measurements. In total, 41 plant traits were measured in 59 of the 60 plant species. These traits described whole-plant, leaf, stem, flower, seed (fine) and root characteristics and were structural, morphological, chemical, physiological and 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, please refer to Supplementary Table 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 were therefore derived from earlier published measurements¹²¹. Detailed information on the individual trait measurements is provided in Supplementary Information.

Quantifying FD and FI. We combined the species-level abundance assessments for each plot with the trait measurements to quantify FD and FI 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 metric¹²⁴ (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: $Q = \sum_{i=1}^{S-1} \sum_{j=i+1}^S d_{ij} p_i p_j$, 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 × 3 m², 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) metric¹⁰, 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 the 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 species-level abundance assessments.

Statistical analyses. We first analysed how each ecosystem property was related to all 41 measured traits. This was done using a separate LMM for each ecosystem property, in which the CWM and 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 'empty' models containing only random factors were first 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; Supplementary Table 3). During each step in our selection procedure, we first tested for the significance (based on two-sided tests and $\alpha = 0.05$) 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) > 5. In case the most significant fixed factor resulted in multicollinearity (maximum VIF > 5), we investigated whether the next most significant factor could be added. This procedure was repeated until we ended up with a model containing only significant fixed factors with VIF ≤ 5, to which no significant ($P \leq 0.05$) fixed factors could be added. LMM fitting was done with a restricted maximum-likelihood procedure, using the lmer function of the lme4

package¹⁴⁸ in R v.3.5.1 (ref. ¹⁴⁹). We calculated the marginal (proportion of variance exclusively explained by fixed factors—that is, traits) and conditional (proportion of variance explained by fixed factors and random factors combined) R^2 values¹⁵⁰ using the `r.squaredGLMM` function of the `MuMIn` package¹⁵¹ in R v.3.5.1 (ref. ¹⁴⁹). We also performed some sensitivity analyses in which we repeated the above analyses, with (1) the only difference being that we corrected for false discovery rates¹⁵², to reduce the risk of type I errors, (2) the only difference being that FD and CWM values based on presence/absence data were used as predictors and (3) replacement of FD and CWM predictor variables by realized species richness.

We then investigated to what extent the proportion of variance explained by traits per se (marginal R^2 values) depended on (1) whether the ecosystem property was vegetation based, animal based or abiotic and (2) whether it described an above- or below-ground ecosystem stock or process. For this we categorized ecosystem properties (Supplementary Table 1) and used a linear model (with two-sided significance tests) to investigate how marginal R^2 values from the final models described above depended on (1) the 'trophic level' of the ecosystem property (that is, primarily vegetation based, heterotroph based or an abiotic property) and (2) 'stratum' (above versus below ground).

We also investigated to what extent links between the FD and FI 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 described above, except that the random factor 'year' was omitted from the models (because ecosystem properties were analysed for each year separately, this random factor had become obsolete). In addition, the random factor 'plot' was omitted from the models because we had only one measurement per plot within each year.

To quantify the overlap in significant predictors among different ecosystem properties, we created a binary matrix of 42 (number of ecosystem properties) \times 41 (number of traits), with cells containing a value of 1 when the FD and/or FI of the corresponding trait significantly drove the ecosystem property, and a value of 0 when neither FD nor 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 Sørensen's index¹²⁷ as $o = \frac{|T_i \cap T_j|}{0.5(|T_i| + |T_j|)}$ where $|T_i|$ and $|T_j|$ are the numbers of traits significantly driving respectively ecosystem properties i and j , respectively, and $|T_i \cap T_j|$ is the number of traits significantly driving both ecosystem properties i and j , and we then calculated the average overlap. Importantly, these overlap estimates could be conservative (that is, underestimated) due to strong correlations between traits. Therefore, we repeated the above-described LMMs (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 FD and FI values as explanatory variables. To this end, we first performed PCA and then selected the 15 PCA axes that explained $>100/82$ (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 properties with PCA axes was the same as that for the main analyses linking ecosystem properties with FD and FI variables. We then repeated the overlap analysis in the way described above and found that, for FD and FI metrics based on PCA variables, the average overlap of 13.4% was somewhat, but not markedly, higher than that based on FD and FI metrics of raw traits.

We then analysed to what extent a subset of the six traits most commonly assessed in other studies—that is, SLA, plant height, leaf N concentration, leaf dry matter content, stem tissue density and leaf area—could explain variance in ecosystem properties. To this end we repeated the modelling procedure described above, except that only the six traits mentioned above were assessed in the model selection procedure rather than the full set of 41 traits. In addition, we also assessed how random subsets of n traits, with n ranging from 1 to 40, could explain ecosystem properties. To this end, we ran 100 simulations for each level of n . In each of these simulations, we first randomly selected a subset of n traits out of the total of 41. For these random subsets of n traits, we again ran the same model selection procedure described above for each ecosystem property to assess which of the traits significantly drove the levels of each property, and to assess the marginal R^2 values of final models. For each simulation, we then calculated the mean (across all ecosystem properties) marginal R^2 value and, for each n , we calculated the mode and 95% percentiles for the mean marginal R^2 value across the 100 simulations (as reported in Fig. 4). Only for $n=1$ and $n=40$ traits was this procedure slightly different, because for both of these levels of n there were only 41 traits or trait combinations possible. Thus, in those cases, we did not take 100 random draws of traits but instead systematically analysed all possible combinations. Based on the resulting relationship between the number of traits analysed and marginal R^2 values, we fitted a nonlinear model using the `nls` function in R 3.5.3, in the form $R^2 = \frac{R_{\max}^2 \times n_{\text{trait}}}{K + n_{\text{trait}}}$ in which R^2 is the marginal R^2 value, R_{\max}^2 is the asymptote in marginal R^2 value, n_{trait} the number of traits analysed and K describes the slope by which R_{\max}^2 is reached. The resulting R_{\max}^2 and K values were 0.184 and 19.21, respectively, and these were used to extrapolate the observed relationship between the number of traits analysed and marginal R^2 values, to calculate how many traits were required to obtain marginal R^2 values of 0.150 and above.

Reporting Summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

The datasets analysed for this study, are available at Figshare: https://figshare.com/articles/dataset/Data_and_R_scripts_of_Plant_traits_alone_are_poor_predictors_of_ecosystem_properties_and_long-term_ecosystem_functioning/12834350.

Code availability

The R scripts used for this study are available at <https://github.com/fonsvanderplas/traits-and-ecosystem-properties/>.

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Author contributions

F.v.d.P., C.W., T.S.-G., A.W. and K.B. conceived the ideas and designed the study. F.v.d.P., T.S.-G., S.M. and A.A. performed analyses. T.S.-G., A.W., K.B., S.M., R.L.B., N.B., H.d.K., A.E., N.E., C.E., M.F., G.G., A.H., E.K.-F., S.L., A.M., L.M., P.A.N., Y.O., C.R., C.S., M.S.-L., S.S., B.S., E.-D.S., V.T., T.T., W.V., W. Weisser, W. Wilcke and C.W. contributed to 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.

Additional information

Extended data is available for this paper at <https://doi.org/10.1038/s41559-020-01316-9>.

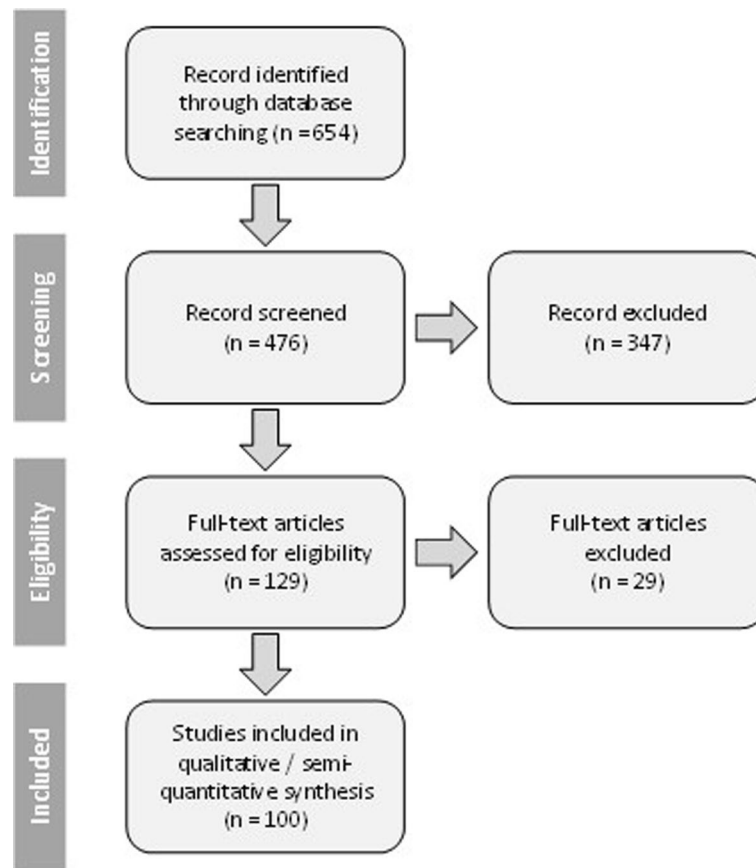
Supplementary information is available for this paper at <https://doi.org/10.1038/s41559-020-01316-9>.

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Extended Data Fig. 1 | A PRISMA flowchart of the literature research. Our literature search yielded 654 publications, of which 476 were screened, and 129 full-text articles were assessed for eligibility. Of these, 100 were eligible and included in our synthesis.

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Study description	The majority of our data was collected in the Jena Main Biodiversity Experiment. In this experiment, 78 20x20 m grassland plots were set up, and each was sown with 1, 2, 4, 8 or 16 grassland plant species, to create variation in plant diversity and composition. From 2003-2012, we collected plant composition and ecosystem function (42 different ecosystem functions) data. In addition, based on field measurements, greenhouse measurements and literature data, we collated information on 41 plant traits. By combining plant community and trait data, we quantified functional diversity and identity of each plot in each year. We then assessed to which extent functional trait diversity and identity data could be used to predict levels of ecosystem functions.
Research sample	Original research data from the Jena Experiment, and published elsewhere (see citations in MS). Data collectors are involved as co-authors.
Sampling strategy	A statistical power analysis was used to chose the sample size (number of plots) of the Jena Main Biodiversity Experiment. For more details, we refer to Roscher et al, 2004, Basic and Applied Ecology
Data collection	Data was collected by original data providers from the major projects involved, most of whom are now listed as co-authors on our manuscript.
Timing and spatial scale	Timing: 2003-2012. Scale: 78 20x20 m plots within one field
Data exclusions	not applicable
Reproducibility	Large-scale and long-term biodiversity experiments observations are hard to replicate, so we have one single experiment only. Data and code are publicly available.
Randomization	Diversity levels and the identity of plant species sown in plots were chosen to be independent from each other, by experimental design. The location of plots were randomized, so that covariation between plot location and plant species compositions or plant diversity levels was avoided. For more details, we refer to Roscher et al, 2004, Basic and Applied Ecology
Blinding	Blinding was not possible, in the sense that when samples are taken from a plot, the observed could more or less see whether it was sown with many or few plant species.
Did the study involve field work?	<input checked="" type="checkbox"/> Yes <input type="checkbox"/> No

Field work, collection and transport

Field conditions	According to Roscher et al (2004, Basic and Applied Ecology): " Mean annual air temperature at the nearest meteorological station, 3 km south of the field site, is 9.3 °C (1961–1990) and mean annual precipitation amounts to 587 mm (Kluge & Müller-Westermeier 2000)". Plots were located in floodplain grasslands near the town of Jena (Germany)
Location	50°55'N, 11°35'E
Access & import/export	According to project guidelines of the involved project (Jena Experiment).
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