Plant community impact on productivity: the interplay of community-level functional attributes, species, and environmental selection

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Abstract

While the impact of biodiversity, notably functional diversity, on ecosystem productivity has been extensively studied, little is known about the effect of individual species. Here, we identified species of high importance for productivity (key species) in over 28,000 diverse grassland communities in the European Alps, and compared their effects with those of community-level measures of functional composition (weighted means, variances, skewness, and kurtosis). After accounting for the environment, the five most important key species jointly explained more deviance than all statistics of functional composition. Key species were generally tall with high specific leaf areas. By dividing the observations according to distinct habitats, the explanatory power of all non-environmental predictors increased considerably, and the relationships between functional composition and productivity varied systematically, presumably because of changing interactions and trade-offs between traits. Our results advocate for a better consideration of species' individual effects on ecosystem functioning in complement to community-level measures.

Introduction

Biotic control of the productivity of ecosystems is still elusive (Chapin *et al.* 2000) because species can act through their numbers (Wardle 2002) or their functions (Cadotte *et al.* 2011). Yet, quantifying this control is pivotal for impact assessments of biodiversity loss (Cardinale *et al.* 2012) and for global vegetation modelling (Prentice & Cowling 2013). It has long been proposed that the emergent properties of ecological communities, particularly the number of species and functional diversity, are the primary drivers of ecosystem processes (Hooper *et al.* 2005). As a corollary, individual species are most often considered to affect ecosystem processes in idiosyncratic and unpredictable ways (Diaz *et al.* 2007), except for a few ecosystem engineers and keystone species (Jones *et al.* 1994). However, beyond the effects of ecosystem-engineers, ecophysiological studies have emphasized the key role of species identity in driving ecosystem processes, and this role cannot be grasped by the properties of communities (e.g., Mahaut *et al.* 2020). This is particularly true for natural systems like grasslands that encompass a wide variety of more or less common species with individual but predictable responses to environmental conditions. Here, we compare the impact of individual species on grassland productivity with that of community-level properties across diverse environments.

While there are many concepts of potential biotic control in terms of individual species and functional community properties, we focus here on two that have sound theoretical links to productivity and are quantifiable at scale: the key and keystone species concept for individual species and the Trait Driver Theory (Enquist *et al.* 2015, TDT) for community-level properties (Box 1). For completeness, however, we also provide results for rare species (Violle *et al.* 2017) and for classical, multivariate measures of functional diversity such as Rao's quadratic entropy (Botta-Dukát 2005; Villéger *et al.* 2008). To identify key(stone) species, Maire *et al.* (2018) provided a comprehensive analytical framework that can be extended to encompass other measures of biotic control, representing a unique opportunity to tease apart the different biotic drivers of ecosystem functioning, as well as the role of environmental context.

Biotic control of grassland productivity cannot be understood without considering environmental context. Environmental conditions define which ecological strategies are successful at a given location and thus which species may thrive (Weiher *et al.* 2011; Enquist *et al.* 2015; Garnier *et al.* 2016). Similarly, they set the limit of achievable productivity (Brun *et al.* 2019). Environmental conditions should therefore be controlled for, when identifying the relationships of individual species and community-level properties with productivity (Maire *et al.* 2018). Furthermore, in order to understand the dependency of biotic productivity control on environmental context, it can be assessed for different, more or less narrowly defined, types of environments (hereafter referred to as habitats). To this end, however, extensive empirical data are necessary.

We investigated how species cover abundance and the moments of trait distributions contributed to explain productivity and how these contributions varied across habitats, using a model-comparison approach and >28’000 grassland community plots covering the diverse environments of the French Alps and Switzerland (Fig. S1). We focused on the productivity-related functional traits specific leaf area (SLA), leaf nitrogen content (LNC), and reproductive height (HGT) (Lavorel & Garnier 2002; Wright & Westoby 2002; Wright *et al.* 2004) and investigated effects of key(stone) species cover abundance and moments of trait distributions on productivity (approximated by the remotely-sensed Soil Adjusted Vegetation Index, SAVI) in diverse habitats. Our analysis demonstrates that the cover abundance of few key species can contribute more to explain productivity than important functional community properties and that the relationships of productivity with biotic predictors vary systematically across habitats, revealing a multitude of cues about the driving, underlying processes.

Material and Methods

Data

Community data

Plant community observations originated from two sources covering the French Alps and Switzerland, respectively (Fig. S1). Data for the French Alps was provided by the French National Alpine Botanical Conservatory (Thuiller *et al.* 2014) and included about 43’000 observations of vascular plant communities from diverse ecosystem types. Data for Switzerland was collected by the dry meadows and pastures initiative run by the Swiss Federal Office for Environment and consisted of almost 24’000 observations of grassland communities. Both datasets contained semi-quantitative dominance information resolved in six cover-abundance classes (as defined by Braun-Blanquet (1946)). We subjected these data to a series of preprocessing and filtering steps (Supplementary Methods) after which 28’171 community observations of 2702 species remained.

Environmental data

Environmental data included the remotely-sensed Soil Adjusted Vegetation Index (SAVI) as a proxy for productivity, as well as key environmental predictors representing climate, soil, terrain, and land cover, mostly with spatial resolutions of 100 m or higher (see Supplementary Methods). We preprocessed these data by deriving relevant statistics and calculating annual averages, where necessary. The final set of environmental predictors included mean temperature, humidity, soil moisture, soil fertility, terrain wetness, exposition, and whether or not a site was sparsely vegetated (vegetation sparsity).

Trait data

Trait data included specific leaf area (SLA), leaf nitrogen content (LNC), and reproductive height (HGT). LNC and SLA are two key traits of the leaf economics spectrum (Wright *et al.* 2004) and HGT is a central trait related to competitive ability and avoidance of environmental stress (Körner 2003). Furthermore, these traits are related to photosynthetic capacity (Wright & Westoby 2002) and primary productivity (Lavorel & Garnier 2002). We also used information on plant life form to exclude communities with trees, large shrubs or aquatic plants, which were not the focus of this study (Supplementary Methods). Trait data mostly originated from in-house measurements which are now available in the TRY database (KATTGE *et al.* 2011) (see Table S1 for a detailed list of references). When multiple measurements were available per species, we averaged them. Full trait information was available for 412 of the 504 species with an occurrence frequency >1%.

Analyses

We first split the community data into one, five, 25, and 50 clusters of similar environmental conditions (throughout the manuscript we refer to these clusters as “habitats”). Then, we repeated the following analysis steps within each habitat (Fig. S2): first, we fitted the relationship between productivity (soil adjusted vegetation index) and important environmental factors, using generalized additive models (Hastie & Tibshirani 1990). The resulting fits provided reference models (M_0) for the next steps. Second, we estimated the community-weighted moments of the distributions of SLA, LNC, and HGT, and investigated to which extent they increased explained deviance when added as predictors in M_0, one at a time. Furthermore, we investigated the partial responses of productivity to each of these community-level predictors. Third, we identified key and keystone species by adding the cover values of each species as linear predictors to M_0, one at a time, and assessing the magnitude of their coefficients and how much they improved explained deviance. We set the added explained deviance of species with negative coefficients to zero and defined those species with added deviance above the 92.5th percentile as key species (high absolute importance) and those species with added deviance *and* linear coefficients above the 92.5th percentile as keystone species (high absolute and relative importance). Finally, we compared the traits of the key(stone) species derived this way to the traits of the remaining, ordinary species.

Creating environmental clusters

We split observed communities into one, five, 25, and 50 clusters of similar environmental conditions to define distinct habitats. We assumed mean annual temperature, humidity, and soil fertility to be the most important factors constraining productivity. In a first step, we conducted a principal component analysis (PCA) of these factors, after scaling and centering them, and used the first two principal components as the basic environmental dimensions. On these dimensions, we then ran partitioning around medoids (PAM) clustering to identify five, 25, and 50 clusters of similar size (Fig. S3, Table S2). Finally, we classified environmental clusters by their average SAVI into classes of 'low' for annual mean SAVI <0.23; 'medium' for annual mean SAVI ≥0.23 and <0.3; and 'high' for annual mean SAVI ≥0.3. Analyses were run in the R environment (R Development Core Team 2008), with package ade4 (Dray & Dufour 2007) for PCA and package cluster (Maechler *et al.* 2018) for PAM clustering. Resulting environmental clusters are described in the Supplementary Results.

Fitting reference models

Reference models (M_0) were used to identify the association between SAVI and important environmental variables. We used generalized additive models (Hastie &

Tibshirani 1990) to fit these relationships for each set of communities associated with an environmental cluster. M_0 included smooth terms for humidity, temperature, soil fertility, soil moisture, the north/south component of exposition, and terrain wetness index, as well as a binary factor for vegetation sparsity. Furthermore, we added a binary factor to correct for potential, systematic differences between the two community datasets (the one for the French Alps and the one for Switzerland). In a few habitats, binary factors were only represented with one level, and thus their terms were removed from the model equation. We fixed all smooth terms at three degrees of freedom and assumed SAVI to follow a Gaussian error distribution. Even though SAVI values are theoretically bounded between -1 and 1, estimated annual means never approached these boundaries and showed a frequency distribution that was in agreement with the Gaussian error assumption. While the formulation of M_0 was identical to analyze the impact of community-level predictors and individual-species cover, 38% fewer observations were available for the analysis of community-level predictors (Table S2). This was because in order to have representative estimates of community-level predictors, we discarded observations with trait data available for less than 80% of the total vegetation cover. For the key(stone)-species analysis, on the other hand, we only considered species that were present in at least 1% of the observations of the habitat, leading to 0-28% fewer species considered (Table S2). We used the R package gam (Hastie 2018) to fit generalized additive models.

Investigating community-level predictors

Community-level predictors included the moments of the distributions of SLA, LNC, and HGT (Enquist *et al.* 2015), i.e., community-weighted mean (CWM), community-weighted variance (CWV), community-weighted skewness (CWS), and community-weighted kurtosis (CWK). CWM was estimated it as

$$CWM = \frac{\sum_i^n w_i x_i}{\sum_i^n x_i}, \tag{1}$$

where w_i is the dominance of species i and x_i is its trait value; CWV was calculated as

$$CWV = \frac{\sum_i^n wi(x_i - CWM)^2}{\sum_i^n w_i}; \tag{2}$$

CWS was calculated as

$$CWS = \frac{\sum_i^n wi\frac{(x_i - CWM)^3}{CWV^{3/2}}}{\sum_i^n w_i}. \tag{3}$$

Since we were not interested in the direction of skewness, we only considered absolute values of CWS. Finally, we estimated CWK as

$$CWK = \frac{\sum_i^n wi\frac{(x_i - CWM)^4}{CWV^2}}{\sum_i^n w_i}, \tag{4}$$

In order to obtain predictors with approximately Gaussian frequency distributions, we log-transformed all CWV, CWK and absolute CWS values, as well as CWM of HGT.

We assessed the relevance of community-level predictors by adding them to reference models, one at a time. We fitted the partial response of productivity to community-level predictors as smooth terms of three degrees of freedom. For each of the twelve resulting models, we assessed how much their explained deviance increased compared to the deviance of M_0 and derived partial response plots of SAVI between the 2.5th and the 97.5th percentiles of the observed values of each community-level predictor. Along these response plots, we assessed how much the predicted SAVI increased based on linear least-square fits. The description of how partial response curves were classified into different response types is provided in the Supplementary Methods.

Identifying key(stone) species

To identify key(stone) species, within each habitat we added linear terms for the cover percentages of all species, one at a time, to the environmental reference model (M_0), fitting a model M_i for each species. For each of these M_i, we assessed how much explained deviance increased compared to M_0. Then, we set the added explained deviance of species with negative coefficients (negative relationships with productivity) to zero and defined those species with added deviance in the top 7.5 percent as key species. For keystone species, we additionally expected linear coefficients to be in the top 7.5 percent. In order to assess the sensitivity of the resulting key(stone)-species sets on this 7.5% threshold, we also investigated key(stone)-species sets defined by the 5% and 10% thresholds.

Testing for differences in added explained deviance

We used a Tukey honest significant difference (HSD) test to test for differences in explained deviance added by community-level predictors and key(stone) species cover. Across the full dataset, we estimated explained deviance added by each individual community-level predictor, and by different groups of key species (top, top five, full set) and keystone species (full set). For each predictor or predictor group, we fitted 100 models based on 1000 randomly drawn observations from the full dataset. Based on these replicates, we tested for significant differences at the $p \leq 0.05$ level, for all pair-wise predictor combinations. Furthermore, we used these model replicates to deduce medians and 95%-confidence intervals of partial productivity responses to community-level predictors.

Investigating key(stone) and ordinary species in trait space

We compared key(stone) species to ordinary species in trait space, focusing on distances and distinctiveness. Trait space was defined by the scaled and centered values of

SLA, LNC, and HGT. Before scaling, HGT measurements were log-transformed so that their frequency distribution assumed an approximately Gaussian shape. For visualization, we ran one global PCA on the trait space of all species and examined species scores on the first two principal components. For greater readability, we also fitted Gaussian mixture density functions to the point sets of key(stone) and ordinary species, by using the R package mclust (Scrucca *et al.* 2016). The algorithm, based on the Bayesian information criterion, thereby defined a number of mixture components for ordinary species (between one and nine) and for key(stone) species (between one and three). Next, within each habitat, we summarized the differences between key(stone) and ordinary species in terms of functional distances, and functional distinctiveness *sensu* Violle *et al.* (2017). We tested whether key(stone)-species traits were different from ordinary-species traits, by conducting permutational multivariate analyses of variance from distance matrices. To this end, we applied the R function ‘adonis2’ from the package vegan (Oksanen *et al.* 2019) on the Euclidean distance matrices of our trait space, running 999 permutations. Finally, we assessed whether key(stone) species occupied eccentric positions in trait space by first calculating functional distinctiveness of each species and then testing for significant differences between key(stone) and ordinary species, using two-sided Wilcoxon tests.

Results

Relationships across the full dataset

Across the full dataset that covered steep environmental gradients, the seven environmental predictors of the reference model explained 70.4% of the deviance of productivity. The explained deviance added by biotic predictors was comparably small (Fig. 1). Community-weighted moments added between 0.2% (CWK of HGT) and 1.1% (CWM of SLA) of explained deviance. Similarly, multivariate measures of functional diversity added between 0.1% and 0.5% explained deviance (Fig. S4). The cover values of key species, on the other hand, contributed between 0.6% and 3.1% when the top, the top five, and the full set (38 species) were added jointly to M_0. The full set of keystone species (11 species) explained 1.2% of deviance, when added jointly to M_0. According to a Tukey HSD test, the contributions to explained deviance by the cover values of the full key-species set and the top five key species were significantly higher than the explained deviance added by any community-level predictor. The explained deviance added by the cover values of the top key species alone was only significantly lower than one community-level predictor, CWM of SLA. Also the summed cover abundance of rare species made a comparably high contribution to explained deviance (2.0%, Fig. S4), but rare-species cover abundance was negatively related to SAVI (Fig. S5).

Community-weighted means and variances mostly had positive associations with productivity across the full dataset while relationships of community-weighted skewness and kurtosis with productivity tended to be negative (Fig. S5). Productivity showed the most positive partial response to CWM of SLA. The response to CWM of HGT was similar, except for the uppermost part of the range, where productivity levelled off. The positive productivity responses to CWVs were fairly consistent for all traits. They started to increase linearly with a moderate slope and then leveled off in the upper third of the range. CWS (absolute values) and CWK negatively influenced productivity for all traits, indicating that productivity tends to decrease when trait distributions are skewed or sharply peaked. However, these latter relationships were comparably weak.

Key species primarily included grasses and forbs, while keystone species consisted of forbs and legumes (Fig. 2a). The 38 key species across all environments (Table S3) individually added ≥0.10% explained deviance to M_0 (Fig. 2a). Among them, eleven species also were of high relative importance and thus keystone species. However, there seemed to be an upper limit to the combination of absolute and relative importance, with no species dominating in both. Many species also had negative linear coefficients and thus a negative association with productivity (Fig. 2a). Yet, these species generally were of low absolute importance.

Keystone species and particularly key species differed from ordinary species when compared in trait space defined by SLA, LNC, and HGT (Fig. 2b, c). Functional distances within both, key and keystone species, were significantly shorter than distances between them and ordinary species (p=0.001 and p=0.050, respectively, Adonis test). Key species generally were taller than average and had higher specific leaf areas, while keystone species were only slightly taller and stood out mainly through high SLA. Furthermore, key(stone) species did not show atypical positions in trait space: key species were even significantly less functionally distinct than ordinary species, while no difference was found for keystone species (p=0.048 and p=0.191, respectively, two-sided Wilcoxon test). Key(stone) species differed from ordinary species in a similar way when defined more strictly on the basis of the

95th percentiles of absolute and relative importance, but the differences began to erode when the 90th percentiles were used as thresholds (Fig. S6).

Relationships by habitat

In most habitats, the top-ranked biotic community-level predictors, mostly CWM of SLA, added more explained deviance to M_0 than the top key species. Explained deviance added by biotic predictors generally increased when the dataset was divided into several habitats, using clustering (Figs. 3, S7, and S8). Furthermore, the added explained deviance was higher under warm conditions with high soil fertility and low humidity than under cool and humid conditions (Fig. 3a, b). In 6-20% of habitats, mostly under cool and moderately humid conditions, top key species added more explained deviance than community-level predictors (Fig. 3c, Figs. S7-S8). Among community-level predictors, community-weighted means most frequently ranked highest (Fig. 3a). This was particularly true for CWM of SLA, which dominated under warm conditions. Top key species were often forbs when conditions were cold and humid, or grasses and legumes when conditions were warmer and less humid (Fig. 3b).

Not only did the strength of the relationships between community-level predictors and productivity vary across habitats, but so did their shape (Fig. 4). Productivity increased with CWM of SLA when conditions were moderately warm, whereas the relationships were mostly unimodal under warm and dry conditions (Fig. 4a). In cold environments with low soil fertility, productivity was often negatively related to CWM of LNC, whereas unimodal relationships prevailed under low humidity (Fig. 4b). Productivity showed increasing partial responses to CWM of HGT in particular in the cooler half of environmental space with lower soil fertility, and unimodal responses in the warmer part (Fig. 4c). For CWVs, relationships were similarly variable: partial productivity responses to CWV of LNC were particularly positive under warm and dry conditions (Fig. 4e), and partial relationships between CWV of plant height and productivity changed from increasing to unimodal with increasing temperature and soil fertility (Fig. 4f). Partial relationships were also variable between productivity and CWS and CWK of traits, although in these cases relationships were more often classified as non-significant (Fig. S9). The patterns remained similar when the number of separated habitats was five or 50 instead of 25 (Figs. S10 and S11).

The traits involved in the most positive associations between community-level predictors and productivity were structured in environmental space (Fig. 4g). In cold habitats, and in cool habitats with low humidity, productivity showed most positive partial responses to CWM or CWV of HGT. In contrast, CWM of SLA drove most positive productivity responses when temperature, soil fertility, and humidity were moderately high. CWV and, to a lesser extent, CWM of LNC showed the most positive relationships with productivity when temperatures were cool and humidity was high, and in some of the warmest habitats. CWS and CWK of traits were rarely associated with the most positive productivity responses among community-level predictors. These patterns remained when the dataset was split into five habitats (Fig. S10), but were less clear when 50 habitats were distinguished (Fig. S11).

Most of the key species found across all habitats were forbs, but grass and legume species were more often identified repeatedly in several habitats (Fig. 5a). Forbs were typically key species only in one to few habitats, and within them their added explained deviance was comparably low. Among the key species with comparably high average explained deviance added, several species, often grasses and legumes, were in the key-species sets of many habitats. This was particularly true for the legume *Trifolium pratense* that was among key species in 23 of 25 habitats (Fig. 5b), but also the grasses *Anthoxanthum* *odoratum*, *Holcus lanatus*, and *Trisetum flavescens* were identified in 18, 15, and 14 habitats, respectively. For *A. odoratum* this was the case for environments of moderate humidity (Fig. 5c), for *H. lanatus* it was primarily the case in warm environments (Fig. 5d), and for *T. flavescens* in moderately warm environments of rather low humidity (Fig. 5e). Keystone species similarly included several species that were identified in multiple habitats. These were mainly forbs, for example *Rumex acetosa* which was identified in nine habitats of mostly warm conditions (Fig. S12).

Key species tended to be taller and to have higher SLA than ordinary species in habitats of intermediate and high productivity, but not when productivity was low (Fig. 5f). Both, key-species and ordinary-species sets, showed variable centroids in trait space across habitats. Generally, these centroids were defined by greater plant height and higher SLA when habitat productivity increased. Moreover, the shifts between key-species centroids and ordinary-species centroids increasingly pointed towards higher SLA and HGT in habitats of increasing productivity (Fig. 5f), and of increasing temperature and soil fertility (Fig. 5g). In low-productivity habitats, trait shifts pointed in various directions and functional distances within key species did not significantly differ from functional distances between key and ordinary species (Adonis test, Fig. 5g). In environments of intermediate and high productivity, on the other hand, trait shifts were significant at the $p \leq 0.05$ level in 50% and 89% of cases, respectively. Relationships remained stable when the dataset was split into five or 50 habitats instead of 25 (Figs. S13 and S14).

Discussion

We investigated the associations of community-level functional properties and key(stone)-species cover with grassland productivity across the French Alps and Switzerland and found them to be similarly strong and heavily modulated by the environment. Key species were generally tall and had high SLA - traits that are associated with high growth rates (Wright *et al.* 2004; Poorter *et al.* 2009; Borgy *et al.* 2017) and competitive ability (Körner 2003; Violle *et al.* 2009). Their lower functional distinctiveness compared to ordinary species indicates that their phenotypes may be selected for in grassland communities (Grime 2006; Brun *et al.* 2019). Advantages from fast growing and competitive strategies may be reinforced by additional traits such as mowing-tolerance, which may be why several key species are important forage crops (Table S3). These include, for example, the cross-habitat top key species *T. pratense* and *T. flavescens* (Fig. 5). Moreover, high ability to disperse may be important for key species: six of the 38 key species of the full dataset are listed among the 468 globally most noxious neophytes (Table S3) and others are known to be regionally invasive (e.g., *Ranunculus acris*; Lamoureaux & Bourdôt 2007). The traits of keystone species, on the other hand, were less distinct, apart from high SLA. The lack of species that ranked very high in absolute and relative importance indicates that keystone plants, with respect to productivity, tend to be specialized to a restricted range of conditions. The required adaptations and traits may therefore be more context-specific and variable.

With respect to community-level predictors, we found the strongest associations between community-weighted means and productivity. This is consistent with the assumption of Trait Driver Theory (TDT) that productivity is primarily determined by the effect of the traits that lead to the best fitness in a given environment, which are reflected by CWMs

(Garnier *et al.* 2004; Enquist *et al.* 2015). Unlike the predictions of TDT, however, productivity increased with trait variance and decreased with kurtosis. It seems that in the diverse grasslands of the European Alps inefficiencies from trait deviations from the optimum are compensated by benefits from niche differentiation, resource-use complementarity, and mutualistic effects like nitrogen fertilization (Darwin 1859; Diamond 1979; Pacala & Tilman 1994; Barneze *et al.* 2020). Finally, as expected by TDT, we found productivity to decline with absolute trait skewness, indicating that skewness may mainly arise from disequilibria with the local environment, rather than from the presence of functionally distinct key species (Enquist *et al.* 2015). It is possible to better understand how different predictors at the community level determine productivity when taking into account the environmental context.

Environmental conditions shape the relationships between community-level predictors and productivity by governing which ecological strategies are capable to thrive, how trade-offs between traits play out, and how species interact. The range of thriving ecological strategies is particularly constrained in cold environments with poor soils, which only support small plants (Körner 2003). In these environments, the relationships between productivity and CWMs of plant height were especially positive (Fig. 4). Additional height among small plants seems to directly translate into higher biomass produced per season, and thus higher productivity. Only when environmental stress is lower, the growth benefits from greater height are eventually offset by costs for increased maintenance of stems (Falster & Westoby 2003) and higher vulnerability to mowing and grazing (Diaz *et al.* 2001), leading to unimodal relationships between height and productivity (Fig. 4). Variations in the relationship between productivity and CWM of SLA may be driven by environmental control of the growth rate-longevity trade-off (Wright *et al.* 2004). Productivity increased with CWM of SLA when conditions were moderately warm and humid, while under warm and dry conditions relationships were mostly unimodal. In principle, growth rates (and thus productivity) increase with SLA, as material costs per photosynthetically active leaf area decrease (Wright *et al.* 2004; Poorter *et al.* 2009; Borgy *et al.* 2017). Yet, this advantage of faster growth comes with shorter leaf life spans and higher water loss through transpiration (Wright *et al.* 2004). When water stress is low and growing seasons comparably short, these disadvantages are of little consequence, but they can be detrimental in warm and dry environments. Finally, environmental control of interactions may have driven the variations in productivity response to CWV of LNC, which was particularly positive under warm and dry conditions. CWV of LNC was more associated with legume coverage than with any community-level predictor (Spearman $r = 0.57$, Fig. S15), indicating that the positive effect of CWV of LNC may be linked to increased biological nitrogen fertilization from more legumes in the community (Barneze *et al.* 2020). Legumes are known for fixing atmospheric nitrogen via symbiosis with root bacteria and making it available to themselves as well as to neighboring plants (Pirhofer-Walzl *et al.* 2012). However, fixing atmospheric nitrogen is energy-intensive and reaction rates of nitrogenase, the enzyme responsible, quickly decrease when temperatures sink below 22°C (Vitousek *et al.* 2013). Biological nitrogen fixation is, therefore, less efficient in cold than in warm environments (Cleveland *et al.* 1999).

We combined large observational datasets to investigate the biotic control of grassland productivity and obtained detailed insight on species-specific effects and environmental context, but we also had to make several limiting assumptions. Firstly, we only considered three traits did not account for intraspecific trait variation. Although SLA, LNC, and HGT are key determinants of productivity (Lavorel & Garnier 2002; Wright & Westoby 2002; Wright *et al.* 2004), additional traits such as mowing tolerance, as discussed above, or physiological rates are important too. Moreover, while intraspecific trait variation may be smaller than interspecific variation, they interact in complex ways with implications that can be significant (Kichenin *et al.* 2013). Secondly, with our empirical approach we have no certainty that the identified associations between biotic predictors and productivity are causal. Although our results generally are plausible and correspond to ecological theory, key(stone)-species effects, for example, could also arise from species associations with unmeasured environmental conditions. Finally, we focused on vascular plants and ignored pteridophytes and mosses. While in most habitats these latter groups may not drive productivity, in some cold and moist places this may have been different.

Once the primary environmental effects are acknowledged, the remaining cross-habitat rules to link biotic properties to grassland productivity are weak, as the nature and importance of relationships varies greatly depending on environmental context. In this study, we have demonstrated that the effect of environmental context can be quantified when dataset and approach are chosen appropriately. This, in turn, allows for deeper insights and a better process understanding with significant benefits, e.g., for global vegetation modeling (Prentice & Cowling 2013). Moreover, we have shown that beside community-level trait attributes the cover values of key(stone) species are powerful indicators of ecosystem productivity. The effect of key(stone) species is linked to trait values characteristic of productive strategies such as high SLA but it cannot be sufficiently captured by traditional concepts like functional groups (Jaillard *et al.* 2018) as other factors, including ability to disperse, play important roles, too. Future studies will be necessary to comprehensively identify the properties of key(stone) plants and establish a more complete picture of the biotic control of productivity.

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References

Barneze, A.S., Whitaker, J., McNamara, N.P. & Ostle, N.J. (2020). Legumes increase grassland productivity with no effect on nitrous oxide emissions. *Plant Soil*, 446, 163–177.

Borgy, B., Violle, C., Choler, P., Garnier, E., Kattge, J., Loranger, J., *et al.* (2017). Sensitivity of community-level trait-environment relationships to data representativeness: A test for functional biogeography. *Glob. Ecol. Biogeogr.*, 26, 729–739.

Botta-Dukát, Z. (2005). Rao's quadratic entropy as a measure of functional diversity based on multiple traits. *J. Veg. Sci.*, 16, 533–540.

Braun-Blanquet, J. (1946). Über den Deckungswert der Arten in den Pflanzengesellschaften der Ordnung Vaccinio-Piceetalia. *Jahresbericht der Naturforschenden Gesellschaft Graubündens*, 130, 115–119.

Brun, P., Zimmermann, N.E., Graham, C.H., Lavergne, S., Pellissier, L., Münkemüller, T., *et al.* (2019). The productivity-biodiversity relationship varies across diversity dimensions. *Nat. Commun.*, 10, 5691.

Cadotte, M.W., Carscadden, K. & Mirotchnick, N. (2011). Beyond species: functional diversity and the maintenance of ecological processes and services. *J. Appl. Ecol.*, 48, 1079–1087.

Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., *et al.* (2012). Biodiversity loss and its impact on humanity. *Nature*, 486, 59–67.

Chapin, F.S., Zavaleta, E.S., Eviner, V.T., Naylor, R.L., Vitousek, P.M., Reynolds, H.L., *et al.* (2000). Consequences of changing biodiversity. *Nature*, 405, 234–242.

Cleveland, C.C., Townsend, A.R., Schimel, D.S., Fisher, H., Howarth, R.W., Hedin, L.O., *et al.* (1999). Global patterns of terrestrial biological nitrogen (N 2) fixation in natural ecosystems. *Global Biogeochem. Cycles*, 13, 623–645.

Darwin, C. (1859). *On the origin of species*. John Murray, London.

Diamond, J.M. (1979). *Assembly of species communities*. The Belknap Press of Harvard University Press, Cambridge.

Diaz, S., Lavorel, S., de Bello, F., Quetier, F., Grigulis, K. & Robson, T.M. (2007). Incorporating plant functional diversity effects in ecosystem service assessments. *Proc. Natl. Acad. Sci.*, 104, 20684–20689.

Diaz, S., Noy-Meir, I. & Cabido, M. (2001). Can grazing response of herbaceous plants be predicted from simple vegetative traits? *J. Appl. Ecol.*, 38, 497–508.

Dray, S. & Dufour, A.-B. (2007). The ade4 Package: Implementing the Duality Diagram for Ecologists. *J. Stat. Softw.*, 22.

Enquist, B.J., Norberg, J., Bonser, S.P., Violle, C., Webb, C.T., Henderson, A., *et al.* (2015). Scaling from Traits to Ecosystems. pp. 249–318.

Falster, D.S. & Westoby, M. (2003). Plant height and evolutionary games. *Trends Ecol. Evol.*, 18, 337–343.

Garnier, E., Cortez, J., Billès, G., Navas, M.-L., Roumet, C., Debussche, M., *et al.* (2004).

PLANT FUNCTIONAL MARKERS CAPTURE ECOSYSTEM PROPERTIES DURING SECONDARY SUCCESSION. *Ecology*, 85, 2630–2637.

Garnier, E., Navas, M.-L. & Grigulis, K. (2016). *Plant Functional Diversity*. Oxford University Press.

Grime, J.P. (1998). Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *J. Ecol.*, 86, 902–910.

Grime, J.P. (2006). Trait convergence and trait divergence in herbaceous plant communities: Mechanisms and consequences. *J. Veg. Sci.*, 17, 255–260.

Gross, N., Bagousse-Pinguet, Y. Le, Liancourt, P., Berdugo, M., Gotelli, N.J. & Maestre, F.T. (2017). Functional trait diversity maximizes ecosystem multifunctionality. *Nat. Ecol. Evol.*, 1, 0132.

Hastie, T. (2018). gam: Generalized Additive Models.

Hastie, T.J. & Tibshirani, R.J. (1990). *Generalized additive models*. Chapman & Hall/CRC, London.

Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., *et al.* (2005). EFFECTS OF BIODIVERSITY ON ECOSYSTEM FUNCTIONING: A CONSENSUS OF CURRENT KNOWLEDGE. *Ecol. Monogr.*, 75, 3–35.

Jaillard, B., Deleporte, P., Loreau, M. & Violle, C. (2018). A combinatorial analysis using observational data identifies species that govern ecosystem functioning. *PLoS One*, 13, e0201135.

Jones, C.G., Lawton, J.H. & Shachak, M. (1994). Organisms as Ecosystem Engineers. *Oikos*, 69, 373.

KATTGE, J., DÍAZ, S., LAVOREL, S., PRENTICE, I.C., LEADLEY, P., BÖNISCH, G., *et al.* (2011). TRY - a global database of plant traits. *Glob. Chang. Biol.*, 17, 2905–2935.

Kichenin, E., Wardle, D.A., Peltzer, D.A., Morse, C.W. & Freschet, G.T. (2013). Contrasting effects of plant inter- and intraspecific variation on community-level trait measures along an environmental gradient. *Funct. Ecol.*, 27, 1254–1261.

Körner. (2003). *Alpine Plant Life - Functional Plant Ecology of High Mountain Ecosystems*. 2nd edn. Springer, New York, USA.

Lamoureaux, S.L. & Bourdôt, G.W. (2007). A review of the ecology and management of Ranunculus acris subsp. acris in pasture. *Weed Res.*, 47, 461–471.

Lavorel, S. & Garnier, E. (2002). Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Funct. Ecol.*, 16, 545–556.

Maechler, M., Rousseeuw, P., Struyf, A., Hubert, M. & Hornik, K. (2018). cluster: Cluster Analysis Basics and Extensions.

Mahaut, L., Fort, F., Violle, C. & Freschet, G.T. (2020). Multiple facets of diversity effects on plant productivity: Species richness, functional diversity, species identity and intraspecific competition. *Funct. Ecol.*, 34, 287–298.

Maire, E., Villéger, S., Graham, N.A.J., Hoey, A.S., Cinner, J., Ferse, S.C.A., *et al.* (2018). Community-wide scan identifies fish species associated with coral reef services across the Indo-Pacific. *Proc. R. Soc. B Biol. Sci.*, 285, 20181167.

Naiman, R.J., Johnston, C.A. & Kelley, J.C. (1988). Alteration of North American Streams by Beaver. *Bioscience*, 38, 753–762.

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., *et al.* (2019). vegan: Community Ecology Package.

Pacala, S.W. & Tilman, D. (1994). Limiting Similarity in Mechanistic and Spatial Models of Plant Competition in Heterogeneous Environments. *Am. Nat.*, 143, 222–257.

Pirhofer-Walzl, K., Rasmussen, J., Høgh-Jensen, H., Eriksen, J., Søegaard, K. & Rasmussen, J. (2012). Nitrogen transfer from forage legumes to nine neighbouring plants in a multi-species grassland. *Plant Soil*, 350, 71–84.

Poorter, H., Niinemets, Ü., Poorter, L., Wright, I.J. & Villar, R. (2009). Causes and consequences of variation in leaf mass per area (LMA): a meta-analysis. *New Phytol.*, 182, 565–588.

Power, M.E., Tilman, D., Estes, J.A., Menge, B.A., Bond, W.J., Mills, L.S., *et al.* (1996). Challenges in the Quest for Keystones. *Bioscience*, 46, 609–620.

Prentice, I.C. & Cowling, S.A. (2013). Dynamic Global Vegetation Models. In: *Encyclopedia of Biodiversity*. Elsevier, pp. 670–689.

R Development Core Team. (2008). R: A Language and Environment for Statistical Computing.

Scrucca, L., Fop, M., Murphy, T.B. & Raftery, A.E. (2016). mclust 5: clustering, classification and density estimation using Gaussian finite mixture models. *R J.*, 8, 205–233.

Thuiller, W., Guéguen, M., Georges, D., Bonet, R., Chalmandrier, L., Garraud, L., *et al.* (2014). Are different facets of plant diversity well protected against climate and land cover changes? A test study in the French Alps. *Ecography (Cop.).*, 37, 1254–1266.

Villéger, S., Mason, N.W.H. & Mouillot, D. (2008). NEW MULTIDIMENSIONAL FUNCTIONAL DIVERSITY INDICES FOR A MULTIFACETED FRAMEWORK IN FUNCTIONAL ECOLOGY. *Ecology*, 89, 2290–2301.

Violle, C., Garnier, E., Lecoeur, J., Roumet, C., Podeur, C., Blanchard, A., *et al.* (2009). Competition, traits and resource depletion in plant communities. *Oecologia*, 160, 747–755.

Violle, C., Thuiller, W., Mouquet, N., Munoz, F., Kraft, N.J.B., Cadotte, M.W., *et al.* (2017). Functional Rarity: The Ecology of Outliers. *Trends Ecol. Evol.*, 32, 356–367.

Vitousek, P.M., Menge, D.N.L., Reed, S.C. & Cleveland, C.C. (2013). Biological nitrogen fixation: rates, patterns and ecological controls in terrestrial ecosystems. *Philos. Trans. R. Soc. B Biol. Sci.*, 368, 20130119.

Wardle, D.A. (2002). Ecology by numbers. *Trends Ecol. Evol.*, 17, 533–534.

Weiher, E., Freund, D., Bunton, T., Stefanski, A., Lee, T. & Bentivenga, S. (2011). Advances, challenges and a developing synthesis of ecological community assembly theory. *Philos. Trans. R. Soc. B Biol. Sci.*, 366, 2403–2413.

Wieczynski, D.J., Boyle, B., Buzzard, V., Duran, S.M., Henderson, A.N., Hulshof, C.M., *et* *al.* (2019). Climate shapes and shifts functional biodiversity in forests worldwide. *Proc. Natl. Acad. Sci.*, 116, 587–592.

Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., *et al.* (2004). The worldwide leaf economics spectrum. *Nature*, 428, 821–827.

Wright, I.J. & Westoby, M. (2002). Leaves at low versus high rainfall: coordination of structure, lifespan and physiology. *New Phytol.*, 155, 403–416.

Figures

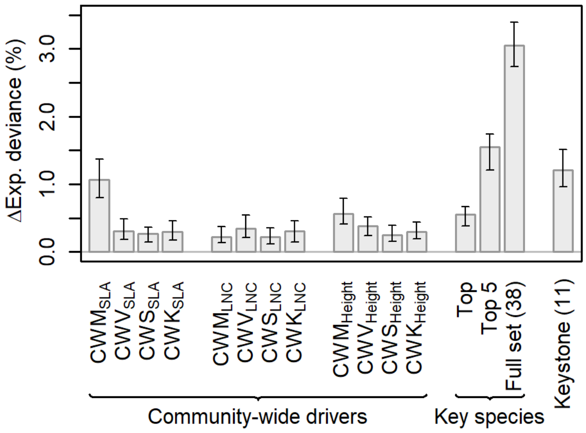
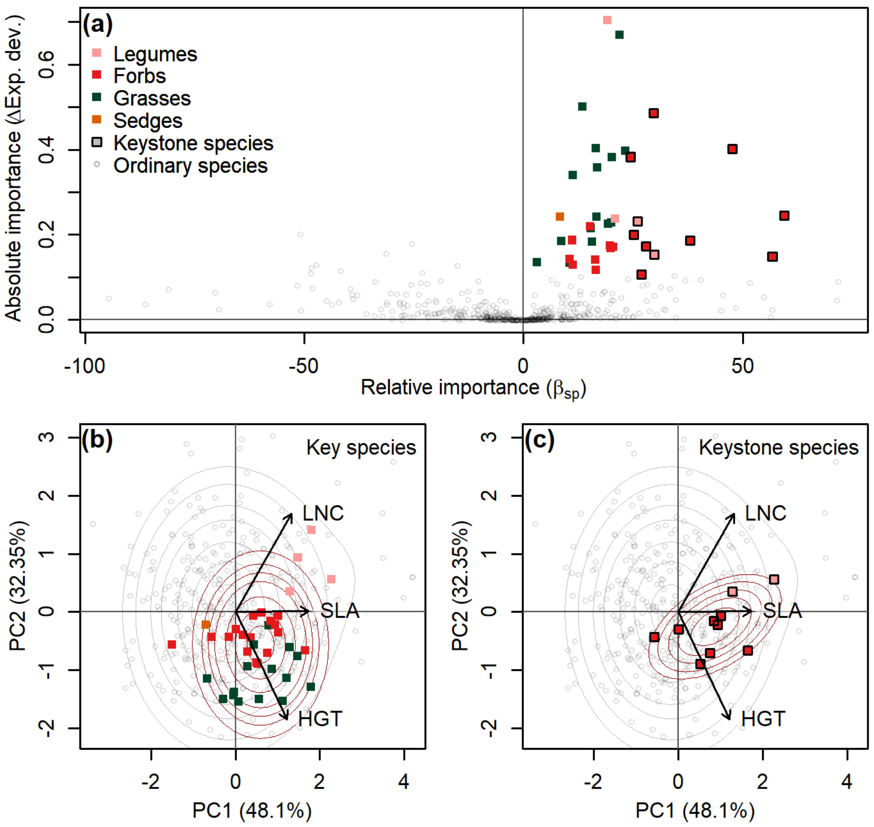


Fig. 1 | Explained deviance added by community-level predictors and individual-species cover.



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616 **Fig. 2 | Importance and traits of key(stone) species**.

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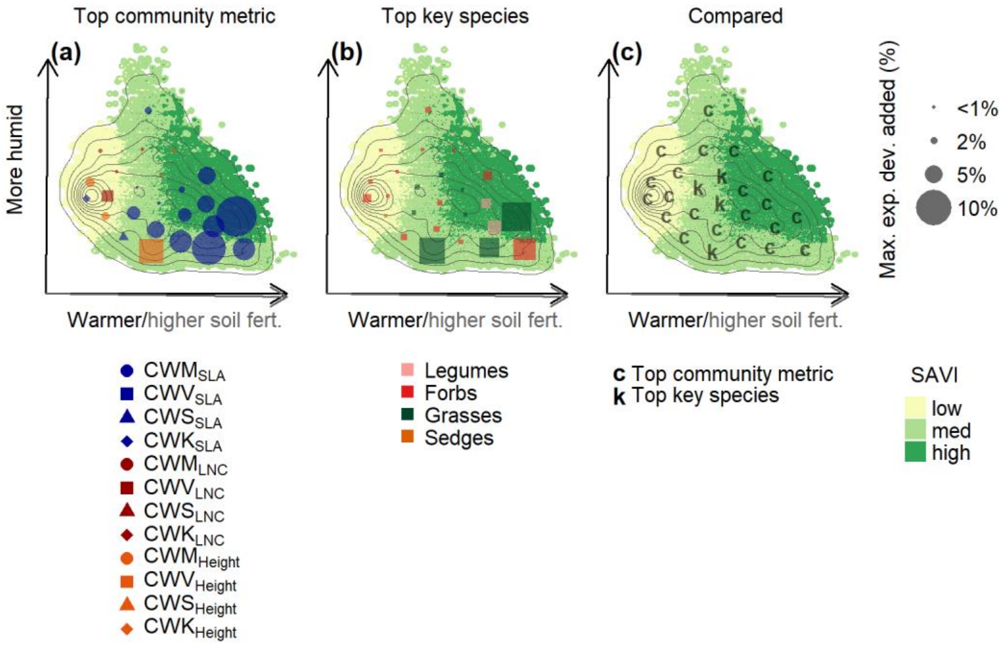

Fig. 3 | Explained deviance added by community-level predictors and key-species cover across 25 habitats.

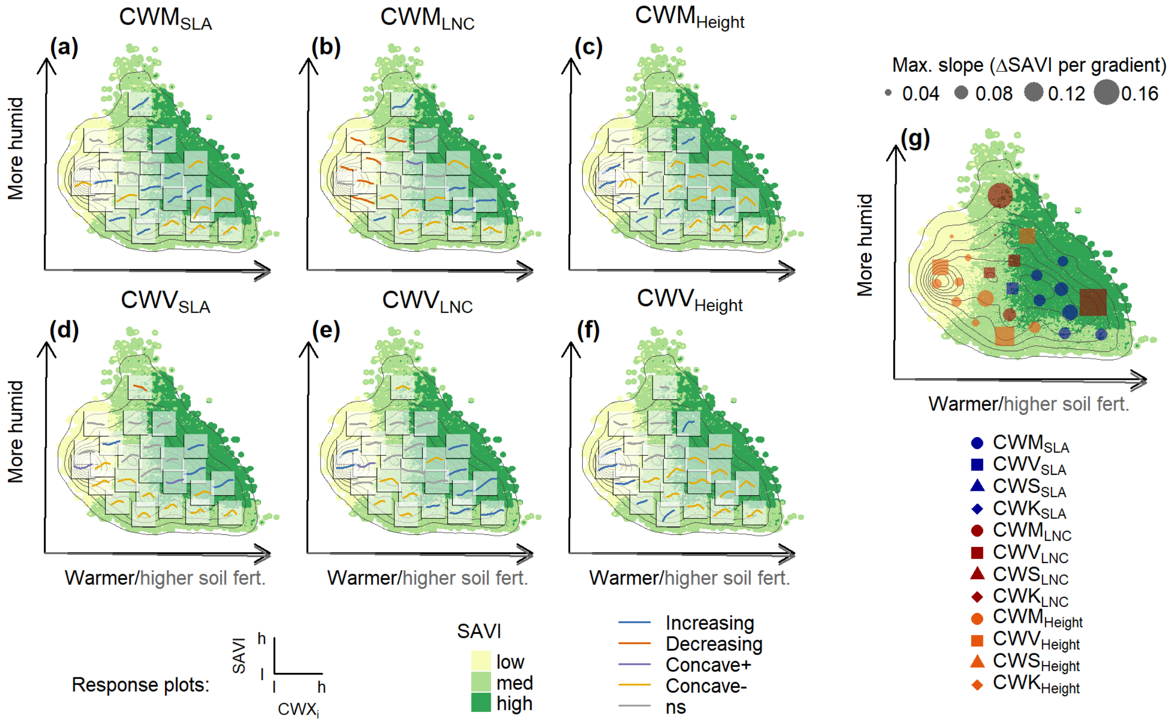

Fig. 4 | Partial responses of productivity to community-weighted means and variances across 25 habitats.

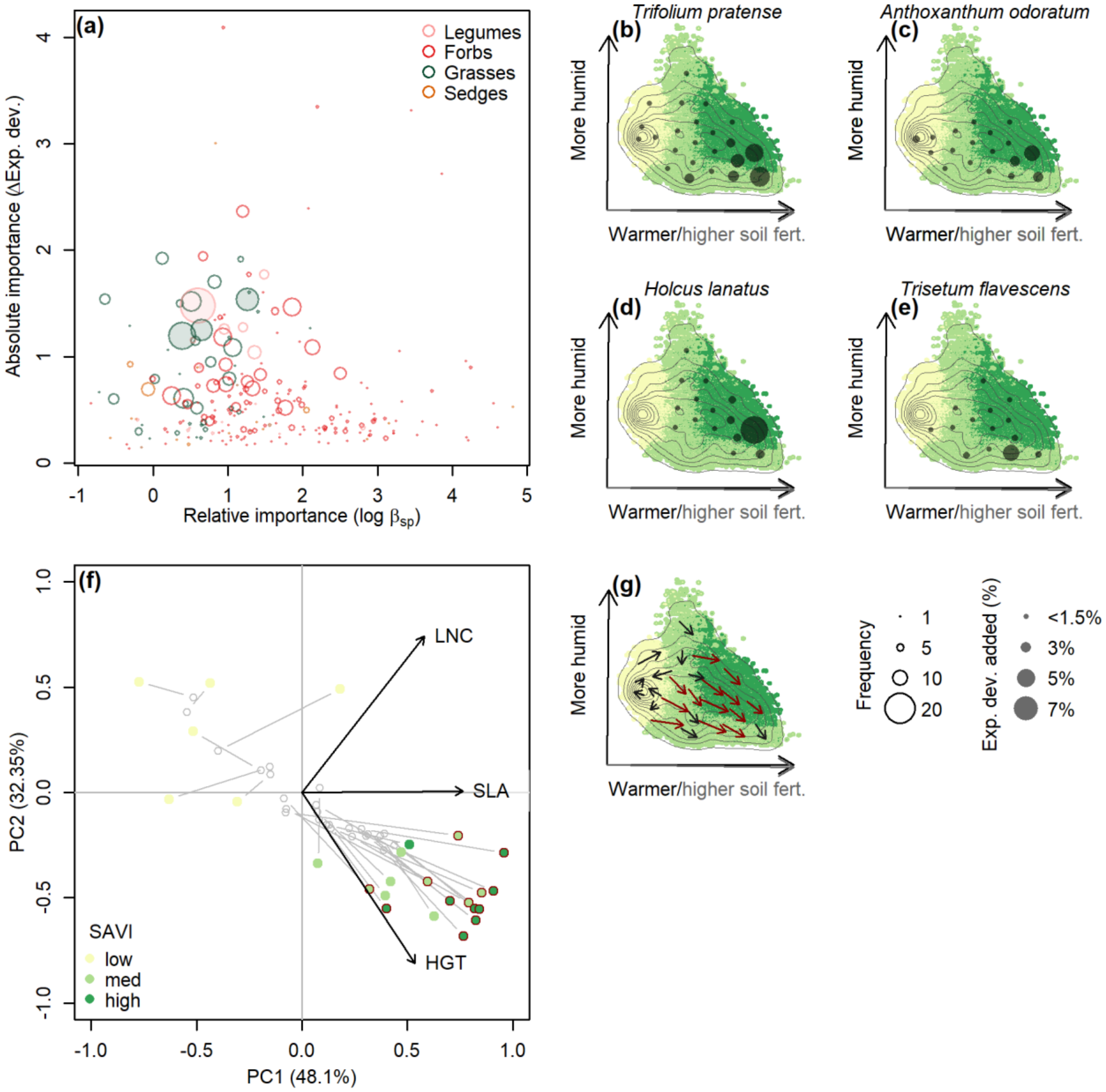

Fig. 5 | Importance and traits of key species across 25 habitats.

Figure legends

Fig. 1 | Explained deviance added by community-level predictors and individual-species cover. Shown are contributions of community-weighted moments, key-species cover, and keystone-species cover to explained deviance of model fits explaining productivity (soil adjusted vegetation index) with environmental conditions. Community-weighted moments were represented with smooth terms of three degrees of freedom while linear coefficients were used to model the effect of the cover values of individual species. Bars represent medians and error bars are interquartile ranges of 100 models fitted on resampled data.

Fig. 2 | Importance and traits of key(stone) species. **a**, productivity improvement per percent cover (relative importance) and explained deviance added to the reference model (absolute importance) of all species considered. Key species are shown as squares and colored according to plant type (see legend), their subset of keystone species is outlined in black, and ordinary species are shown as grey circles. **b** and **c**, key species and keystone species, respectively, in a two-dimensional representation of trait space (PCA axes with explained variance in brackets, see Methods). Isolines are Gaussian mixture density functions of the distributions of key species (dark red) and ordinary species (grey), respectively. Note that for one key species trait information was not available (see Table S1).

Fig. 3 | Explained deviance added by community-level predictors and key-species cover across 25 habitats. **a**, identity and added explained deviance of smooth terms of best-performing community-level predictors. **b**, plant type and explained deviance of best-performing key species. **c**, class of predictor with highest explained deviance added: community-level predictor (c) or key-species coverage (k). Axes are a rotation of the first two principal components of environmental space (see Methods) with arrows representing loadings for increasing temperature, soil fertility, and humidity. Surface depicts inverse-squared-distance interpolation of productivity (soil adjusted vegetation index, SAVI) levels and superimposed isolines represent the density of observations.

Fig. 4 | Partial responses of productivity to community-weighted means and variances across 25 habitats. Partial responses of productivity (soil adjusted vegetation index, SAVI) to community-weighted means (**a**-**c**) and community-weighted variances (**d**-**f**) of SLA (**a**, **d**), LNC (**b**, **e**), and HGT (**c**, **f**) across 25 subsampled datasets from similar environments. Curve types are classified as increasing (blue), decreasing (red), concave positive (purple), unimodal (yellow), and non-significant (grey, see Supplementary Methods). Axes are a rotation of the first two principal components of environmental space with arrows representing loadings for increasing temperature, soil fertility, and humidity. Surface depicts inverse-squared-distance interpolation of productivity levels and superimposed isolines represent the density of observations. **g**, identity (shape) and slopes (size) of community-level predictors with steepest slopes across the observed gradient. Figs. S7-S9 show partial responses to additional predictors, and partial responses to CWMs and CWVs when five and 50 habitats are distinguished.

Fig. 5 | Importance and traits of key species across 25 habitats. a, increase in productivity per percent cover (relative importance), and explained deviance added to the reference model (absolute importance) of key species of all habitats. Key species are colored according to plant type (see legend); ring size represents the number of habitats in which a species belongs to the key-species set; the four most global key species are highlighted with semi-transparent filling. **b**-**e**, added explained deviance across environmental space for the four most global key species. Circles are only shown for habitats where the species are in the set of key species. **f**, centroids of key-species sets (colored circles) and ordinary-species sets (grey rings) from each habitat in a two-dimensional representation of trait space (PCA axes with explained variance in brackets). Point pairs are connected by grey lines. **g**, magnitude and direction of shifts between the centroids of keystone and ordinary species, with directions corresponding to the axes in panel **f**. Axes in panels **b**-**e** and **g** are a rotation of the first two principal components of environmental space with arrows representing loadings for increasing temperature, soil fertility, and humidity. Surface depicts inverse-squared-distance interpolation of productivity levels and superimposed isolines represent the density of observations.

Text boxes

Box 1: Definitions of key(stone) species and trait driver theory

Key(stone) species: The effect of individual species on ecosystem functioning can be measured in absolute terms or relative to their abundance. Species that are important in absolute terms, i.e., that significantly promote ecosystem functioning across the studied region, are called ‘key’ species (Maire *et al.* 2018). The common surgeonfish *Acanthurus albipectoralis*, for instance, is a key species to fish biomass and coral cover in the reefs of the Indo-Pacific (Maire *et al.* 2018). Species that are disproportionately important relative to their abundance distinctly increase ecosystem functioning locally, when they are present, but they may be geographically rare and thus have a small impact at the study-system level. If species are important in both absolute and relative terms they are called ‘keystone’ species (Power *et al.* 1996), including, for example, the North American beaver with its capacity to change the structure of riverine ecosystems (Naiman *et al.* 1988).

Trait driver theory (TDT): TDT states that the moments of the functional trait distribution (mean, variance, skewness, and kurtosis) of a given community serve as proxies for several ecosystem processes. Community-weighted means (CWMs) represent the traits of the dominant phenotype, which indicate the potential productivity of the individuals, according to the Mass-Ratio Hypothesis (Grime 1998; Garnier *et al.* 2004). Community-weighted variance (CWV) and kurtosis (CWK) are expected to capture different aspects of the diversity of ecological strategies, which increases the average deviation of individuals from the optimal strategy, and thus reduces productivity (Enquist *et al.* 2015). Community-weighted skewness (CWS) depicts the asymmetric nature of the trait distribution, and thus the imbalance of ecological strategies present in an ecosystem. Imbalances result, for example, from rapid environmental change, and they tend to have negative effects on productivity (Enquist *et al.* 2015). There is growing evidence that these different moments are useful to better understand the functional structure of plant communities and to predict their implications on ecosystem functioning (Garnier *et al.* 2016; Gross *et al.* 2017; Wieczynski *et al.* 2019).