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Plant community impact on productivity: Trait diversity or key(stone) species effects?

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Abstract

Outside controlled experimental plots, the impact of community attributes on primary productivity has rarely been compared to that of individual species. Here, we identified plant species of high importance for productivity (key species) in >29,000 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 of productivity than any measure of functional composition alone. Key species were generally tall with high specific leaf areas. By dividing the observations according to distinct habitats, the explanatory power of key species and functional composition increased and key-species plant types and functional composition-productivity relationships varied systematically, presumably because of changing interactions and trade-offs between traits. Our results advocate for a careful consideration of species' individual effects on ecosystem functioning in complement to community-level measures.

KEYWORDS
community-weighted moments, European Alps, grassland, keystone species, trait driver theory

INTRODUCTION

The ways through which grassland communities control primary productivity, the amount of photosynthesised carbon per area and time, remain imbricated and poorly understood (Chapin et al., 2000). Species can act through their numbers (Wardle, 2002) and their functional traits (Cadotte et al., 2011), and they act differently depending on the environmental context (Baert et al., 2018; Brun et al., 2019). In addition, the contribution of individual

species to productivity can be significant (Gotelli et al., 2011; Vitousek & Hooper, 1994). Understanding these relationships, however, is pivotal for assessing the impacts of biodiversity loss (Cardinale et al., 2012) and for global vegetation modelling (Prentice & Cowling, 2013). Comparably few studies have jointly studied the contributions of community-level properties and individual species to ecosystem productivity, and if they have (e.g. Loreau & Hector, 2001), not in real-world ecosystems and without systematically accounting for environmental context. Here, we followed the call for more such integrative approaches (Mahaut et al., 2020) and investigated how community-level properties and individual-species abundances contribute to explain productivity in the diverse environments of the European Alps.

While there are many concepts of biotic control in terms of community properties and individual species, we focus on two that have sound theoretical links to productivity (Box 1): the Trait Driver Theory (Enquist et al., 2015) for community-level functional properties and the key and keystone species concepts for individual species (Maire et al., 2018; Power et al., 1996), summarised as 'key(stone)' species in the following. For completeness, however, we also provide results for classical multivariate measures of functional diversity such as the Rao's quadratic entropy (Botta-Dukát, 2005; Villéger et al., 2008) and functional rarity such as functional distinctiveness (Violle et al., 2017).

Biotic control of community productivity cannot be understood without considering environmental conditions. Environmental conditions define which ecological strategies are successful at a given location and thus which species may thrive (Enquist et al., 2015; Garnier et al., 2016; Weiher et al., 2011). 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 control of productivity 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.

BOX 1 Definitions of Trait Driver Theory and key and keystone species

TRAIT DRIVER THEORY

Trait Driver Theory 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 (Garnier et al., 2004; Grime, 1998). 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).

KEY AND KEYSTONE SPECIES

If the presence or abundance of a species is linked to distinctly higher levels of ecosystem function, for example primary productivity, across a studied region, it is a 'key' species with respect to this function (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). Across the study system, key species occurrence is therefore linked to a high overall contribution to an ecosystem function. According to Power et al. (1996) 'keystone' species are species whose effects on ecosystem function are large, and disproportionally large relative to their abundance. A conspicuous example for a keystone species is the North American beaver, with its capacity to change the structure of riverine ecosystems (Naiman et al., 1988). As key species, keystone species occurrence is thus associated with a high overall contribution to an ecosystem function. But there is a second condition: keystone species need to have a high per-abundance effect, that is a large statistical effect size. Here, we investigate key and keystone species in a relative fashion, by identifying those species whose abundance contributes most to explain productivity and—in case of keystone species—also shows the strongest per-abundance effects on productivity (see Methods). While the key and keystone plant species identified this way likely play crucial roles, they are not selected based on their absolute impact which may be smaller than that of more iconic keystone species.

Here, we tested and compared the power of established community-based and species-based theories to explain differences in the remotely-sensed productivity of diverse real-world ecosystems. We focused on the moments of functional trait distributions and species cover abundance as key indicators for Trait Driver Theory and the key(stone) species concept respectively (Box 1). We employed a multi-model-comparison approach and >29,000 grassland community plots covering the French Alps and Switzerland (Figure S1), accounting for key environmental factors and considering the productivity-related traits specific leaf area (SLA), leaf nitrogen content (LNC) and reproductive height (HGT) (Lavorel & Garnier, 2002; Wright et al., 2004; Wright & Westoby, 2002). Specifically, we addressed the following questions (1) to which extent do community-weighted moments contribute to explain productivity compared to key(stone) species cover abundance? (2) do the relationships between community-weighted moments and productivity in the grasslands of the European Alps match the expectations postulated by Trait Driver Theory (formulated in Box 1)? and (3) how do the traits of key, keystone and the remaining, ordinary species differ from each other? Our analysis demonstrates that the cover abundance of few species can contribute more to explain productivity than estimates of functional community properties and that the relationships of productivity with species cover abundance and functional composition vary systematically across habitats, revealing a multitude of clues about the underlying processes.

MATERIAL AND METHODS

Data

Community data

Plant community observations originated from two sources covering the French Alps and Switzerland respectively (Figure 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 were 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 applied a series of preprocessing and filtering steps to these data (Supplementary Methods), after which 29'091 community observations remained.

Environmental data

Environmental data included the remotely sensed soil adjusted vegetation index as a proxy for productivity, as well as predictors representing climate, soil, topography and land cover, mostly with spatial resolutions of 100 m or higher. Satellite-derived vegetation indices have been shown to be accurate proxies of gross primary productivity (GPP), the rate at which vegetation canopies fix carbon through photosynthesis (Bannari et al., 1995; Zhou et al., 2014). Over the past decades, dozens of vegetation indices have been introduced, which are optimised for various ecosystem types (Xue & Su, 2017). For grasslands, in particular when including sparsely vegetated, high-alpine sites, the soil adjusted vegetation index (SAVI, Huete, 1988) has shown tight associations with GPP (Zhou et al., 2014). We calculated annual means of SAVI based on 18 years of observations made by the Landsat project (landsat.gsfc.nasa.gov; Figure S2). The environmental predictors included mean temperature, mean humidity (potential evapotranspiration minus precipitation), soil moisture and soil fertility proxies (derived from plant indicator values), terrain wetness index, exposition and whether or not a site was sparsely vegetated (vegetation sparsity). See Supplementary Methods for a description of data sources and preparations steps.

Trait data

Trait data included specific leaf area (SLA), leaf nitrogen content (LNC) and reproductive height (HGT). LNC and SLA are key traits of the leaf economics spectrum (Wright et al., 2004), and HGT is a central trait related to competitive ability (Violle et al., 2009) 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 that were taken within or close to the study region (now available in the TRY database; Kattge et al., 2020). For 0.4%, 5.8% and 20.4% of the 500 species with an occurrence frequency >1%, HGT, SLA and LNC measurements, respectively, were taken from the TRY database, originating from various sources (see Table S1 for detailed references). When multiple measurements were available per species, we averaged them. Full trait information was available for 412 species.

Analyses

Creating environmental clusters

In addition to running the analysis on the full data set, we ran it on five, 25 and 50 clusters of similar environmental conditions (hereafter referred to as 'habitats').

Splitting the data this way allowed us to assess how the relationships were affected by environmental context. We assumed mean annual temperature, water availability (humidity) and nutrient availability (soil fertility index) to be the most important factors constraining productivity. In order to facilitate the interpretability of the environmental space, we further summarised these factors by the first two first axes of a principal component analysis (PCA) that was run on the scaled and centred values. In this space, we then ran partitioning around medoids clustering to identify five, 25 and 50 clusters of similar size (Figure S3). Finally, we classified environmental clusters by their average SAVI into classes of 'low' for annual mean SAVI <0.23; 'medium' for mean SAVI ≥0.23 and <0.3; and 'high' for mean SAVI ≥0.3. Analyses were run in the R environment (R Development Core Team, 2008), with packages ade4 (Dray & Dufour, 2007) and cluster (Maechler et al., 2018). Resulting environmental clusters are described in the Supplementary Results.

Fitting reference models

We defined reference models (M_0) to identify the association between SAVI and environmental variables. We used generalised additive models (Hastie & Tibshirani, 1990) to fit these relationships for each set of communities associated with a habitat. 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 (for the French Alps and Switzerland respectively). 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 bounded between −1 and 1, annual means never approached these boundaries and showed a frequency distribution that was in agreement with the Gaussian error assumption. Once fitted, we calculated goodness of fit of all models based on adjusted explained deviance (referred to as explained deviance hereafter) using the R package ecospat (Broennimann et al., 2018).

While the formulation of M_0 was identical to analyse the impact of community-level predictors and individual-species cover, 39% 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 <80% of the total vegetation cover. For the key(stone)-species analysis, on the other hand, we only considered species that were present in ≥1% of the observations in a given habitat, leading to 0–33% fewer species considered (Table S2). We used the R package gam (Hastie, 2018) to fit generalised additive models.

Investigating community-level predictors

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

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

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

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

and CWS was calculated as

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

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

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

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 12 resulting models, we assessed how much their explained deviance increased compared to 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. The description of how partial response curves were classified into response types is provided in the Supplementary Methods.

Identifying key and keystone species

We identified key species, which were tightly and positively linked to SAVI (strong predictors), and keystone species, which were strong predictors too but also considerably increased SAVI, where they were present (strong per-abundance effect, see Box 1). 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 (Maire et al., 2018). Then, we set the added explained deviance of species with negative coefficients to zero (as by definition key species are positively associated with productivity) and defined those species with added deviance in the top 7.5% as key species. For keystone species, we additionally expected linear coefficients to be in the top 7.5%. Note, that while keystone species may also have negative effects on productivity (Power et al., 1996), for simplicity we only focused on those with positive effects. 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 Tukey honest significant difference (HSD) 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 community-level predictor individually, 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.

Comparing key and keystone species with 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 centred values of SLA, LNC and HGT. Before scaling, HGT measurements were log-transformed so that their frequency distribution assumed an approximately Gaussian shape. For visualisation, we ran one 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 (1–9) and for key(stone) species (1–3). Next, within each habitat, we summarised 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 (using the R package vegan (Oksanen et al., 2019)). We derived the Euclidean distance matrices of our trait space and tested based on 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. The workflow of the analysis is illustrated in Figure S4.

RESULTS

Explanatory power of environmental and biotic controls

Across the full dataset that covered steep environmental gradients, the seven environmental predictors of the reference model explained 70.3% of the deviance of SAVI. The explained deviance added by biotic predictors was comparably small (Figure 1). Community-weighted moments added between 0.2% (CWS of LNC) and 1.3% (CWM of SLA) of explained deviance. Similarly, multivariate measures of functional diversity added between 0.2% and 0.6% explained deviance (Figure S5). The cover values of key species, on the other hand, contributed between 0.5% and 3.3% 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 but also only 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. However, when community-weighted moments were modelled jointly (all community-weighted moments of one trait or one community-weighed moment of all traits) the full set of CWMs and all moments of SLA added significantly more explained deviance to M_0 than the top five key species, while the other combinations added significantly less (Figure S5). Also the summed cover abundance of rare species made a comparably high

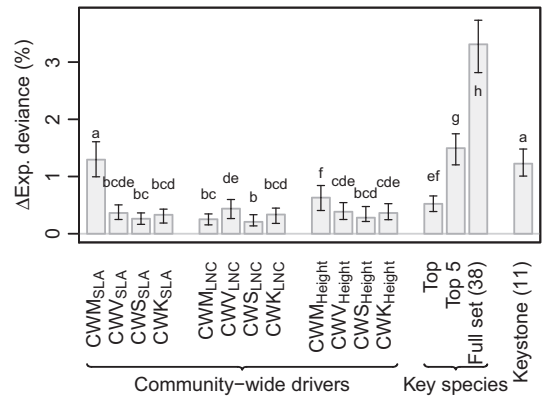

FIGURE 1 Explained deviance added by community-level predictors and individual-species cover. Shown are contributions of community-weighted moments, key-species cover, and keystone-species cover to explained deviance of model fits explaining productivity (soil adjusted vegetation index) with environmental 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. Letters on top of bars indicate groups according to a Tukey HSD test: if two bars share any letter, they are not significantly different from each other

contribution to explained deviance (2.0%, Figure S5), but rare-species cover abundance was negatively related to SAVI (Figure S6).

Community-weighted moments

Community-weighted means and variances mostly had positive associations with SAVI across the full dataset while relationships of community-weighted skewness and kurtosis with SAVI tended to be negative (Figure S6). SAVI 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 SAVI levelled off. The positive SAVI responses to CWVs were fairly consistent for all traits. They started to increase linearly with a moderate slope and then levelled off in the upper third of the range. CWS (absolute values) and CWK negatively influenced SAVI for all traits, indicating that SAVI tends to decrease when trait distributions are skewed or sharply peaked. However, these latter relationships were comparably weak.

Keystone and key species

Key species primarily included grasses and forbs, while keystone species consisted of forbs and legumes (Figure 2a). The 38 key species across all environments (Table S3) individually added ≥0.10% explained deviance to M_0 (Figure 2a). Among them, eleven species also showed high per-abundance effects and thus were keystone species. However, there seemed to be an upper limit to the combination of overall contribution and effect size, with no species dominating in both. Many species also had negative linear coefficients and thus a negative association with SAVI (Figure 2a). Yet, these species generally added little explained deviance.

Keystone and particularly key species differed from ordinary species when compared in trait space (Figure 2b, c). Functional distances within both, key and keystone species, were significantly shorter than distances between them and ordinary species ($p = 0.001$ and $p = 0.048$, 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 the 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 $p = 0.194$, respectively, two-sided Wilcoxon test). Key(stone) species similarly differed from ordinary species when defined more strictly based on the 95th percentiles of overall contribution and effect size, but differences began to erode when the 90th percentiles were used as thresholds (Figure S7).

Relationships by habitat

Explained deviance added by both community-weighted moments and key species-cover was higher under warm conditions with high soil fertility and low humidity than under cool and humid conditions (Figure 3). Among community-level predictors, community-weighted means most frequently ranked highest (Figure 3a). This was particularly true for CWM of SLA, which dominated under warm conditions. Among key species, the top-ranked ones were often forbs when conditions were cold and humid, or grasses and legumes when conditions were warmer and less humid (Figure 3b).

Not only did the strength of the relationships between community-level predictors and SAVI vary across habitats, but so did their shape (Figure 4). SAVI increased with CWM of SLA when conditions were moderately warm, whereas the relationships were mostly unimodal under warm-dry conditions (Figure 4a). In colder environments with low soil fertility, SAVI was often negatively related to CWM of LNC, whereas unimodal relationships prevailed under low humidity (Figure 4b). SAVI 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 (Figure 4c). For CWVs, relationships were similarly variable: partial SAVI responses to CWV of LNC were particularly positive under warm conditions (Figure 4e), where partial relationships between CWV of plant height and SAVI were most distinctly unimodal

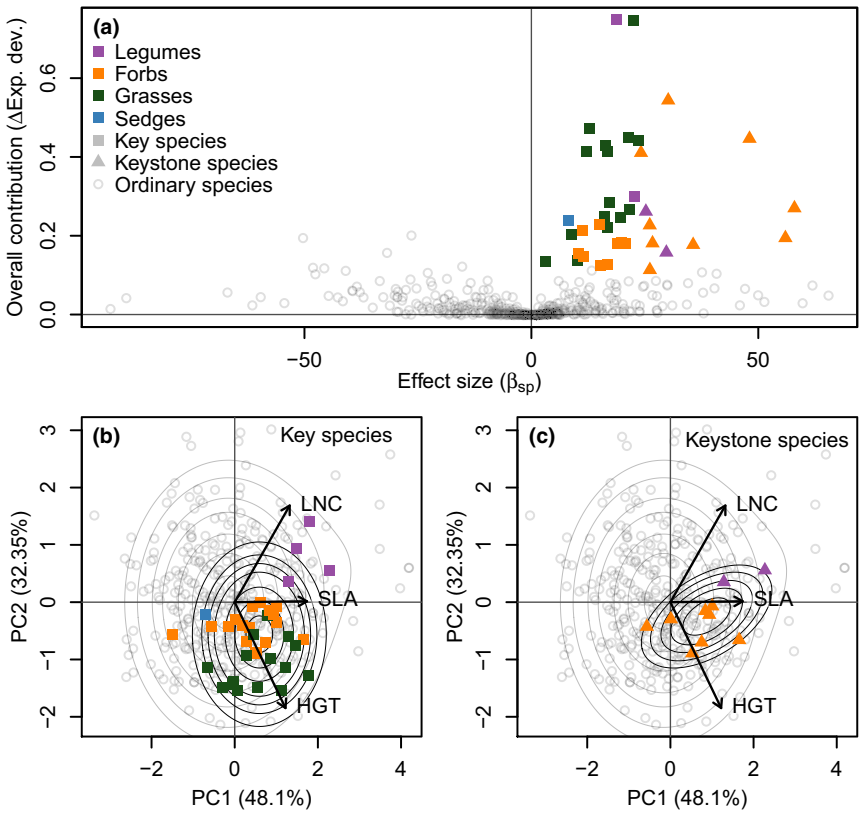

FIGURE 2 Importance and traits of key and keystone species. (a) productivity improvement per percent cover (effect size) and explained deviance added to the reference model (overall contribution) of all species considered. Key species are shown as squares and coloured according to plant type (see legend), their subset of keystone species is shown as triangles, 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 (black) and ordinary species (grey) respectively. Note that for one key species trait information was not available (see Table S1)

(Figure 4f). Partial relationships were also variable between SAVI and CWS and CWK of traits, although in these cases relationships were more often classified as non-significant (Figure S8).

Most of the key species found across all habitats were forbs, but grass and legume species were more often identified repeatedly in several habitats (Figure 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 (Figure 5b), but also the grasses *Anthoxanthum odoratum* and *Trisetum flavescens*, and the forb *Plantago lanceolata* were identified in 16, 15 and 15 habitats respectively. For *A. odoratum* this was the case for environments of moderate humidity (Figure 5c) and for *T. flavescens* and *P. lanceolata* it was mostly, although not as strictly, in moderately warm environments of rather low humidity (Figure 5d, e). 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 (Figure S9).

Key species tended to be taller and to have higher SLA than ordinary species in habitats of intermediate and high SAVI, but not when SAVI was low (Figure 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 SAVI of the habitat increased. Moreover, the shifts between key-species centroids and ordinary-species centroids more often pointed toward higher SLA and HGT in habitats of moderate to high SAVI (Figure 5f), and temperature and soil fertility (Figure 5g). In low-SAVI 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, Figure 5g). In environments of intermediate and high SAVI, on the other hand, trait shifts were significant at the $p \leq 0.05$ level in 67% and 64% of cases respectively. When five or 50 instead of 25 habitats were distinguished, the strength and the shape of relationships of community-weighted moments and key(stone) species with SAVI remained similar (Figures S10–S15).

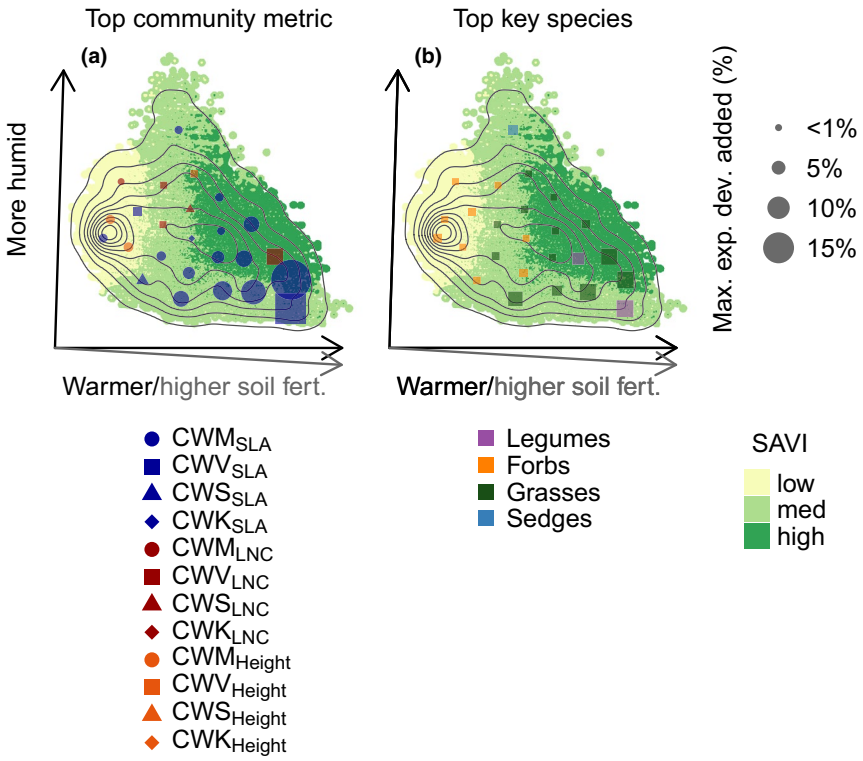

FIGURE 3 Explained deviance added by community-level predictors and key-species cover across 25 habitats. (a) identity and added explained deviance of smooth terms of best-performing community-level predictors. (b) plant type and added explained deviance of best-performing key species. Axes are a rotation 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

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 influent and heavily modulated by the environment. In our full-data analysis, the explained deviance added by biological predictors was relatively low (e.g. 0.7% for the top key species). This is because the steep environmental gradients in our study area primarily constrained productivity and the quantification of biological contributions were accounted for only after environmental effects (Maire et al., 2018), rather than because biotic predictors were unimportant: key-species contributions were still two orders of magnitude higher than random expectation (Figure S16). Moreover, when the data was grouped by habitats, explained deviance added by biotic predictors increased markedly (e.g. 0.5–6.7% for the top key species in 25 habitats). When environmental conditions were not corrected for, biotic predictors explained up to 41% of deviance in the full-data analysis, highlighting that environmental and biotic predictors are entwined (Grace et al., 2016).

Key species were generally tall and had high SLA—traits that are associated with high competitive ability (Körner, 2003; Violle et al., 2009) and high growth rates (Poorter et al., 2009; Wright et al., 2004). The lower functional distinctiveness of key species compared to ordinary species indicates that grassland species associated with unexpectedly high productivity tend to converge to one particularly successful phenotype (Enquist et al., 2015; Grime, 2006). 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 *Trifolium pratense* and *Trisetum flavescens* (Figure 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 overall contribution and per-abundance effect indicates that keystone plants, with respect to productivity, tend to be specialised 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

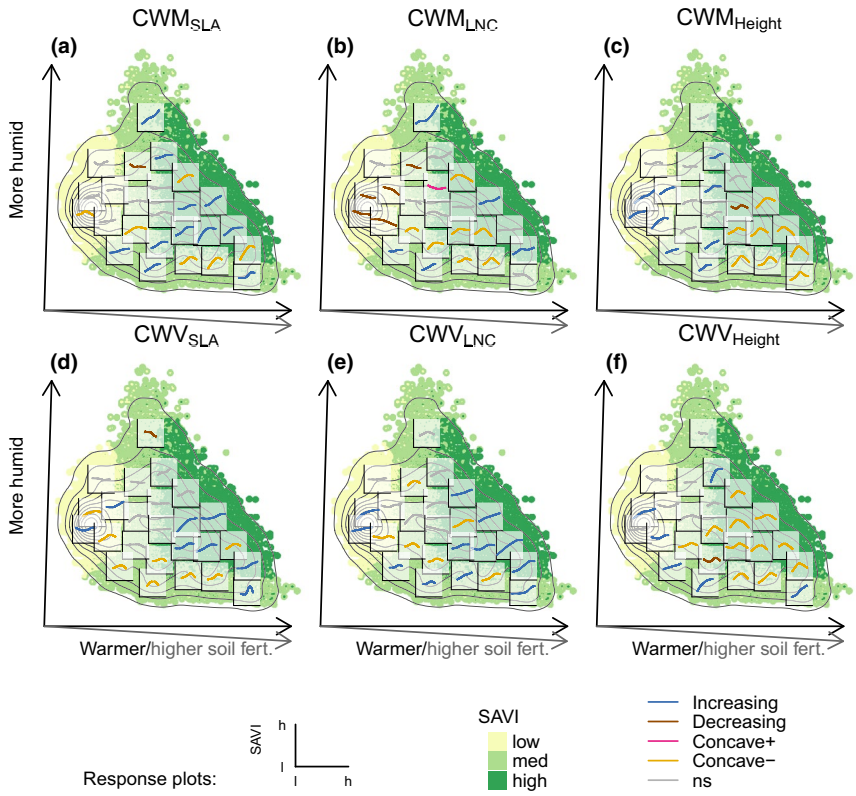

FIGURE 4 Partial responses of productivity to community-weighted means and variances across 25 habitats. Partial responses of productivity (soil adjusted vegetation index, SAVI) to community-weighted means (a–c) and community-weighted variances (d–f) of SLA (a, d), LNC (b, e) and HGT (c, f) across 25 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

assumption of Trait Driver Theory (TDT) that productivity is primarily determined by the effect of the traits that lead to the highest fitness in a given environment, which are reflected by CWMs (Enquist et al., 2015; Garnier et al., 2004). 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, deviations from the optimal ecological strategy are compensated by benefits from niche differentiation, resource-use complementarity and mutualistic effects like nitrogen fertilisation (Barneze et al., 2020; Pacala & Tilman, 1994). 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). A deeper understanding of how different predictors at the community level determine productivity may be obtained by considering 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, productivity increases especially steeply with CWMs of plant height (Figure 4). Additional height among small plants may 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 (Figure 4). Variations in the relationship between productivity and CWM of SLA may be driven by environmental control of the growth rate-longevity trade-off (Borgy et al., 2017; 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 rate (and thus productivity) increase with SLA, as material costs per photosynthetically active leaf area decrease (Poorter et al., 2009; Wright et al., 2004). Yet, this advantage comes with shorter leaf life spans and higher water loss through transpiration (Wright et al., 2004). When water stress is low and growing season comparably

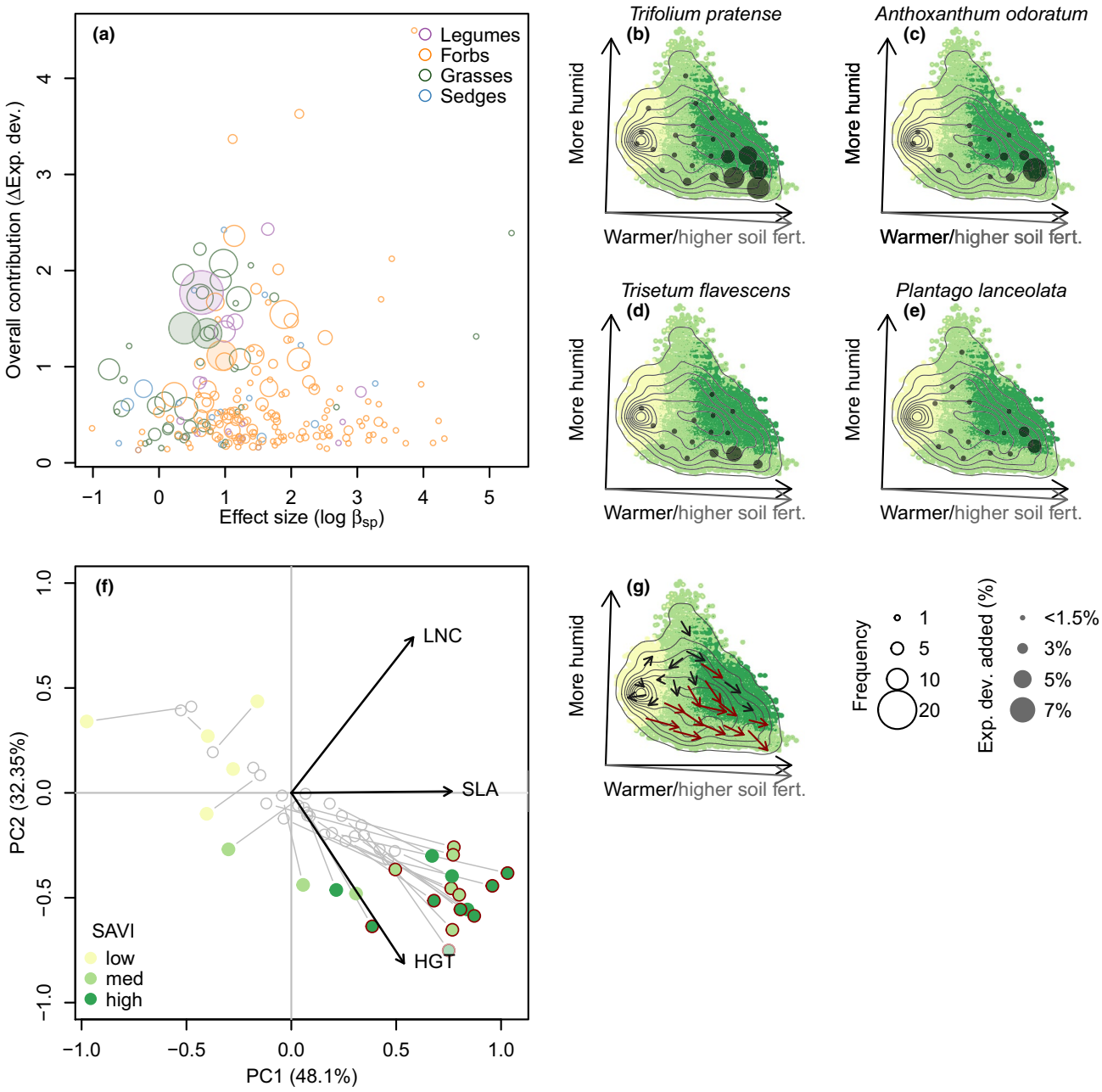

FIGURE 5 Importance and traits of key species across 25 habitats. (a) increase in productivity per percent cover (effect size), and explained deviance added to the reference model (overall contribution) of key species of all habitats. Key species are coloured according to plant type (see legend); ring 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 (coloured 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). Significant shifts are highlighted in dark red. 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

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 abundance than with any community-level predictor (Spearman r = 0.57, Figure S17), indicating that the positive effect of CWV of LNC may be linked to increased biological nitrogen fertilisation 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 neighbouring 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 fall below 22°C (Vitousek et al., 2013). Biological nitrogen fixation is, therefore, less efficient in cold than in warm environments (Cleveland et al., 1999).

To gain insight on how community-level properties and individual species are associated with productivity in diverse habitats, we relied on large observational datasets and had to make several assumptions. First, we only considered three traits and did not account for intraspecific trait variation. Although SLA, LNC and HGT are key determinants of productivity (Lavorel & Garnier, 2002; Wright et al., 2004; Wright & Westoby, 2002), 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 (Kichenin et al., 2013), they interact in complex ways with implications that can be significant (Des Roches et al., 2018). Especially in the full-data analysis with its steep environmental gradients, this may have limited the predictive power of the functional community metrics. Second, 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 which, in a few cool and moist habitats, may distinctly contribute to productivity.

The nature and importance of processes linking biotic properties to grassland productivity are known to vary greatly depending on the environmental context (Grace et al., 2016). In this study, we have demonstrated that the effect of environmental context can be quantified when data set and approach are chosen appropriately. This, in turn, sets the scene for deeper insights and a better process understanding. For global vegetation modelling (Prentice & Cowling, 2013), for example formulations of trade-offs may be improved (Peaucelle et al., 2019). Moreover, we have shown that, beside community-level trait attributes, the cover values of key(stone) species may be used as indicators of productivity in real-world ecosystems—a useful finding for ecosystem management, given that species cover is readily quantified. While our approach did not allow us to identify the mechanisms that underlie these associations, it indicates that in addition to established properties of productive species, such as high SLA (Lavorel & Garnier, 2002) or membership of certain functional groups (Jaillard et al., 2018), the effect of key(-stone) species may be linked to other factors, including ability to disperse. Future studies will be necessary to comprehensively identify the roles and properties of important key(stone) species and establish a more complete picture of the biotic control of productivity.

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AUTHORSHIP

W.T., C.V. and D.M. conceived the general idea of the analysis. P.B. designed the study with the help of W.T., C.V., B.J.E., D.M., N.M, F.M., T.M., A.O. and N.E.Z. P.B. performed the analysis and led the writing of the manuscript. All authors significantly interpreted results and contributed to writing and editing.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

The data supporting the results of this study are available on Dryad and can be accessed with the following link: https://doi.org/10.5061/dryad.n5tb2rbx9.

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REFERENCES

Baert, J.M., Eisenhauer, N., Janssen, C.R. & De Laender, F. (2018) Biodiversity effects on ecosystem functioning respond unimodally to environmental stress. *Ecology Letters*, 21, 1191–1199.

Bannari, A., Morin, D., Bonn, F. & Huete, A.R. (1995) A review of vegetation indices. *Remote Sensing Reviews*, 13, 95–120.

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

Borgy, B., Violle, C., Choler, P., Denelle, P., Munoz, F., Kattge, J. et al. (2017) Plant community structure and nitrogen inputs modulate the climate signal on leaf traits. *Global Ecology and Biogeography*, 26, 1138–1152.

Botta-Dukát, Z. (2005) Rao's quadratic entropy as a measure of functional diversity based on multiple traits. *Journal of Vegetation Science*, 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.

Broennimann, O., Di Cola, V. & Guisan, A. (2018) ecospat: Spatial Ecology Miscellaneous Methods.

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. *Nature Communications*, 10, 5691.

Cadotte, M.W., Carscadden, K. & Mirotchnick, N. (2011) Beyond species: functional diversity and the maintenance of ecological processes and services. *Journal of Applied Ecology*, 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 III, 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 Biogeochemical Cycles*, 13, 623–645.

Des Roches, S., Post, D.M., Turley, N.E., Bailey, J.K., Hendry, A.P., Kinnison, M.T. et al. (2018) The ecological importance of intraspecific variation. *Nature Ecology & Evolution*, 2, 57–64.

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

Dray, S. & Dufour, A.-B. (2007) The ade4 Package: Implementing the duality diagram for ecologists. *Journal of Statistical Software*, 22, 1–20.

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 in Ecology & Evolution*, 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: Oxford University Press.

Gotelli, N.J., Ulrich, W. & Maestre, F.T. (2011) Randomization tests for quantifying species importance to ecosystem function. *Methods in Ecology and Evolution*, 2, 634–642.

Grace, J.B., Anderson, T.M., Seabloom, E.W., Borer, E.T., Adler, P.B., Harpole, W.S. et al. (2016) Integrative modelling reveals mechanisms linking productivity and plant species richness. *Nature*, 529, 390–393.

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

Grime, J.P. (2006) Trait convergence and trait divergence in herbaceous plant communities: mechanisms and consequences. *Journal of Vegetation Science*, 17, 255–260.

Gross, N., Bagousse-Pinguet, Y.L., Liancourt, P., Berdugo, M., Gotelli, N.J. & Maestre, F.T. (2017) Functional trait diversity maximizes ecosystem multifunctionality. *Nature Ecology & Evolution*, 1, 0132.

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

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

Huete, A. (1988) A soil-adjusted vegetation index (SAVI). *Remote Sensing of Environment*, 25, 295–309.

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.

Kattge, J., Bönisch, G., Díaz, S., Lavorel, S., Prentice, I.C., Leadley, P. et al. (2020) TRY plant trait database – enhanced coverage and open access. *Global Change Biology*, 26, 119–188.

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. *Functional Ecology*, 27, 1254–1261.

Körner (2003) *Alpine plant life - functional plant ecology of high mountain ecosystems*, 2nd edition. New York, USA: Springer.

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

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

Loreau, M. & Hector, A. (2001) Partitioning selection and complementarity in biodiversity experiments. *Nature*, 412, 72–76.

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. *Functional Ecology*, 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. *Proceedings of the Royal Society B-Biological Sciences*, 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. *American Naturalist*, 143, 222–257.

Peaucelle, M., Bacour, C., Ciais, P., Vuichard, N., Kuppel, S., Peñuelas, J. et al. (2019) Covariations between plant functional traits emerge from constraining parameterization of a terrestrial biosphere model. *Global Ecology and Biogeography*, 28, 1351–1365.

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 and 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 Phytologist*, 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: Levin, S.A. (Ed.) *Encyclopedia of biodiversity*. Waltham, MA: 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. *The R Journal*, 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 in Ecology & Evolution*, 32, 356–367.
Vitousek, P.M. & Hooper, D.U. (1994) Biological diversity and terrestrial ecosystem biogeochemistry. In: Schulze, E.-D. & Mooney, H.A. (Eds.) *Biodiversity and ecosystem Function*. Berlin Heidelberg, Berlin, Heidelberg: Springer, pp. 3–14.
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. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 368, 20130119.
Wardle, D.A. (2002) Ecology by numbers. *Trends in Ecology & Evolution*, 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. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 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. *Proceedings of the National Academy of Sciences*, 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 Phytologist*, 155, 403–416.
Xue, J. & Su, B. (2017) Significant remote sensing vegetation indices: a review of developments and applications. . *Journal of Sensors*, 2017, 1–17.
Zhou, Y., Zhang, L., Xiao, J., Chen, S., Kato, T. & Zhou, G. (2014) A comparison of satellite-derived vegetation indices for approximating gross primary productivity of grasslands. *Rangeland Ecology & Management*, 67, 9–18.

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