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Trade-offs and synergies between ecosystem productivity and stability in temperate grasslands

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Abstract

Aim: It is crucial to monitor how the productivity of grasslands varies with its temporal stability for management of these ecosystems. However, identifying the direction of the productivity–stability relationship remains challenging because ecological stability has multiple components that can display neutral, positive or negative covariations. Furthermore, evidence suggests that the direction of the productivity–stability relationship depends on the biotic interactions and abiotic conditions that underlie ecosystem productivity and stability. We decipher the relationships between grassland productivity and two components of its stability in four habitat types with contrasting environments and flora.

Location: France.

Time period: 2000–2020.

Major taxa: Grassland plant species.

Methods: We used c. 20,000 vegetation plots spread across French permanent grasslands and remotely sensed vegetation indices to quantify grassland productivity and temporal stability. We decomposed stability into constancy (i.e., temporal invariability) and resistance (i.e., maximum deviation from average) and deciphered the direct and indirect effects of abiotic (namely growing season length and nitrogen input) and biotic (namely plant taxonomic diversity, trait diversity and community-weighted mean traits) factors on productivity–stability relationships using structural equation models.

Results: We found a positive relationship between productivity and constancy and a negative relationship between productivity and resistance in all habitats. Abiotic factors had stronger effects on productivity and stability compared with biotic factors. A longer growing season enhanced grassland productivity and constancy. Nitrogen input had positive and negative effects on grassland productivity and resistance, respectively. Trait values affected the constancy and resistance of grassland more

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than taxonomic and trait diversity, with effects varying from one habitat to another. Productivity was not related to any biotic factor.

Main conclusions: Our findings reveal how vital it is to consider both the multiple components of stability and the interaction between environment and biodiversity to gain an understanding of the relationships between productivity and stability in real-world ecosystems, which is a crucial step for sustainable grassland management.

KEYWORDS

biodiversity, constancy, ecosystem functioning, eutrophication, functional traits, remote sensing, resistance

1 | INTRODUCTION

Quantifying the link between the rate of an ecosystem function, such as productivity, and its temporal stability is pivotal in the perspective of monitoring and managing ecosystems world-wide (Albrich et al., 2018; Montoya et al., 2019). This is particularly crucial for grasslands that are subject to highly variable climate and severe disturbances, such as drought (Bardgett et al., 2021), which can affect the provision of major ecosystem services, including carbon sequestration and forage production for livestock (Bengtsson et al., 2019). Given that several years can be necessary to recover grassland productivity after a disturbance (e.g., Fu et al., 2017), temporal stability is as important as the average level of productivity for the long-term provisioning of these ecosystem services. However, studies that have investigated the drivers of grassland productivity and its year-to-year stability largely neglect the covariation that potentially exists between ecosystem productivity and stability (Wang et al., 2021). Whether grassland productivity can be simultaneously enhanced and sustained over time thus remains an open question.

The relationship between stability and ecosystem productivity is shaped by biodiversity and biotic interactions (Isbell et al., 2009; Wang et al., 2021). Years of biodiversity–ecosystem functioning research have demonstrated positive, saturating relationships between species or trait diversity and productivity (Cardinale et al., 2007; Duffy et al., 2017; Tilman et al., 1997) and stability (Craven et al., 2018; Isbell et al., 2015). Although the positive effects of biodiversity on ecosystem productivity and stability might have suggested a positive covariation between these two ecosystem properties, these positive effects have been shown to be independent of each other (Cardinale et al., 2013). Recent findings also indicate that the sign of the relationship between ecosystem productivity and stability depends on the mechanisms that drive these biodiversity effects (Wang et al., 2021; Yan et al., 2021). The positive effect of plant diversity on productivity is frequently related to the mechanism of niche complementarity. Complementarity usually occurs when interspecific interactions limit the similarity of traits (i.e., enhance trait diversity) between coexisting species, notably for those traits that are related to resource use strategy (e.g., specific leaf area, leaf nitrogen content and leaf dry matter content; Garnier et al., 2016; Wright et al., 2004), resulting in maximized use of the

available resources. The coexistence of species with different values of response traits to the environment can also increase the stability of ecosystem productivity because one species can compensate for the decline of another following a change in environmental conditions (i.e., asynchronous dynamics; Hallett et al., 2017; Loreau & de Mazancourt, 2013). Accordingly, both ecosystem productivity and stability are expected to increase with trait diversity of plant communities. Alternatively, and especially in the most productive habitats, interspecific interactions can lead to the dominance of a restricted number of species that display the highest competitive ability, for example by being taller than others (Garnier et al., 2016). In that case, the traits of the dominant species, rather than trait diversity, drive ecosystem productivity (i.e., mass ratio hypothesis; Grime, 1998). Yet, if communities dominated by tall, fast-growing and resource-acquisitive species are generally more productive than those dominated by slow-growing, conservative ones (Garnier et al., 2016), they might also show lower resistance to environmental fluctuations (Grime et al., 2000; Májeková et al., 2014).

Environmental conditions, by shaping the nature of species interactions (Lortie et al., 2004; Maestre et al., 2009) and determining which ecological strategies dominate in a particular location (Enquist et al., 2015; Garnier et al., 2016), can affect the role of plant diversity and functional traits in driving ecosystem productivity and stability. Growing season length is a major regulatory factor of the distribution of functional traits related to resource use strategies in grassland communities (Borgy, Violle, Choler, Denelle, et al., 2017). Increased growing season length also promotes the coexistence of species with different phenologies (Rathcke & Lacey, 1985), which can, in turn, increase both ecosystem productivity and stability (Oehri et al., 2017). In addition, resource availability, and especially nitrogen, exerts a strong control on the distribution of plant functional traits (de Bello et al., 2013; Grime, 1977), with major repercussions on ecosystem productivity and stability (Grman et al., 2010; Hautier et al., 2020; van Ruijven & Berendse, 2005).

Finally, deciphering the relationship between ecosystem productivity and stability can be particularly challenging given that ecological stability consists of several components (de Bello et al., 2021), including temporal invariability (hereafter, constancy) and the maximum deviation from the average level of functioning (hereafter, resistance) (Donohue et al., 2013). These components can be

uncorrelated or can display either positive or negative covariation (Donohue et al., 2013; Polazzo & Rico, 2021). Analysis of the relationships between productivity and different components of its stability is therefore crucial to understand whether productivity is consistently linked to stability or whether some stability components increase with productivity whereas others decrease.

Here, we used 19,884 vegetation plots across France to quantify the relationships between grassland productivity and two components of its stability (constancy and resistance) and to disentangle the joint roles played by abiotic and biotic factors on these relationships. The dataset covers four major types of grassland habitats, namely calcareous, mesic, mountain and ruderal grasslands, which are characterized by contrasting growing season length (GSL; computed from both temperature and soil water balance) and nitrogen inputs (Borgy, Violle, Choler, Denelle, et al., 2017; Denelle et al., 2020; Violle et al., 2015). We used satellite-sensed surface spectral reflectance to derive proxies for annual productivity and the two stability components (White et al., 2020). Initially, we tested whether the four grassland habitats show differences in terms of productivity, constancy and resistance. We expected higher productivity, constancy and resistance in habitats with longer GSL and higher productivity but lower constancy and resistance in habitats with high levels of N inputs. Then, we performed cross-correlation analyses to quantify whether the relationship between productivity and stability varies among grassland habitats. Finally, we used structural equation models (SEMs) to disentangle the direct and indirect effects of abiotic factors (GSL and N inputs), taxonomic diversity, trait diversity and community-weighted mean (CWM) values of a set of traits related to resource use strategy, plant size and reproductive phenology. We built one SEM per grassland habitat to test whether the effects of plant diversity and functional traits change between habitats with contrasting abiotic conditions.

2 | MATERIALS AND METHODS

2.1 | Ecosystem productivity and stability in French permanent grasslands

We first delineated all grasslands in France at a resolution of 500 m \times 500 m by combining data from Corine Land Cover (2010), a European-scale land cover database, and from the *Registre Parcellaire Graphique*, an administrative database of land management based on on-farm survey data (Supporting Information Figure S1). To select only the most representative pixels, we kept 93,524 pixels with a grassland cover >70%.

For all selected pixels and for the years 2000–2020, we computed the kernel-normalized difference vegetation index (kNDVI; Camps-Valls et al., 2021). The kNDVI is a nonlinear generalization of the normalized difference vegetation index (NDVI), which quantifies photosynthetically active vegetation from the ratio of red and near-infrared reflected light. Recent advances showed that kNDVI gives a better approximation of primary productivity than

NDVI (Camps-Valls et al., 2021). We used the Moderate Resolution Imaging Spectrometer (MODIS) of NASA's Terra satellite (product MOD09A1.006), which has a temporal resolution of 8 days and a spatial resolution of 500 m. According to MODIS quality flag, we removed reflectance scores that had low-quality class values (i.e., QA_Overall < 1; Friedl et al., 2019) and followed Choler et al. (2021) to process the time series of vegetation indices. Briefly, we reduced the noise of the raw values of kNDVI using the best index slope extraction (BISE) algorithm (Viovy et al., 1992). The acceptable difference in kNDVI values within the sliding period was set to $n = 0.2$, and the length of the forward sliding period was set to $p = 3$. We then applied a low-pass filter using the Savitzky–Golay algorithm (Savitzky & Golay, 1964), with the following parameters: $n = 3$ (the filter order) and $p = 7$ (the filter length).

Annual primary productivity was approximated, for each pixel, by the integrated kNDVI over a vegetation cycle (i.e., between the onset and the end of each growing season; Supporting Information Figure S2). Each year, onset of growth and senescence correspond to the first dates when kNDVI crosses the $0.5 \times$ maximum (kNDVI) threshold in ascendant and descendent directions, respectively. Then, we computed the mean of annual productivity for the 2000–2020 period to quantify grassland productivity in each 500 m pixel (Supporting Information Figure S2). We detrended by time the 21-year annual kNDVI series using second-order polynomial regressions before calculating the constancy and resistance of grassland productivity (Supporting Information Figure S2).

Constancy was approximated as the inverse of the coefficient of variation for each 500 m pixel, i , according to the equation:

$$\text{Constancy}_i = \text{mean}(\text{kNDVI}_i) / \text{SD}(\text{dtrd_kNDVI}_i),$$

where $\text{mean}(\text{kNDVI}_i)$ is the average value of annual integrated kNDVI over the vegetation season and $\text{SD}(\text{dtrd_kNDVI}_i)$ its time-detrended standard deviation (SD) over the whole period, 2000–2020.

We approximated resistance as the inverse of the deviation of plant productivity from “baseline” functioning (White et al., 2020). For each pixel, i , and year, t , deviations were the scaled anomalies of annual productivity ($A_{i,t}$):

$$A_{i,t} = [(\text{kNDVI}_{i,t}) - \text{mean}(\text{kNDVI}_i)] / \text{SD}(\text{dtrd_kNDVI}_i),$$

with $\text{kNDVI}_{i,t}$ being the value of grid cell i of the year t over the whole period, 2000–2020. Positive values of $A_{i,t}$ correspond to a higher annual productivity relative to baseline productivity, whereas negative values represent a lower value. The minimum value of $A_{i,t}$ is thus obtained for the lower estimated annual productivity over the 2000–2020 period. Given that the core issue of this work is to test whether a high yield can be maintained stable through time, we focused on the minimum value of $A_{i,t}$ to characterize ecosystem resistance (R_i):

$$R_i = |1 / \min(A_{i,t})|,$$

so that the larger the value of R_p , the greater is the resistance of the ecosystem. For >90% of the 500 m pixels, the maximal deviation from mean grassland productivity was observed in 2003, 2005 or 2018 (Supporting Information Figure S3), which corresponds to the major drought events in France over the last 20 years. Our resistance index thus characterized the response of grassland productivity to these extreme climatic events.

2.2 | Vegetation, habitat types and plant traits

The dataset of permanent grasslands in France includes 96,132 botanical plots and 2930 species, coming from multiple data sources and gathered in the DivGrass project (Borgy, Violle, Choler, Denelle, et al., 2017; Denelle et al., 2020; Violle et al., 2015). The area of each plot varied from 50 to 100 m², and they were visited a single time. Most of the plots (75,872) consist of plant species relative cover estimated among a six-level scale: 0–1, 1–5, 5–25, 25–50, 50–75 and 75–100%. The median of each class provides a quantitative scale. Only botanical plots surveyed after 1980 and data considering all the species and estimating their cover were retained (80% of DivGrass database).

Each plot was assigned to one of four types of grassland habitats (i.e., dry calcareous, mountain, mesic and ruderal), defined from an analysis of modularity of the global species–site network (Denelle et al., 2020). Dry calcareous grasslands were characterized by higher soil pH and low water availability caused either by low precipitation or by fine, sloping soil that does not retain water. Mountain grasslands included sites with lower annual temperature and higher precipitation. Mesic grasslands represented sites at low elevation, with mean annual temperature and precipitation that lay in between those of the other habitats. Sites associated with high temperatures, low precipitation and more ruderal species represented disturbed ruderal communities with many Mediterranean taxa.

For each species, we extracted five functional traits from several databases and local datasets (including the TRY database; Kattge et al., 2020); see Borgy, Violle, Choler, Denelle, et al. (2017) and Violle et al. (2015) for details about trait data compilation. We considered three traits related to resource use strategy, namely specific leaf area (SLA; in metres squared per gram), mass-based leaf nitrogen content (LNC; in milligrams of N per gram) and leaf dry matter content (LDMC), which discriminate resource-acquisitive versus conservative plant strategies well (Garnier et al., 2016; Wright et al., 2004). Plant height (in metres) characterized plant size. Finally, flowering time (Julian day) represented reproductive phenology, a dimension of the functional space of plants that is rather independent from resource use strategy and size (Segrestin et al., 2020). We considered mean trait values for each species, assuming that interspecific variation in trait values has more influence than intraspecific variation on the functional turnover of community composition at large biogeographical scales (Siefert et al., 2015). Given that trait values were not available for all species (Violle et al., 2015), we removed botanical plots where >60% of the coverage was occupied by a species with

information missing for at least one trait (for a detailed discussion on issues related to threshold values, see Borgy, Violle, Choler, Garnier, et al., 2017).

2.3 | Abiotic and biotic drivers

We used an index of growing season length (GSL) that accounts for both daily temperature and soil water content that has been calculated by Borgy, Violle, Choler, Denelle, et al. (2017) for the DivGrass dataset. Briefly, this index corresponds to the mean number of days in the year for which: (1) mean daily temperature was >5°C, and (2) the ratio between soil available water content and soil water-holding capacity was >.2 for the 1961–1990 period. We chose to use this integrative index rather than mean annual precipitation and temperature because Borgy, Violle, Choler, Denelle, et al. (2017) demonstrated that it best predicted the distribution of plant functional traits in the DivGrass dataset.

Nitrogen input was computed as the sum of organic fertilization, mineral fertilization and atmospheric deposition. Data were obtained from the census Noplu-Agri information system of the French Ministry of Agriculture (<http://www.statistiques.developpement-durable.gouv.fr>) and the European Monitoring and Evaluation Program (<http://www.emep.int/>). These data were available for each French municipality, whose mean area is c. 8 km² (see details in the paper by Borgy, Violle, Choler, Denelle, et al., 2017).

Biotic drivers corresponded to taxonomic diversity, trait diversity and community-weighted mean (CWM) values of SLA, LNC, LDMC, plant height and flowering time. The exponential of the Shannon diversity index [$\exp(H')$] quantified taxonomic diversity as an effective species number (Jost, 2006). We measured the multivariate functional dispersion index (FDis) to quantify the functional diversity of each community (Laliberté & Legendre, 2010).

2.4 | Data aggregation at 5 km resolution

Given that the botanical plots were geo-referenced at a precision ≤5 km (Violle et al., 2015), we conducted the analyses at that resolution to account for the geo-location uncertainty of the vegetation data. We aggregated grassland productivity, constancy and resistance in a 5 km × 5 km grid using the *aggregate* function of the *raster* R library (Hijmans et al., 2022). We used the median of the value of each ecosystem property of the 500 m pixels with grassland cover >70%, meaning that ecosystem properties at 5 km resolution were computed from k 500 m subpixels, with k varying between 1 and 100 (Supporting Information Figure S2). We also computed the median of taxonomic and functional diversity, in addition to the median of the CWM of each trait for each 5 km pixel, while discarding pixels with fewer than three botanical plots. The N input and GSL were downsampled at the 5 km resolution using the *resample* function of the *raster* R library (Hijmans et al., 2022). Finally, a few 5 km pixels comprised plots of different grassland types. We considered these pixels

as many times as necessary to ensure that each habitat was represented in the final dataset. The final dataset comprised 19,884 plots and 2002 plant species spread across 1914 5 km pixels. Of these, 477, 889, 353 and 195 5 km pixels corresponded to dry calcareous, mesic, mountain and ruderal grasslands, respectively.

2.5 | Data analyses

Initially, we compared ecosystem productivity, constancy and resistance among the different grassland habitats using ANOVA and Tukey's post-hoc tests.

Next, we analysed ecosystem productivity–stability relationships for all grassland habitats together and then separately for each of the four types of grassland habitats. We computed the Pearson correlation index between ecosystem constancy and ecosystem productivity, between ecosystem resistance (\log_{10} -transformed) and ecosystem productivity, and between both components of ecosystem stability.

To sort out the roles of climate (GSL), nitrogen input and biotic factors [$\exp(H')$, FDis and CWMs of each trait] on grassland productivity, constancy and resistance, SEMs were used. Given that we expected that abiotic conditions would affect the roles of plant diversity and functional traits on ecosystem productivity and stability, we built one SEM per habitat, with the four grassland habitats displaying contrasting environmental conditions (Supporting Information Figure S1). We considered covariations between ecosystem productivity, constancy and resistance, between GSL and N inputs, and between all facets of biodiversity. We modelled the direct effects of GSL and N inputs and of each biotic factor on the three ecosystem variables. We also accounted for the effects of GSL and N inputs on biodiversity (the indirect effects of abiotic factors on grassland productivity, constancy and resistance). Given that ecosystem productivity and stability were spatially autocorrelated (data not shown), we used a spatial regression method in the SEM in order to reduce type I errors. We used generalized least squares (GLS) that seek to model the spatial structure in the distribution of

residuals as a distance-based correlation function (Beale et al., 2010). We evaluated the potential of five forms of distance-based correlation function: linear, Gaussian, exponential, rational and spherical. Then, we used the Akaike information criterion (AIC) to select the best correlation structure as the one having the lowest AIC. In all cases, models with an exponential function fitted the data best (data not shown). We standardized all variables before analysis. The SEMs were built using the *piecewiseSEM* R library (Lefcheck et al., 2020). All analyses were performed in R v.4.0.3.

3 | RESULTS

Grassland productivity, constancy and resistance showed significant differences between habitats (Figure 1). Productivity and constancy were higher in mesic and ruderal grasslands, which also had a longer GSL and the highest level of N input, and lower in mountain grasslands, which had a shorter GSL and a lower level of N inputs (Supporting Information Figure S4). Conversely, ruderal grasslands had the lowest resistance and mountain grasslands the highest (Figure 1).

Our analyses also revealed that grassland productivity was positively correlated with constancy and negatively correlated with resistance (Figure 2). These marginal relationships (i.e., they do not account for other effects) were consistent across habitats, although the coefficients of correlation changed slightly from one habitat to another (Figure 2). Furthermore, we observed positive, marginal correlations between the constancy and the resistance of grassland productivity, with the strongest link for ruderal habitat (Figure 2).

Next, we focused on the direct and indirect effects of abiotic factors (i.e., GSL and N inputs) and on the direct effects of biotic factors (i.e., taxonomic diversity, trait diversity and CWM of the different traits) on the productivity, constancy and resistance of each grassland habitat using SEMs. We showed that ecosystem productivity was mostly affected by abiotic factors (Figure 3), with grassland productivity increasing with the level of N inputs and with GSL in all habitats except in ruderal grasslands, where GSL

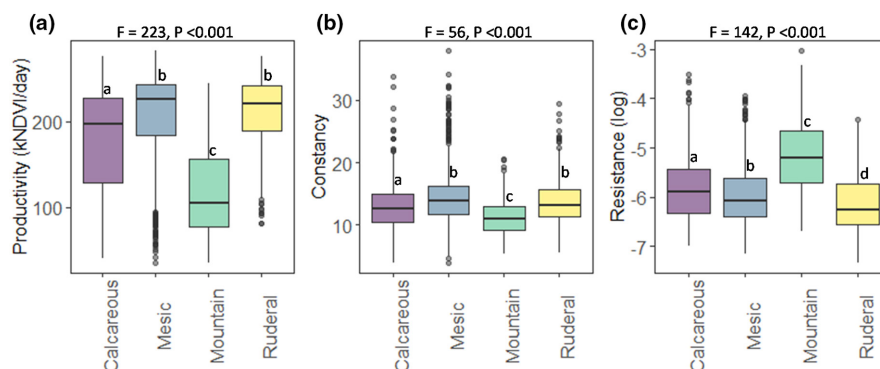


FIGURE 1 Productivity and stability (constancy and resistance) of permanent grasslands across four habitat types. (a) Productivity, (b) constancy and (c) resistance of calcareous ($n = 464$), mesic ($n = 877$), mountain ($n = 320$) and ruderal ($n = 193$) grassland habitats. The results of the ANOVAs are indicated above the box plots, and letters show significant differences between habitats according to Tukey's post hoc tests (two habitats sharing a similar mean have the same letter).

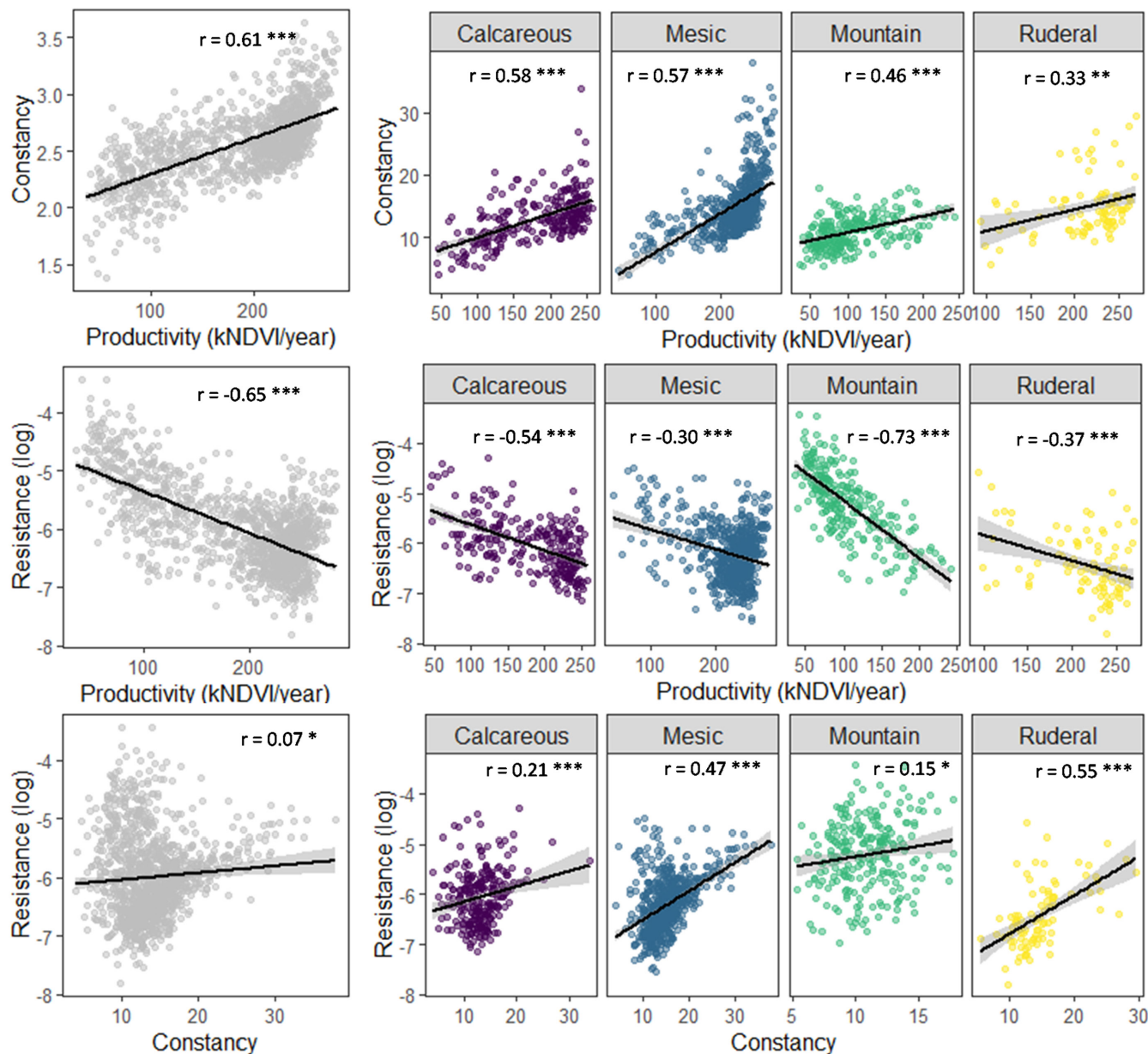


FIGURE 2 Marginal correlations between grassland productivity, constancy and resistance. Left panels show relationships when all grassland habitats are combined. Right panels show relationships for each habitat. * $p < .05$, ** $p < .01$, *** $p < .001$; ns, non-significant.

had no effect on productivity (Figure 4). Abiotic factors were also the main drivers of ecosystem stability in all habitats, except in ruderal grasslands (Figure 3). Constancy increased with N input in mesic (Figure 4b) and mountainous (Figure 4c) grasslands and increased with GSL in calcareous (Figure 4a) and mesic (Figure 4b) habitats. Conversely, resistance decreased with N input in calcareous (Figure 4a) and mountainous (Figure 4c) grasslands and decreased with GSL in mountainous habitat (Figure 4c). Moreover, we found that biotic factors had a stronger influence on grassland stability than on productivity (Figure 3). The constancy of grassland productivity decreased with LDMC CWM in mesic habitat and with LNC CWM in ruderal habitat (Figure 4b,d). The resistance of grassland productivity decreased with SLA CWM and increased with Height CWM in calcareous habitat (Figure 4a). Grassland

resistance increased with Flower CWM (i.e., late-flowering plants) in mountainous habitat (Figure 4c), whereas it decreased with Flower CWM (i.e., early-flowering plants) in ruderal habitat (Figure 4d). The resistance of ruderal grassland also decreased with LNC CWM (Figure 4d). The constancy and resistance of ruderal grassland were the only ecosystem properties that were significantly affected by plant diversity (Figure 3), with both stability components decreasing with functional diversity (FD; Figure 4d). Finally, abiotic factors indirectly affected the stability of grasslands by modulating the functional traits and the diversity of plant communities (Figure 3). Nitrogen input was notably associated with high Height CWM and SLA CWM in calcareous habitat (Figure 4a), low LDMC CWM in mesic grassland (Figure 4b) and high Flower CWM (i.e., late-flowering plants) in ruderal habitat

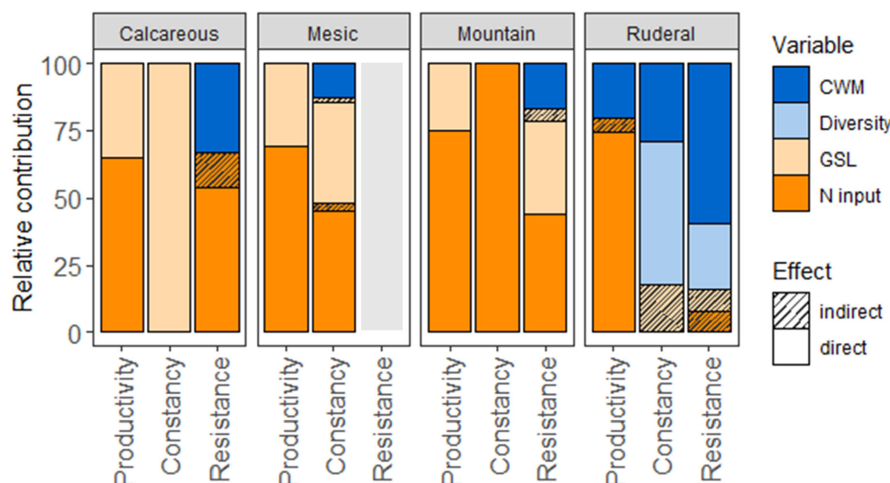


FIGURE 3 Relative contribution of abiotic and biotic factors to grassland productivity, constancy and resistance in four grassland habitats. Growing season length (GSL; light orange) and nitrogen input (N input; dark orange) affect grassland productivity and stability both directly (non-hatched colour) and indirectly (hatched colour) via their effects on the diversity and functional traits of grassland communities. The relative contribution of each factor corresponds to the standardized path coefficient of structural equation models (for details, see the Materials and Methods). The relative contribution of plant diversity is the sum of the standardized path coefficients of taxonomic diversity and functional diversity. The relative contribution of the mean functional traits of grassland communities is the sum of the standardized path coefficients of community-weighted mean (CWM) values of traits. No covariate significantly affected resistance in mesic habitat.

(Figure 4d). GSL was associated to low LDMC CWM in mesic habitat (Figure 4b) and low Flower CWM (i.e., early-flowering plants) in mountainous habitat (Figure 4c). GSL also had a negative effect on the functional diversity (FDIs) of ruderal grassland (Figure 4d).

4 | DISCUSSION

Direct relationships between the rate of an ecosystem function and its stability have long been postulated in ecology, but the first evidence of such links is recent and based on simulation exercises (e.g., Albrich et al., 2018; Montoya et al., 2019). These works report consistent trade-offs between ecosystem functioning and stability, whereas our empirical study reveals that the direction of the productivity–stability relationship depends on the stability component considered. We report positive links between ecosystem productivity and constancy but negative ones between ecosystem productivity and resistance in four types of grassland habitats. In addition, we find opposite effects of climate and nitrogen inputs on the two stability components, with constancy increasing with GSL and N inputs and resistance decreasing with both abiotic factors. These findings have profound implications for land managers because they indicate that, although the most productive grasslands are on average more constant from year to year, they have less resistance to extreme climatic events. They also suggest that increased use of nitrogen fertilization can reduce the resistance of grasslands to extreme climatic events, with yield losses being greater in the more productive grasslands. Grassland managers will therefore have to choose whether to maximize productivity or reduce the risk of yield loss, knowing that extreme climatic events will become more frequent in the coming years (Tebaldi et al., 2006).

A positive mean productivity–constancy relationship might appear somewhat obvious given that both ecosystem properties are intrinsically linked, with constancy corresponding to the inverse of the coefficient of variation of annual productivity (i.e., the ratio between the mean and its SD). However, given that the mean and SD are positively related (Taylor, 1961), a positive productivity–constancy relationship could occur only if the mean of annual productivity increases more strongly than its SD. Recent theory (Wang et al., 2021) and experiment (Yan et al., 2021) suggest that this arises when niche complementarity between coexisting species drive ecosystem functioning. However, under the niche complementarity hypothesis, functional diversity is expected to promote ecosystem productivity (Cadotte, 2017) and stability (Hallett et al., 2017). Our results do not support the complementarity hypothesis, because the effects of functional diversity found here were negative effects on the constancy and resistance for ruderal grasslands. Although unusual, such a negative role of trait diversity might underline the fact that traits that lead to the greatest fitness in a given environment determine ecosystem functioning and stability (Enquist et al., 2015; Garnier et al., 2016). Accordingly, we show that mean trait values exert a significant influence on the productivity and stability of grasslands, as previously observed in large-scale empirical studies (e.g., Brun et al., 2022; van't Veen et al., 2020). In addition, the negative relationship between ecosystem productivity and resistance found here echoes a well-known trade-off in functional ecology, with fast-growing, resource-acquisitive plant species being more productive but less resistant to environmental disturbance (Garnier et al., 2016; Grime et al., 2000; Májeková et al., 2014). The fact that SLA CWM and LNC CWM are negatively related to resistance and constancy in calcareous and ruderal grasslands partly supports this hypothesis, although these traits do not affect grassland productivity. Future

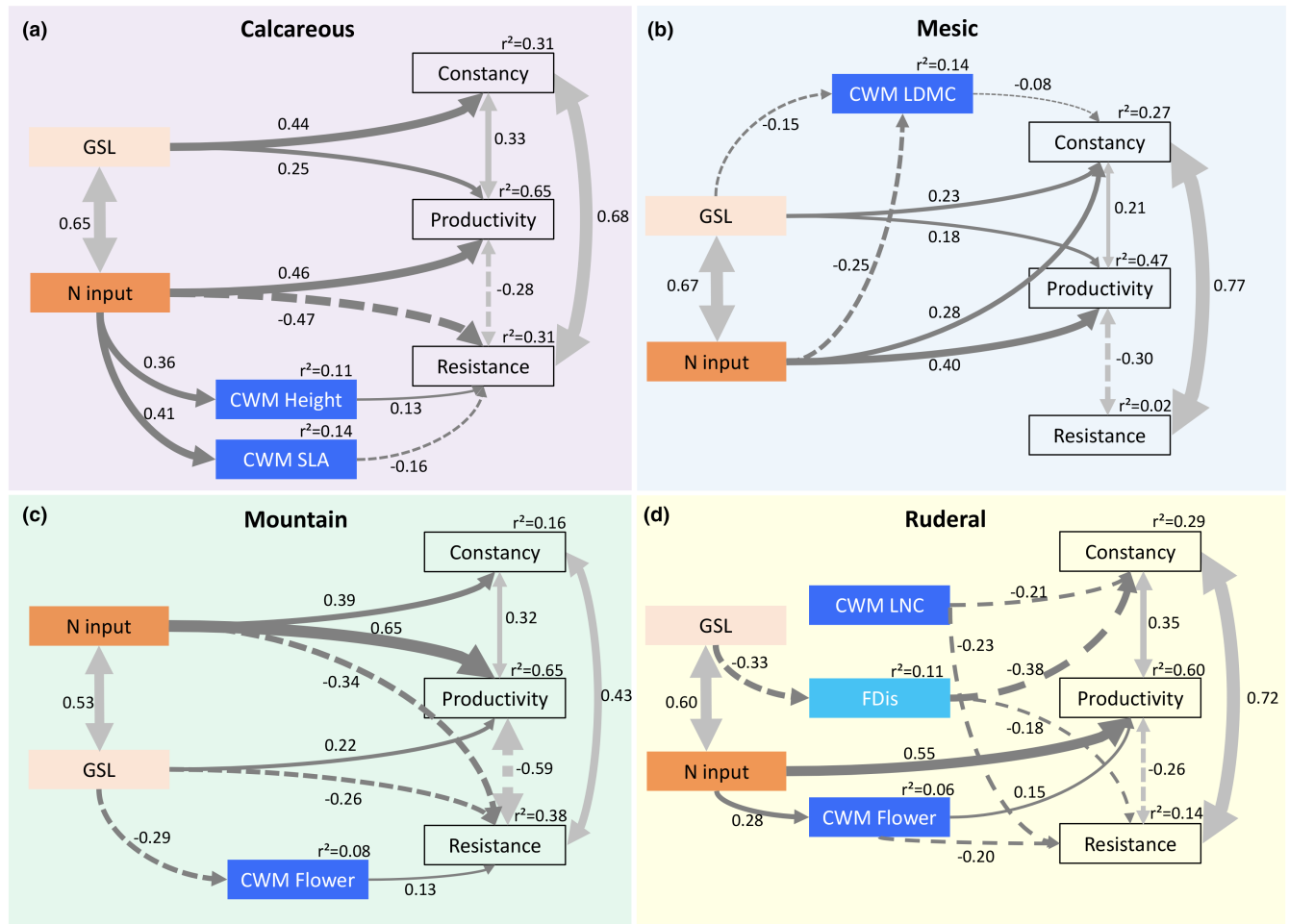


FIGURE 4 Path diagram of the effects of climate, nitrogen input and biodiversity on grassland productivity, constancy and resistance in four grassland habitats. (a) Calcareous grasslands, (b) mesic grasslands, (c) mountain grasslands, and (d) ruderal grasslands. Standardized path coefficients are shown along each arrow, with continuous and dashed arrows indicating positive and negative relationships, respectively. Double-headed arrows show correlations. Only significant relationships are shown. Abbreviations: CWM, community weighted mean; FDis, functional diversity; Flower, flowering time; GSL, growing season length; LDMC, leaf dry matter content; LNC, leaf nitrogen content; N input, nitrogen input; SLA, specific leaf area.

dedicated experiments that consider different dimensions of stability are therefore needed to unravel the mechanisms that drive productivity–stability relationships.

In this large-scale study, environmental conditions exert much stronger controls on ecosystem productivity and stability than plant diversity and trait values. Increasing GSL enhances grassland productivity and constancy in most habitats. Indeed, prolonged vegetation activity promotes temporal niche complementarity, a process that, in turn, increases grassland productivity and constancy (Oehri et al., 2017). However, we observe that the resistance of mountain grasslands is negatively related to GSL, potentially because the probability that a disturbance occurs during the growing season would increase with the length of the growing season. In addition, we show that N input increases grassland productivity in all habitats but simultaneously reduces the resistance of calcareous and mountain grasslands. This agrees with numerous field experiments reporting higher productivity but lower stability in fertilized compared with non-fertilized plots (e.g., Hautier et al., 2014; Isbell

et al., 2013; Liu et al., 2019). However, our analysis is conducted on a much larger grain size (i.e., c. 5 km²). As such, it de facto integrates the roles of the multiple ecological processes that operate at the landscape level (e.g., species dispersal and environmental heterogeneity), which can greatly affect the response of local communities to changes in environmental conditions (Hodapp et al., 2018). Finally, our results provide further evidence that environmental conditions strongly affect the roles of plant diversity and trait values in driving ecosystem productivity and stability (García-Palacios et al., 2018; Hautier et al., 2014). The cross-habitats analysis reveals that the role of functional traits can change substantially from one habitat to another. Notably, we show that communities dominated by late-flowering plants display stronger and lower resistance in mountain and ruderal habitats, respectively. These patterns are probably the result of plant adaptation to the climatic conditions specific to these different habitats. Late-flowering plants can avoid late frosts that are frequent in mountain habitats, whereas flowering early can avoid high summer temperatures that characterize Mediterranean ruderal

habitats. In addition, within-habitat analysis shows that abiotic conditions affect trait values of plant communities. Notably, we report increasing CWM values of SLA and height along the N input gradient in calcareous grassland and decreasing LDMC CWM in mesic grassland, confirming that competitive species with fast-growing strategies dominate communities in resource-rich environments (Garnier et al., 2016).

The joint roles played by biodiversity and environment on ecosystem productivity and stability have been tested widely in experiments that explicitly manipulate species composition and/or resource levels within a few square metres (Hautier et al., 2014; Isbell et al., 2013; Liu et al., 2019). Meta-analyses have also contributed to a better understanding of how the interplay between biodiversity and environment affects the productivity and stability of ecosystems (e.g., García-Palacios et al., 2018; Grace et al., 2016; Hong et al., 2022). At a local scale, biodiversity components and the resulting biotic interactions are generally as important as abiotic factors for the functioning and stability of ecosystems (García-Palacios et al., 2018; Hautier et al., 2014). In contrast, studies conducted at a larger spatial extent and grain size, like ours, report a marginal role of biodiversity on ecosystem functioning (Brun et al., 2022). This can reflect the fact that when increasing grain size, diversity no longer reflects local plant–plant interactions but rather the distribution of species in different vegetation patches (Chisholm et al., 2013). The influences of biodiversity and biotic interactions on ecosystem functioning therefore decrease as grain size increases (Chisholm et al., 2013).

The multidimensional nature of ecosystem functioning and stability has been the focus of an increasing number of studies over the past few years (e.g., Bagousse-Pinguet et al., 2021; Donohue et al., 2013; Polazzo & Rico, 2021). These studies have contributed greatly to clarification of the intrinsic links that exist between different aspects of ecosystem functioning or stability and how different ecological factors, especially biodiversity, affect these relationships. Our work directly expands these findings by considering the relationships that exist between a particular ecosystem function and different components of its stability. We reveal that the sign of the relationship between grassland productivity and stability varies according to the component(s) of stability considered. Furthermore, although opposite productivity–constancy and productivity–resistance relationships would have suggested a negative link between both stability components, we find that the constancy and the resistance of grassland productivity are positively correlated. Such a complex pattern echoes the Simpson paradox, a statistical situation where confounding factors reverse the link between two variables (Dong, 2005). This finding is particularly important given that the nature of the correlation between stability components determines the dimensionality of ecological stability (Donohue et al., 2013, 2016; Polazzo & Rico, 2021). According to these studies, positive correlation between stability components indicates that a unique dimension characterizes ecological stability, such that a single component can capture the stability of the whole system. Yet, despite being positively related, the two stability components

display opposite relationships with N input on the one hand and mean productivity on the other. Our work thus emphasizes how crucial it is to consider multiple components of ecological stability to provide a thorough understanding of the relationships between ecosystem functioning and stability, even if ecological stability is thought to have only one dimension.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data and the scripts used for processing and analysing them have been published on Dryad and are freely accessible at: <https://doi.org/10.5061/dryad.1zcrjdfwm>

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BIOSKETCH

This scientific consortium works on plant functional diversity to understand the effects of biodiversity on ecosystem functioning across spatial and temporal scales. We use French permanent grasslands as a case study (<https://www.fondationbiodiversite.fr/en/the-frb-in-action/programs-and-projects/le-cesab/divgrass/>).

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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