Journal of Vegetation Science IAVS

Functional biogeography of weeds reveals how anthropogenic management blurs trait–climate relationships

Bérenger Bourgeois[1,2] iD | François Munoz[3] iD | Sabrina Gaba[2,4,5] iD |
Pierre Denelle[6] iD | Guillaume Fried[7] iD | Jonathan Storkey[8] iD | Cyrille Violle[9] iD

[1]Centre de Synthèse et d'Analyse sur la Biodiversité — Fondation pour la Recherche sur la Biodiversité, Montpellier, France

[2]LTSER Zone Atelier "Plaine & Val de Sèvre", CNRS, Villiers-en-Bois, France

[3]Laboratoire Interdisciplinaire de Physique, Université Grenoble-Alpes, Grenoble, France

[4]Centre d'Études Biologiques de Chizé, USC Agripop, INRAE, Villiers-en-Bois, France

[5]Centre d'Études Biologiques de Chizé, UMR 7372, CNRS — Université de La Rochelle, Villiers-en-Bois, France

[6]Biodiversity, Macroecology and Biogeography, University of Göttingen, Göttingen, Germany

[7]Anses, Laboratoire de la Santé des Végétaux, Unité Entomologie et Plantes Invasives, Montferrier-sur-Lez, France

[8]Sustainable Agriculture Sciences, Rothamsted Research, Harpenden, Hertfordshire, UK

[9]CEFE, Univ. Montpellier, CNRS, EPHE, IRD, Univ. Paul Valéry, Montpellier, France

Correspondence
Bérenger Bourgeois, Centre de Synthèse et d'Analyse sur la Biodiversité — Fondation pour la Recherche sur la Biodiversité, Montpellier, France.
Email: berengerbourgeois@gmail.com

Funding information
European Research Council; Nouvelle Aquitaine Region; CESAB-FRB

Co-ordinating Editor: Meelis Pärtel

Abstract

Questions: Studies in functional biogeography have mostly focused on unmanaged ecosystems, and neglected testing how management intensity affects community-level response of plant traits to bioclimatic gradients. We hypothesize that trait–climate relationships for arable weeds spontaneously establishing in croplands subject to intensive management should differ from the relationships characterizing less intensively managed grassland ecosystems.

Location: France.

Methods: We computed community-weighted means (CWM) and variances (CWV) of 954 and 5,619 cropland and grassland plant assemblages, respectively, for three fundamental leaf traits (specific leaf area, SLA; leaf dry matter content, LDMC; leaf nitrogen content, LNC). Based on growing season length accounting for both temperature and soil water limitations (GSL_{tw}), we compared trait–climate relationships between herbicide-free croplands and grasslands, and between herbicide-free and herbicide-sprayed cropland assemblages. The contribution of beta-diversity to the trait–climate relationships was then evaluated using multiple regression on distance matrices.

Results: Distinct trait–climate relationships characterized herbicide-free cropland and grassland plant assemblages. CWM of all traits showed weaker relations with GSL_{tw} in cropland relative to grassland assemblages. CWV of LDMC and LNC responded more sharply in croplands. Furthermore, no herbicide effect on trait–climate relationships was detected within cropland assemblages. These results seem to be explained by a greater taxonomic beta-diversity along the GSL_{tw} gradient for grasslands.

Conclusions: Specific trait–environment relationships characterize croplands, underlining that management intensity greatly affects trait–climate relationships for plant assemblages. Deciphering the interplay between land use intensification and climate is critical to accurately forecast functional vegetation changes in response to global changes, and hence to foster actions enhancing ecosystem resilience.

KEYWORDS
Agroecosystems, arable weeds, croplands, environmental filtering, functional biogeography, grasslands, leaf traits, management intensification, plant assemblages, trait-environment relationships

1 | INTRODUCTION

Understanding and predicting the functional response of plant assemblages to bioclimatic variations is a long-standing quest in ecology (Lavorel & Garnier, 2002), and an essential objective in the context of global changes. Revealing the trait–climate relationships shaping plant assemblages is a critical step in forecasting plant diversity shifts under a changing climate, to model potential feedback on ecosystem functioning, and to adapt ecosystem management to improve their resilience (Díaz & Cabido, 2001; Bruelheide et al., 2018). For these purposes, trait-based approaches examine the functional composition of communities and reveal the nature of underlying niche-based processes (McGill et al., 2006; Violle et al., 2007, 2014). Specifically, leaf traits reflect essential aspects of plant growth and survival (the trade-off between resource acquisition and conservation), respond to abiotic environmental conditions, and relate to the key role of plants in biogeochemical cycles (Reich & Oleksyn, 2004; Wright et al., 2004, 2017; Díaz et al., 2016).

Functional biogeography addresses how functional composition varies along broad, continental-scale climatic gradients (Violle et al., 2014). This recent macroecological discipline has so far mostly focused on the response of leaf traits in natural ecosystems as well as extensively managed ecosystems such as grasslands and woodlands (Lamanna et al., 2014; Borgy et al., 2017a; Šímová et al., 2018, 2019; Sandel, 2019). Whether the emerging functional macroecological laws governing trait–climate relationships apply to intensively managed ecosystems remains unknown (McGill, 2019; Mahaut et al., 2020). Most studies have indeed overlooked the role of anthropogenic drivers such as land use and/or management in affecting biophysical leaf traits at the community level. Such effects may explain discrepancies in trait–climate relationships (Cunningham et al., 1999; Ordoñez et al., 2009; Hodgson et al., 2011), e.g. either positive, negative or neutral relationships of community-level specific leaf area (SLA) with mean annual temperature (MAT) or mean annual precipitation (MAP; Wright et al., 2004, 2005; Sandel et al., 2010; Onoda et al., 2011; Moles et al., 2014; Read et al., 2014). In French grasslands, Borgy et al. (2017a) reported that variations in community-level leaf traits (i.e. SLA, leaf nitrogen and phosphorus contents, resp. LNC and LPC, and leaf dry matter content, LDMC) are better related to growing season length accounting for both temperature and water limitations (GSL_{tw}) than to MAT, MAP or growing season length accounting solely for temperature limitation (GSL_t). In addition, trait–climate relationships along the GSL_{tw} gradient were found to be sharper at low vs high nitrogen inputs, partly due to lower species turnover. This buffering effect of management intensity on trait–climate relationships observed in grasslands remains, however, to be generalized to other types of ecosystems.

Croplands cover 12% of the Earth's ice-free land surface (Ramankutty et al. 2008) and now represent, along with pastures, one of the largest terrestrial habitats on the planet (Foley et al., 2005). Croplands, therefore, represent a widespread model of intensively managed ecosystems, with which to test and challenge the universality of macroecological trait–climate relationships (Mahaut

et al., 2020). The composition of plant assemblages spontaneously establishing in croplands, i.e. arable weeds colonizing agricultural fields cultivated with annual crops (Godinho, 1984), is influenced by agricultural management practices, landscape structure and composition, and environmental factors including climate parameters such as rainfall (Fried et al., 2008; José-María et al., 2010; Armengot et al., 2016; Gaba et al., 2018; Alignier et al., 2020; Bourgeois et al., 2020). The environmental constraints prevailing in croplands due to intensive management practices — high disturbance frequency and intensity, high level of resources and intense competition by a dominant species (i.e. the crop) — results in strong anthropogenic habitat filters restricting the functional niche of weed species (Gaba et al., 2014; Bourgeois et al., 2019; Mahaut et al., 2020), and potentially blurring large-scale trait–climate relationships evidenced elsewhere. Weaker trait–climate relationships in community-weighted mean (CWM) and variance (CWV) should thus characterize cropland assemblages compared to more extensively managed open ecosystems such as grasslands. Besides affecting the average trait values of plant assemblages (in terms of CWM), intensive management can filter a limited spectrum of plant strategies and thus reduce globally the range of leaf trait values in assemblages (in terms of CWV).

Within croplands, distinct crop types are related to varying the competitive ability and management practices of crops, including sowing season, fertilizer inputs or herbicide use, that filter weed species (Fried et al., 2008; Gunton et al., 2011; Perronne et al., 2015; Gaba et al., 2018; Mahaut et al., 2018; Bourgeois et al., 2020). Beside affecting species composition, such differential environmental filtering associated with crop types strongly impacts the functional structure of weed assemblages (Gunton et al., 2011; Fried et al., 2012; Perronne et al., 2015). Therefore, we also expect the functional structure of weed assemblages to change with the intensity and/or the nature of crop management. Herbicides act as a major environmental filter on weed species (Mahn, 1984; Mahn & Kästner, 1985; Gaba et al., 2016; Catarino et al., 2019; Fried et al., 2019), and we thus hypothesized that herbicide use affects trait–climate relationships in cropland assemblages. Hence, while anthropogenic activities might have a greater influence on weed assemblages established in croplands compared to grassland assemblages, within croplands, herbicide use might induce a further constraint on weed communities.

In this study, we investigated how trait–climate relationships in weed community-level leaf traits are affected by management, compared to those of less intensively managed grassland assemblages. We designed a trait-based comparative approach to contrast the functional response of plant assemblages to bioclimatic gradients, first between croplands and grasslands, and second among croplands between herbicide-free and herbicide-sprayed plant assemblages. Based on extensive plot-based cropland and grassland surveys conducted across France, using three leaf traits (SLA, LDMC and LNC), and growing season length accounting for both temperature and water limitations (GSL_{tw}) as a bioclimatic descriptor, we addressed the following questions: (1) does management intensity lead to weaker trait–climate relationships in

cropland relative to grassland assemblages; (2) does herbicide application further modulate the response of community-level weed leaf traits to bioclimatic gradients within cropland assemblages; and (3) how do the detected trait–climate relationships relate to taxonomic beta-diversity in both croplands and grasslands? As a result of more intensive management, we expected weaker trait–climate relationships in cropland than in grassland assemblages, as well as in herbicide-sprayed compared to herbicide-free cropland assemblages.

2 | METHODS

2.1 | Cropland surveys

We compiled weed assemblage data from the Biovigilance-Flore network including surveys in 1,440 arable fields across France from 2002 to 2010, for a total of 332 taxa (Fried et al., 2008). Sampled fields were selected to represent the diversity of agricultural practices and environmental conditions in France, thereby covering 20 major crop types. In this study, we focused on the four most frequent and widespread crops, namely winter cereals (mostly winter wheat and barley), maize, oilseed rape and sunflower, and only kept weed assemblages sheltering at least five species for subsequent analyses.

Cropland assemblages were surveyed twice a year in two plots within each field. The two plots were subjected to similar agricultural practices, except that herbicides were used in the first 2,000-m^2 plot but excluded in the second 140-m^2 plot. The first surveys were conducted one month after sowing the crop and before post-emergence herbicide treatment, and the second after the last herbicide treatment. Only the second surveys were investigated in this study. Species densities were evaluated on the field using a semi-quantitative scale, which was transformed for analyses into a quantitative metric using each class median: +, 1, 2, 3, 4, 5 indices were transformed into 0.0005, 0.1, 1.5, 3.0, 11.5, 35.5 and 75.0 plants/m^2, respectively. For clonal plants, the density refers to the number of individual stems. Although herbicide-sprayed plots were larger than herbicide-free ones (given that a larger area is generally required to reach species saturation under herbicide pressure; Chauvel et al., 1998; Krähmer et al., 2020), they sheltered significantly less species (i.e. 9 ± 5 species vs 13 ± 6 species, mean $\pm$ standard deviation), supporting a negative herbicide effect on species richness.

2.2 | Grassland surveys

We obtained grassland assemblage data from the Divgrass database including 51,486 surveys conducted in permanent grasslands across France, mostly from 2000 to 2010, for a total of 5,245 species recorded (Violle et al., 2015). This database includes vegetation plots ranging from 25 m^2 to 100 m^2 to reach species saturation, and species abundances were assessed following the Braun-Blanquet scale (i.e. six cover classes: 0%–1%, 1%–5%, 5%–25%, 25%–50%,

50%–75% and 75%–100%; Braun-Blanquet, 1932). We defined a quantitative index of species abundance as the median of each class.

To ensure comparability between grassland and cropland plant assemblages, only the grassland surveys sheltering at least five species and included within the climatic envelope of croplands in the Biovigilance-Flore dataset were kept for analyses (Figure 1).

2.3 | Community-level plant leaf traits

Three major leaf traits were retrieved from the TRY database (Kattge et al., 2011, 2020), namely specific leaf area (SLA, in m^2/kg), leaf dry matter content (LDMC, in mg/g) and leaf nitrogen content (LNC, in mg/g). We selected these three traits because of their major role in nutrient, carbon and water cycles in terrestrial ecosystems (Chapin et al., 2000; Wang et al., 2012), through their relations with primary productivity (Pontes et al., 2007; Lavorel et al., 2011) and litter decomposition (Fortunel et al., 2009; Pakeman et al., 2011).

For each trait and plant assemblage, we calculated two community-level trait values, namely community-weighted mean (CWM) and community-weighted variance (CWV), as follows:

$$CWM_j = \sum_i^n p_{ij} T_i$$

$$CWV_j = \sum_i^n p_{ij} (T_i - CWM_i)^2$$

where p_{ij} and T_i are, respectively, the relative abundance and the trait value of species i in community j, and n is the total number of species with known trait value in community j.

To make sure the community-level plant trait values were sufficiently representative, only plant assemblages for which species with known trait values represented at least 60% of the total cover were kept for analyses (Borgy et al., 2017a, 2017b).

2.4 | Bioclimatic variable

We considered growing season length based on both temperature and water (GSL$_{tw}$, in days) as a bioclimatic predictor, as it was previously shown to better depict trait–climate relationships in French grasslands, compared to mean annual temperature, mean annual precipitation or growing season length solely based on temperature (Borgy et al., 2017a). GSL$_{tw}$ is the number of days per year with a mean daily temperature higher than 5°C and a ratio of soil available water content/soil water-holding capacity higher than 20%.

Several sources were used to calculate this bioclimatic predictor. The 1-km resolution gridded dataset from MétéoFrance (Benichou & Le Breton, 1987) provided monthly mean temperature and monthly rainfall across the French metropolitan territory over the period 1961–1990. We retrieved soil water-holding capacity (WHC) from the French Soil Geographical Database,
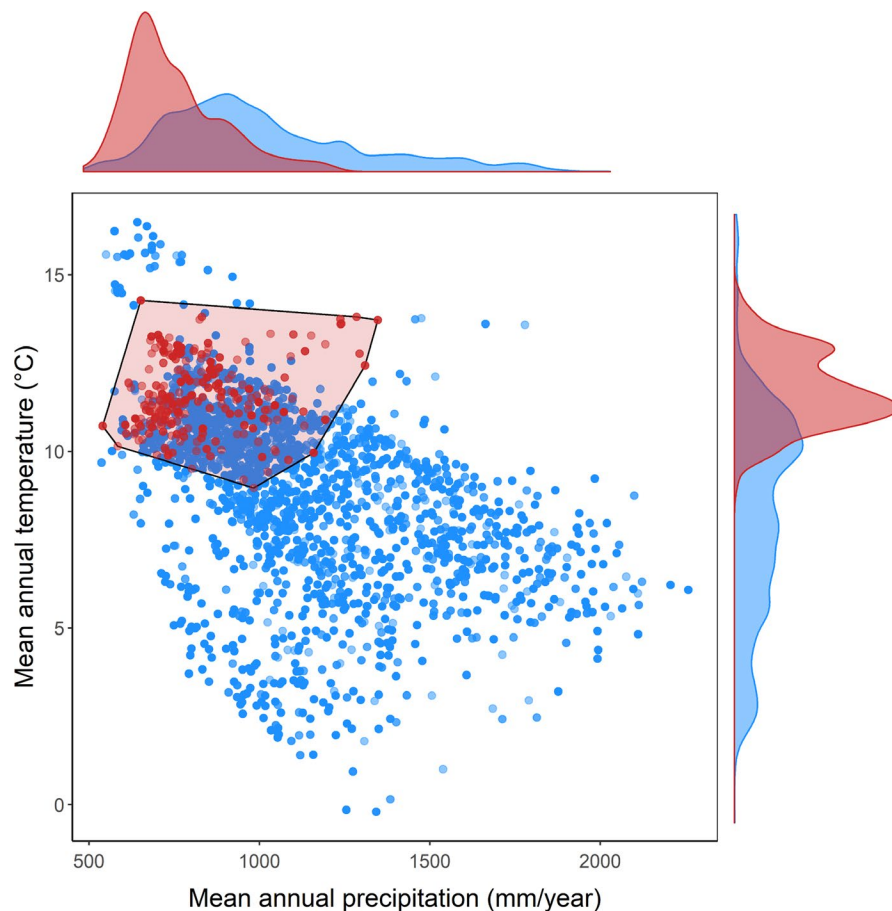
FIGURE 1 Climate envelope of the cropland (red) and grassland (blue) assemblages studied. Only grasslands included in the climate envelope of arable fields (black line, calculated by convex hull) were kept for analyses. Curves show the distribution of mean annual temperature and precipitation within croplands and grasslands.

based on the methodology from Le Bas et al. (1997) and the pedotransfer functions from Al Majou et al. (2008). The dynamic of soil available water content (AW) was estimated from a one-bucket water balance model using a Turc-based estimate (Turc, 1961) of potential evapotranspiration (PET), and based on incoming net solar radiation accounting for topographic effect (Piedallu & Gégout, 2008). After interpolating monthly climate times series at a daily time step for GSL_{tw} computation, AW at day n was calculated as AW at day $n - 1$, plus precipitation and minus PET (see Borgy et al., 2017a for further methodological information).

2.5 | Data analyses

We examined trait–climate relationships linking each CWM/V value to GSL_{tw}, in herbicide-free cropland and grassland assemblages separately. For this, we constructed generalized least-squares models in grasslands, and linear mixed models including crop type as a random effect in croplands (given the residual distribution of preliminary simple linear models differed between crops). To acknowledge the influence of spatial autocorrelation, we performed for each generalized least-squares and linear mixed model a selection based on the Akaike information criterion (AIC) between competing models including either no spatial autocorrelation structure, a linear, a

Gaussian, an exponential, a spherical or a rational quadratic spatial autocorrelation structure. For each CWM/V, we compared the 95% confidence intervals of slope estimates between herbicide-free cropland and grassland assemblages to assess the effect of management intensity on trait–climate relationships. We used a similar approach to assess the effect of herbicide on trait–climate relationships in cropland assemblages.

We assessed taxonomic beta-diversity along GSL_{tw} to evaluate and discuss its contribution to the trait–climate relationships. For each type of plant assemblage (i.e. grassland, herbicide-free cropland, herbicide-sprayed cropland), the Euclidean distance in GSL_{tw} between pairs of survey was related to the Bray–Curtis dissimilarity in species abundance, using multiple regression on distance matrices (Lichstein, 2007).

Overall, we analyzed 5,619 grassland surveys including 1,360 species (among which 78%, 74% and 44% had known SLA, LDMC and LNC values, respectively), 477 herbicide-free cropland surveys including 231 species (among which 73%, 76% and 54% had known SLA, LDMC and LNC values, respectively), and 477 herbicide-sprayed cropland surveys including 212 species (among which 74%, 77% and 57% had known SLA, LDMC and LNC values, respectively). We used R v. 3.5.1 (R Core Team, 2018), with packages *nlme* (Pinheiro et al., 2018), *ecodist* (Goslee & Urban, 2007), *vegan* (Oksanen et al., 2019), *graphics* (R Core Team, 2018) and *ggplot2* (Wickham, 2016).

3 | RESULTS

3.1 | Habitat effect on trait–climate relationships

We detected distinct trait–climate relationships (i.e. significant slope differences in GSL_{tw}–CWM or GSL_{tw}–CWV relationships) between grassland and herbicide-free cropland assemblages, the strength of these trait–climate relationships depending on the community-level plant trait considered (Figures 2 and 3; Appendix S1). Increases in CWM of SLA and in CWM of LNC as well as decreases in CWM of LDMC with GSL_{tw} were sharper in grasslands compared to herbicide-free croplands (Figures 2 and 3). Conversely, CWV of LNC increased with GSL_{tw} more sharply in herbicide-free croplands compared to grasslands. For LDMC, we found a positive CWV–GSL_{tw} relationship in herbicide-free croplands and a negative relationship in grasslands (Figures 2 and 3). Only CWV of SLA showed a similar trait–climate relationship between herbicide-free croplands and grasslands (Figures 2 and 3). We obtained similar results when ignoring in the analyses the plant surveys located at $GSL_{tw} = 365$ days (Appendix S2). Overall, our results indicated that trait–climate relationships tended to be weaker in croplands for community-level trait means, but stronger for community-level trait variances.

3.2 | Herbicide effect on trait–climate relationships in cropland assemblages

For all three traits, no significant difference in trait–climate relationships was detected between herbicide-free and herbicide-sprayed cropland assemblages for both CWMs and CWVs (Figures 4 and 5), either when removing or not from analyses plant surveys located at $GSL_{tw} = 365$ days (Appendix S3; Appendix S4). More precisely, CWM of SLA in herbicide-sprayed plots and LNC in both plot types as well as CWV of LDMC in herbicide-free plots and LNC in both plot types increased significantly, or tended to increase, with GSL_{tw} (Figures 4 and 5). Only CWM of LDMC and CWV of SLA were found to be independent of GSL_{tw} in both herbicide-free and herbicide-sprayed cropland assemblages.

3.3 | Taxonomic beta-diversity along the bioclimatic gradient

For all types of plant assemblages (i.e. grasslands, herbicide-free croplands, herbicide-sprayed croplands), plant beta-diversity calculated from Bray–Curtis dissimilarity between pairs of surveys significantly increased with survey differences in growing season length (calculated as the Euclidean distance in GSL_{tw} between pairs of surveys; Figure 6). Increases in beta-diversity along the GSL_{tw} were, however, 2.5 to five times higher in grasslands compared to herbicide-free and herbicide-sprayed croplands, respectively.

4 | DISCUSSION

We found that intense anthropogenic management in croplands strongly affects trait–climate relationships on community-level leaf traits, compared to grasslands, which challenges the generality of
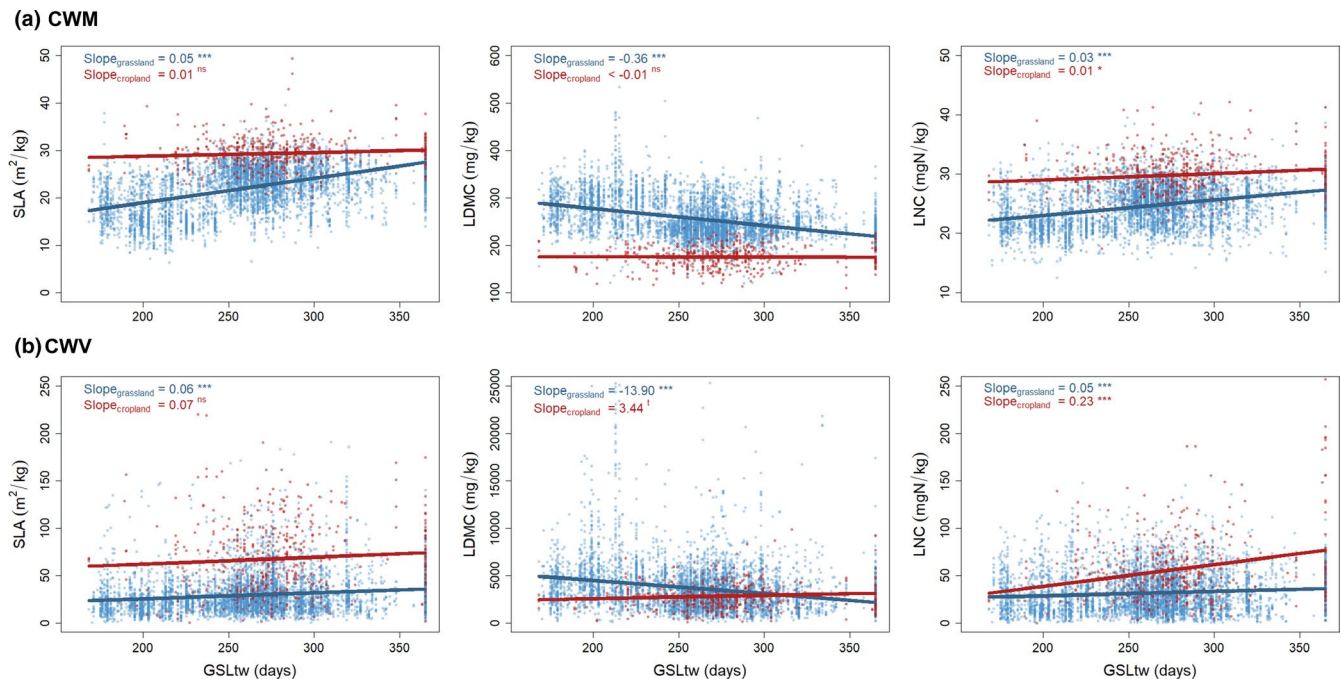

FIGURE 2 Relationships between leaf traits and growing season length (GSL_{tw}) in grassland (blue, n = 5619) and cropland (red, n = 477) plant assemblages. Community-Weighted Means (a) or Variances (b) were computed based on Specific Leaf Area (SLA), Leaf Dry Matter Content (LDMC) or Leaf Nitrogen Content (LNC) and related to GSL_{tw} which depicts growth limitations by both temperature and soil water availability. Asterisks indicate the slope significance of each linear model (***: $p \leq 0.001$; **: $0.001 < p \leq 0.01$; *: $0.01 < p \leq 0.05$; t: $0.05 < p \leq 0.1$; ns: $p > 0.1$).
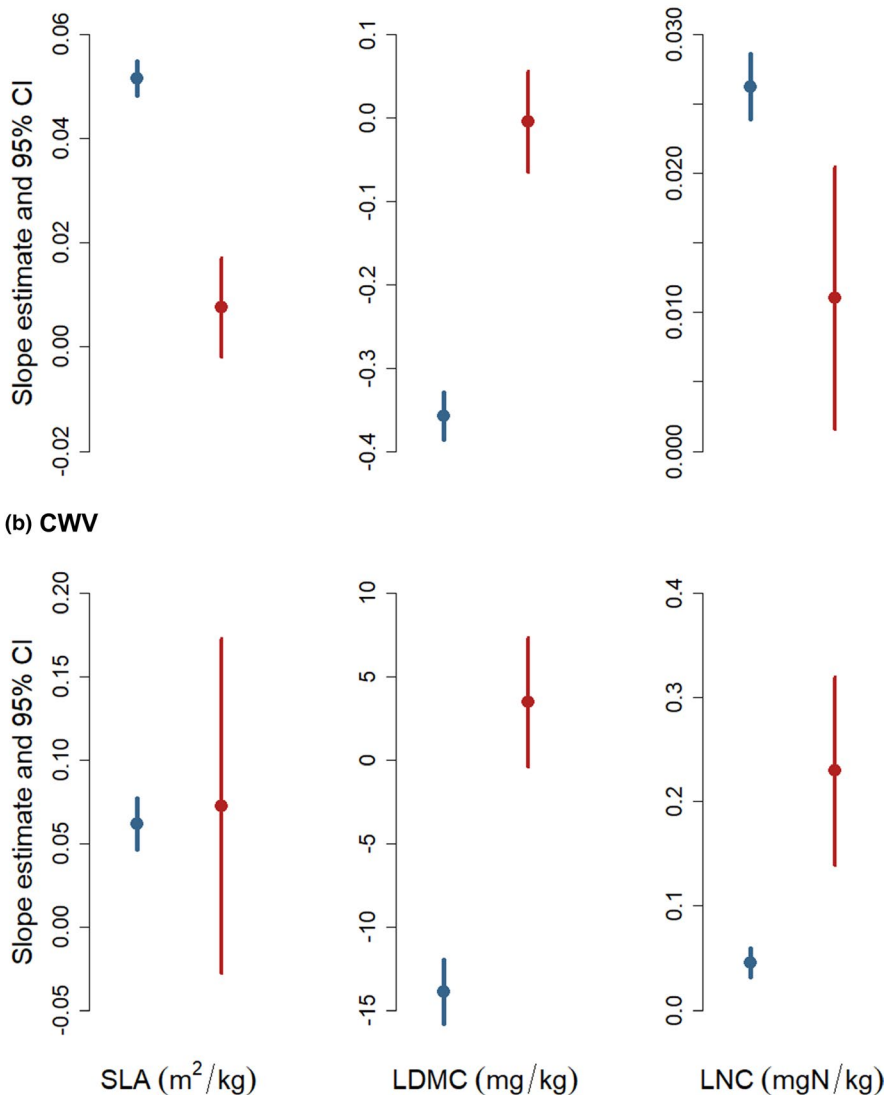
(a) CWM

(b) CWV

SLA (m²/kg)   LDMC (mg/kg)   LNC (mgN/kg)

FIGURE 3 Differences in the slopes of trait-climate relationships between grassland (blue, n = 5619) and cropland (red, n = 477) plant assemblages. Community-Weighted Means (a) or Variances (b) were computed based on Specific Leaf Area (SLA), Leaf Dry Matter Content (LDMC) or Leaf Nitrogen Content (LNC) and related to GSL_{tw} which depicts growth limitations by both temperature and soil water availability.

emerging macroecological laws reported in functional biogeography (Violle et al., 2014; McGill, 2019). Specifically, community-weighted means generally displayed weaker responses to bioclimatic gradients in weed assemblages, while community-weighted variances showed stronger responses. These trait–environment relationships were mostly associated with stronger shifts of abundance-weighted species composition within grassland assemblages along the detected bioclimatic gradient.

Our study first revealed that trait–climate relationships in plant assemblages were largely weaker in croplands compared to grasslands. These results indicate that higher management intensity is associated with a reduced sensitivity of plant assemblages to bioclimatic variations, revealing that other factors are at play. Croplands are characterized by a disturbance regime allowing plant species to develop only during a limited time window. This "patch availability" that contrasts with grasslands strongly affects plant assemblages in croplands (Mahaut et al. 2018). Such an effect of management intensity can have contributed to the discrepancies in trait–climate relationships previously reported in functional biogeographic

studies (Wright et al., 2004, 2005; Sandel et al., 2010; Onoda et al., 2011; Moles et al., 2014; Read et al., 2014; Simpson et al., 2016; Forrestel et al., 2017) that have often neglected to account for local environmental drivers affecting leaf traits (Cunningham et al., 1999; Ordoñez et al., 2009; Hodgson et al., 2011). As previously pointed out (Shipley et al., 2016; Bruelheide et al., 2018), there is an urgent need to better determine the selective forces controlling trait variation among which this study identified land use as a prominent local environmental filter, and to reveal the interplay between local drivers and bioclimatic gradients as shown here.

Although higher management intensity resulted in weaker trait–climate relationships of community-weighted means, it was conversely associated with stronger trait–climate relationships of community-weighted variances. While increase in grassland management intensity through higher fertilizer inputs was shown to lessen constraints on nutrient availability, leading to weaker trait–climate relationships in high- compared to low-fertilized grassland (Borgy et al., 2017a), a different mechanism seems to be involved in croplands. Agricultural practices aiming to favour crop growth
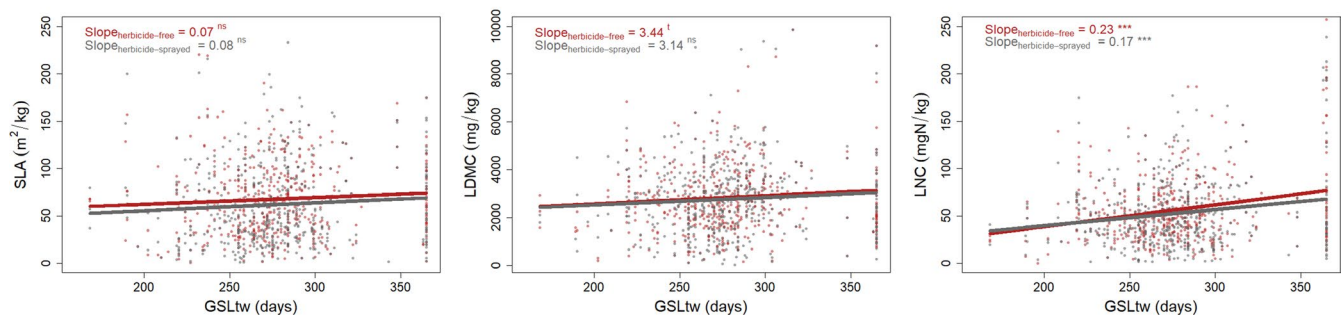
(a) CWM
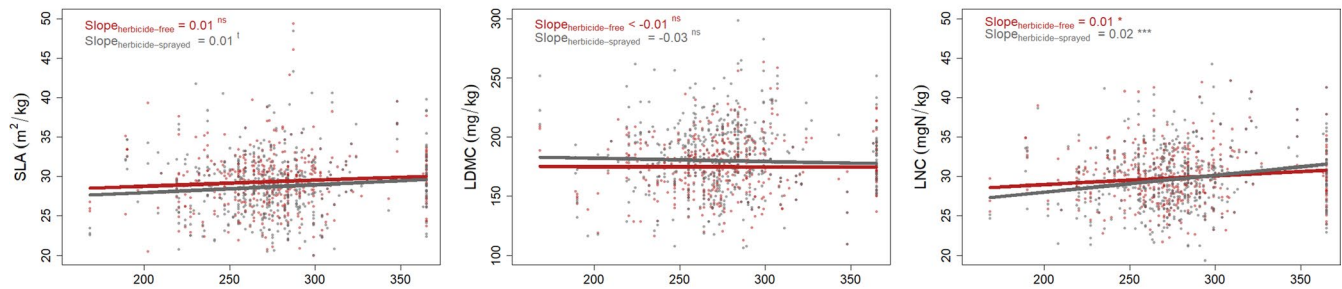
(b) CWV

FIGURE 4 Relationships between leaf traits and growing season length (GSL_{tw}) in herbicide-free (red, n = 477) and herbicide-sprayed (grey, n= 477) cropland plant assemblages. Community-Weighted Means (a) or Variances (b) were computed based on Specific Leaf Area (SLA), Leaf Dry Matter Content (LDMC) or Leaf Nitrogen Content (LNC) and related to GSL_{tw} which depicts growth limitations by both temperature and soil water availability. Asterisks indicate the slope significance of each linear model (***: $p \leq 0.001$; **: $0.001 < p \leq 0.01$; *: $0.01 < p \leq 0.05$; t: $0.05 < p \leq 0.1$; ns: $p > 0.1$).

(e.g. tillage, fertilizer inputs, weed control) have indeed selected for specific plant strategies (Storkey et al., 2005; Weiner et al., 2010; Bagavathiannan & Norsworthy, 2012; Fried et al., 2012; Gaba et al., 2014; Pinke & Gunton, 2014; Wagner et al., 2017) resulting in a narrower functional niche of the most tolerant weeds (i.e. specialist weeds mostly occurring in agricultural fields) while generalist weeds occurring in different types of habitats (among which croplands) are generally functionally similar to grassland species (Bourgeois et al, 2019). The dominance of highly tolerant weeds in croplands could, therefore, blur trait–climate relationships of CWM. Yet, as bioclimatic conditions became more favourable (i.e. as GSL_{tw} increased), additional weeds may have been able to establish in croplands and co-exist with the most tolerant weeds, leading to sharper increases in CWV with GSL_{tw}.

We observed lower taxonomic beta-diversity in croplands compared to grasslands along the GSL_{tw} gradient. This result also supports the view that the dominance of a few species with similar trait values in cropland assemblages is one of the main mechanisms buffering trait–climate relationships. Dominant weed species also generally show trait values similar to the crop (Perronne et al., unpublished data; Gunton et al., 2011) which could have contributed to less pronounced trait–climate relationships. As previously demonstrated (Siefert et al., 2014, 2015), accounting for intraspecific trait variation should provide a better understanding of the mechanisms shaping trait–climate relationships, especially in the case of arable weeds that are generally characterized by high phenotypic plasticity (Storkey, 2005; Perronne et al., 2014; Borgy et al., 2016). Further

investigations including cropland assemblages from Nordic or mediterrannean areas should also help in this process as the bioclimatic envelope of the cropland assemblages studied here only represented a limited fraction of grassland conditions (Figure 1). Despite these potential limitations and based on our results, management intensity nevertheless seems to buffer trait–climate relationships on plant assemblages primarily by constraining the pool of species tolerant to harsher local environmental constraints.

Previous research at the arable field scale showed that traits shaping cropland assemblage response to crop type involved predominantly morphological and phenological traits (Gunton et al., 2011; Fried et al., 2012; Perronne et al., 2015). Locally abundant weeds are indeed generally characterized by low seed mass, early and short flowering and high SLA, such as *Poa annua* L., *Stellaria media* (L.) Vill. or *Veronica persica* Poir. (Fried et al., 2021). In this study, we demonstrated that despite unique trait–climate relationships, leaf traits also contribute to a certain extent to variations in cropland assemblages along bioclimatic gradients. Interestingly, herbicide use had no influence on trait–climate relationships in cropland assemblages. Yet, it is also likely that herbicides have cumulative impacts through time notably by depleting soil seed banks (Bennett & Shaw, 2000; Clay & Griffin, 2000; Brewer & Oliver, 2007; Walker & Oliver, 2008) and hence induce a legacy effect so that the absence of herbicide for only one growing season as carried out here does not counter-balance for an impoverished flora, even if the larger plot size of herbicide-sprayed cropland assemblages may have also contributed to lessen the effect of herbicides on trait–climate relationships
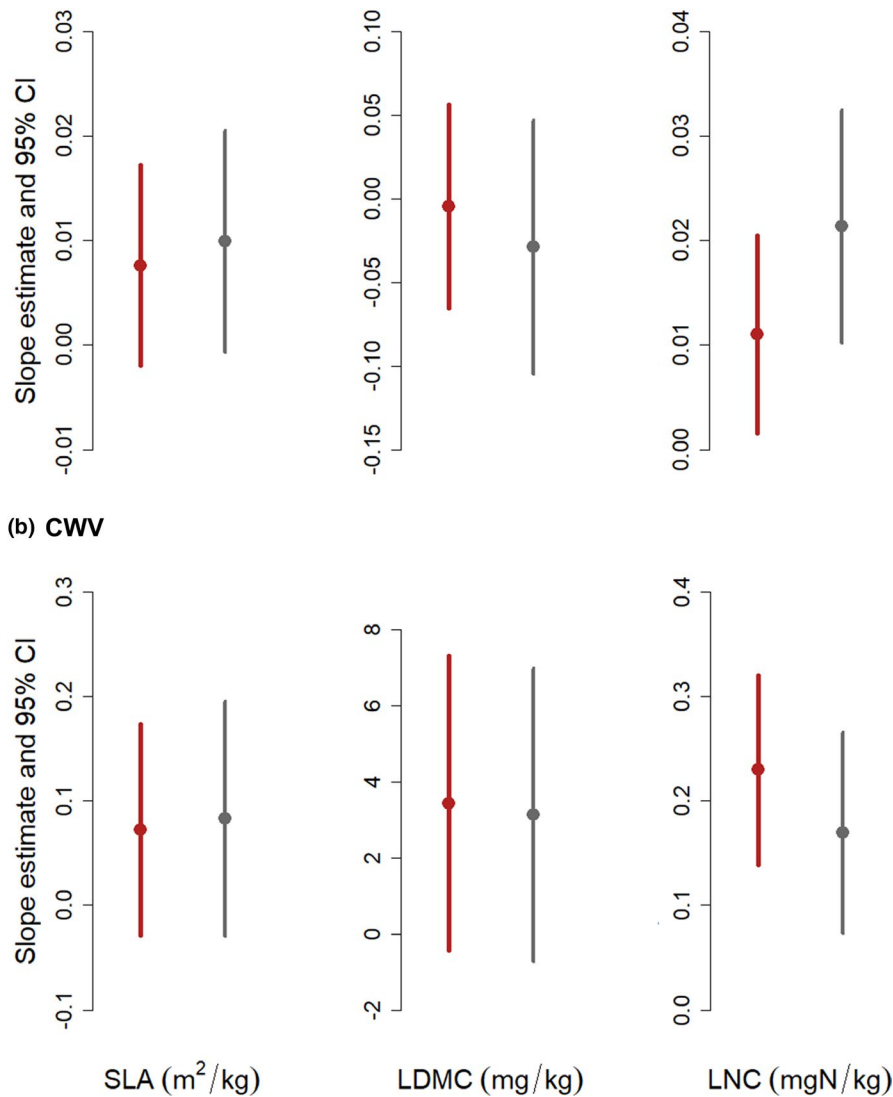
(a) CWM

FIGURE 5 Differences in the slopes of trait-climate relationships between herbicide-free (red, n = 477) and herbicide-sprayed (grey, n= 477) cropland plant assemblages. Community-Weighted Means (a) or Variances (b) were computed based on Specific Leaf Area (SLA), Leaf Dry Matter Content (LDMC) or Leaf Nitrogen Content (LNC) and related to GSL_{tw} which depicts growth limitations by both temperature and soil water availability.
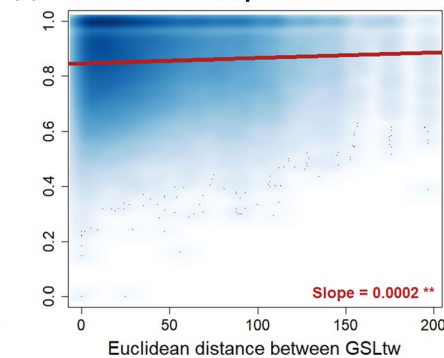
(b) CWV

SLA (m²/kg)   LDMC (mg/kg)   LNC (mgN/kg)
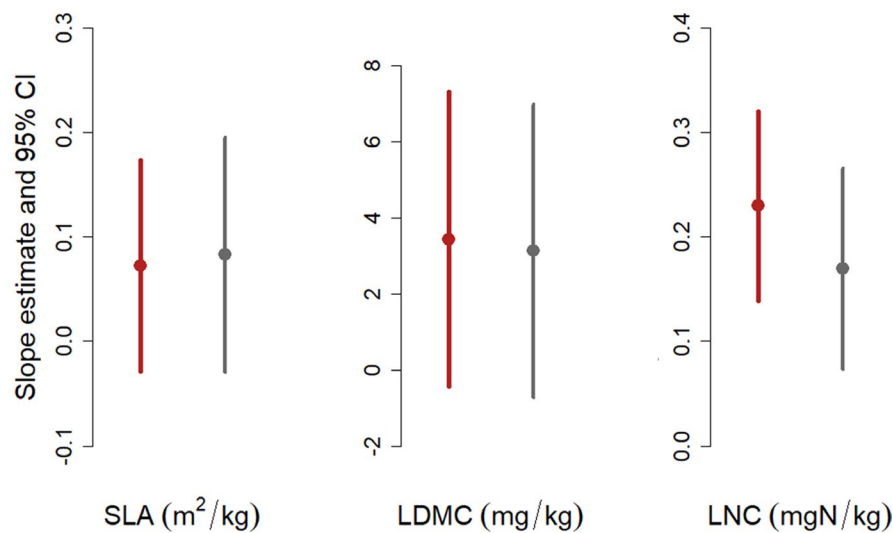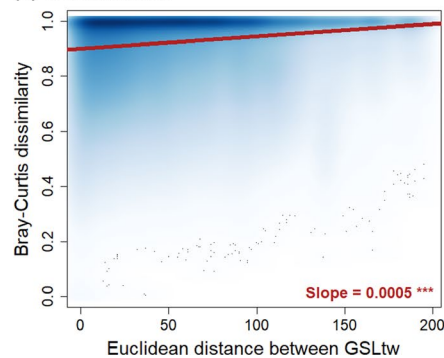
(a) Grasslands (b) Herbicide-free croplands (c) Herbicide-sprayed croplands

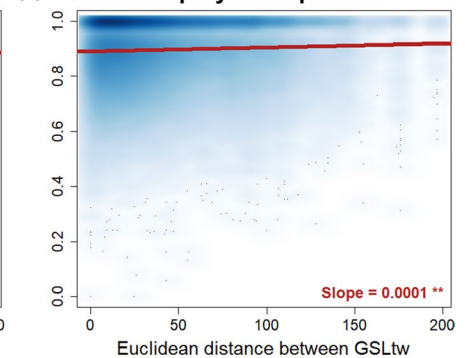Slope = 0.0005 ***   Slope = 0.0002 **   Slope = 0.0001 **

FIGURE 6 Relationships between beta-diversity and differences in growing season length (GSL_{tw}) in grassland (a, n = 5619), herbicide-free (b, n = 477) and herbicide-sprayed (c, n= 477) cropland plant assemblages, obtained by multiple regression on distance matrices (red line). Plant beta-diversity was calculated as Bray-Curtis dissimilarity and differences in growing season length as Euclidean distance between pairs of plant assemblages. GSL_{tw} depicts growth limitations by both temperature and soil water availability. Asterisks indicate the slope significance based on 100,000 permutations (***: p ≤ 0.001; **: 0.001 < p ≤ 0.01).

(despite a negative effect on plant species richness). Long-term monitoring or experiments replicated along bioclimatic gradients are, however, required in croplands to fully decipher the ecological mechanisms at play. Phenological traits such as early flowering onset and long flowering period were also previously demonstrated to promote greater tolerance to the environmental constraints induced by agricultural practices (Zanin et al., 1997; Storkey et al., 2010; Bagavathiannan & Norsworthy, 2012; Pinke & Gunton, 2014; Armengot et al., 2016). Investigating additional plant traits on top of leaf ones such as phenological traits should, therefore, help to disentangle the effect of local filters on trait–climate relationships in cropland assemblages.

5 | CONCLUSION

The establishment of trait–environment relationships across broad environmental gradients has been identified as a priority in functional ecology and biogeography in order to reveal the ecophysiological meaning of plant functional traits (Violle et al. 2014, Shipley 2016). Indeed, such large-scale patterns are thought to be able to produce much more general results than ecophysiological experimental studies that by nature focus on a limited number of species and abiotic conditions. As such, helped by big-data efforts, there has been a spectacular rise of trait–climate gradient analyses over the last decades. Here we found that land use intensification can greatly challenge the generality of the macroecological laws emerging from functional biogeography studies. By selecting for a restricted range of plant strategies, higher management intensity can indeed blur trait–environment relationships as demonstrated here from the comparison of cropland and grassland assemblages. Integrating land use into functional biogeographic studies is, therefore, a promising perspective to refine the response of plant assemblages to broad-scale bioclimatic gradients, and thereby more accurately forecast plant diversity shifts under climate changes, model potential feedback on ecosystem functioning, or adapt ecosystem management to improve resilience. Reaching this target will imply the development of innovative approaches and/ or a statistical framework for producing uncorrelated environmental and spatial gradients. Functional biogeography is at its infancy, and we need to bring much more effort to test the robustness of trait–environment relationships from a predictive perspective, notably by more thoroughly investigating sampling bias, spatial autocorrelation, trait–trait covariation among others, as already done by its sister field, biogeography, for more than one century.

ORCID
Bérenger Bourgeois https://orcid.org/0000-0002-2885-2518
François Munoz https://orcid.org/0000-0001-8776-4705
Sabrina Gaba https://orcid.org/0000-0002-7145-6713
Pierre Denelle https://orcid.org/0000-0002-4729-3774
Guillaume Fried https://orcid.org/0000-0002-3653-195X
Jonathan Storkey https://orcid.org/0000-0003-1094-8914
Cyrille Violle https://orcid.org/0000-0002-2471-9226

REFERENCES

Al Majou, H., Bruand, A., Duval, O., Le Bas, C. & Vautier, A. (2008) Prediction of soil water retention properties after stratification by combining texture, bulk density and the type of horizon. *Soil Use and Management*, 24, 383–391. https://doi.org/10.1111/j.1475-2743.2008.00180.x

Alignier, A., Solé-Senan, X., Robleño, I., Baraibar, B., Fahrig, L., Giralt, D. et al. (2020) Configurational crop heterogeneity increases within-field plant diversity. *Journal of Applied Ecology*, 57, 654–663. https://doi.org/10.1111/1365-2664.13585

Armengot, L., Blanco-Moreno, J.M., Bàrberi, P., Bocci, G., Carlesi, S., Aendekerk, R. et al. (2016) Tillage as a driver of change in weed communities: a functional perspective. *Agriculture, Ecosystems and Environment*, 222, 276–285. https://doi.org/10.1016/j.agee.2016.02.021

Bagavathiannan, M.V. & Norsworthy, J.K. (2012) Late-season seed production in arable weed communities: management implications. *Weed Science*, 60, 325–334. https://doi.org/10.1614/WS-D-11-00222.1

Benichou, P. & Le Breton, O. (1987) Prise en compte de la topographie pour la cartographie des champs pluviométriques statistiques. *Météorologie*, 19, 23–34.

Bennett, A.C. & Shaw, D.R. (2000) Effect of preharvest desiccants on weed seed production and viability. *Weed Technology*, 14, 530–538. https://doi.org/10.1614/0890-037X(2000)014[0530:EOPDOW]2.0.CO;2

Borgy, B., Perronne, R., Kholer, C., Grison, A.-L., Amiaud, B. & Gaba, S. (2016) Changes in functional diversity and intraspecific trait variability in response to crop sequence and climate. *Weed Research*, 56, 102–113. https://doi.org/10.1111/wre.12190

Borgy, B., Violle, C., Choler, P., Denelle, P., Munoz, F., Kattge, J. et al. (2017a) Plant community structure and nitrogen inputs modulate the climate signal on leaf traits. *Global Ecology and Biogeography*, 26, 1138–1152. https://doi.org/10.1111/geb.12623

Borgy, B., Violle, C., Choler, P., Garnier, E., Loranger, J., Amiaud, B. et al. (2017b) Sensitivity of community-level trait-environment relationships to data representativeness: a test for functional biogeography. *Global Ecology and Biogeography*, 26, 729–739. https://doi.org/10.1111/geb.12573

Bourgeois, B., Gaba, S., Plumejeaud, C. & Bretagnolle, V. (2020) Weed diversity is driven by complex interplay between multi-scale dispersal and local filtering. *Proceedings of the Royal Society B: Biological Sciences*, 287, 20201118. https://doi.org/10.1098/rspb.2020.1118

Bourgeois, B., Munoz, F., Fried, G., Mahaut, L., Armengot, L., Denelle, P. et al. (2019) What makes a weed a weed? A large-scale evaluation of arable weeds through a functional lens. *American Journal of Botany*, 106, 90–100. https://doi.org/10.1002/ajb2.1213

Braun-Blanquet, J. (Ed.) (1932) *Plant sociology*. New York: McGraw-Hill.

Brewer, A.C. & Oliver, L.R. (2007) Reducing weed seed rain with late-season glyphosate applications. *Weed Technology*, 21, 753–758. https://doi.org/10.1614/WT-06-145.1

Bruelheide, H., Dengler, J., Purschke, O., Lenoir, J., Jiménez-Alfaro, B., Hennekens, S.M. et al. (2018) Global trait–environment relationships of plant communities. *Nature Ecology and Evolution*, 2, 1906–1917. https://doi.org/10.1038/s41559-018-0699-8

Catarino, R., Gaba, S. & Bretagnolle, V. (2019) Experimental and empirical evidence shows that reducing weed control in winter cereal fields is a viable strategy for farmers. *Scientific Reports*, 9, 9004. https://doi.org/10.1038/s41598-019-45315-8

Chapin, F.S., Zavaleta, E.S., Eviner, V.T., Naylor, R.L., Vitousek, P.M., Reynolds, H.L. et al. (2000) Consequences of changing biodiversity. *Nature*, 405, 234–242. https://doi.org/10.1038/35012241

Chauvel, B., Colbach, N. & Munier-Jolain, N.M. (1998) How to estimate weed flora in a field? Comparison of sampling methods. Zeitschrift für Pflanzenkrankheiten und Pflanzenschutz, Sonderheft XVI, pp. 265–272.

Clay, P.A. & Griffin, J.L. (2000) Weed seed production and seedling emergence responses to late-season glyphosate applications. *Weed Science*, 48, 481–486. https://doi.org/10.1614/0043-1745(2000)048[0481:WSPASE]2.0.CO;2

Cunningham, S.A., Summerhayes, B. & Westoby, M. (1999) Evolutionary divergences in leaf structure and chemistry, comparing rainfall and soil nutrient gradients. *Ecological Monographs*, 69, 569–588. https://doi.org/10.1890/0012-9615(1999)069[0569:EDILSA]2.0.CO;2

Díaz, S. & Cabido, M. (2001) Vive la différence: plant functional diversity matters to ecosystem processes. *Trends in Ecology and Evolution*, 16, 646–655. https://doi.org/10.1016/S0169-5347(01)02283-2

Díaz, S., Kattge, J., Cornelissen, J.H.C., Wright, I.J., Lavorel, S., Dray, S. et al. (2016) The global spectrum of plant form and function. *Nature*, 529, 167–171. https://doi.org/10.1038/nature16489

Foley, J.A., Defries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R. et al. (2005) Global consequences of land use. *Science*, 309, 570–574. https://doi.org/10.1126/science.1111772

Forrestel, E.J., Donoghue, M.J., Edwards, E.J., Jetz, W., du Toit, J.C.O. & Smith, M.D. (2017) Different clades and traits yield similar grassland functional responses. *Proceedings of the National Academy of Sciences of the United States of America*, 114, 705–710. https://doi.org/10.1073/pnas.1612909114

Fortunel, C., Garnier, E., Joffre, R., Kazakou, E., Quested, H., Grigulis, K. et al. (2009) Leaf traits capture the effects of land use changes and climate on litter decomposability of grasslands across Europe. *Ecology*, 90, 598–611. https://doi.org/10.1890/08-0418.1

Fried, G., Armengot, L., Storkey, J., Bourgeois, B., Gaba, S., Violle, C. et al. (2021) Do ecological specialization and functional traits explain the abundance-frequency relationship? Arable weeds as a case study. *Journal of Biogeography*, 48, 37–50. https://doi.org/10.1111/jbi.13980

Fried, G., Cordeau, S., Metay, A. & Kazakou, E. (2019) Relative importance of environmental factors and farming practices in shaping weed communities structure and composition in French vineyards. *Agriculture, Ecosystems and Environment*, 275, 1–13. https://doi.org/10.1016/j.agee.2019.01.006

Fried, G., Kazakou, E. & Gaba, S. (2012) Trajectories of weed communities explained by traits associated with species' response to management practices. *Agriculture, Ecosystems and Environment*, 158, 147–155. https://doi.org/10.1016/j.agee.2012.06.005

Fried, G., Norton, L.R. & Reboud, X. (2008) Environmental and management factors determining weed species composition and diversity in France. *Agriculture, Ecosystems and Environment*, 128, 68–76. https://doi.org/10.1016/j.agee.2008.05.003

Gaba, S., Caneill, J., Nicolardot, B., Perrone, R. & Bretagnolle, V. (2018) Crop competition in winter wheat has a higher potential than farming practices to regulate weeds. *Ecosphere*, 9, e02413. https://doi.org/10.1002/ecs2.2413

Gaba, S., Fried, G., Kazakou, E., Chauvel, B. & Navas, M.-L. (2014) Agroecological weed control using a functional approach: a review of cropping systems diversity. *Agronomy for Sustainable Development*, 34, 103–119. https://doi.org/10.1007/s13593-013-0166-5

Gaba, S., Gabriel, E., Chadoeuf, J., Bonneu, F. & Bretagnolle, V. (2016) Herbicides do not ensure for higher wheat yield, but eliminate rare plant species. *Scientific Reports*, 6, 30112. https://doi.org/10.1038/srep30112

Godinho, I. (1984) Les définitions d' 'adventices' et de 'mauvaise herbes'. *Weed Research*, 24, 121–125. https://doi.org/10.1111/j.1365-3180.1984.tb00579.x

Goslee, S.C. & Urban, D.L. (2007) The ecodist package for dissimilarity-based analysis of ecological data. *Journal of Statistical Software*, 22, 1–19. https://doi.org/10.18637/jss.v022.i07

Gunton, R.M., Petit, S. & Gaba, S. (2011) Functional traits relating arable weed communities to crop characteristics. *Journal of Vegetation Science*, 22, 541–550. https://doi.org/10.1111/j.1654-1103.2011.01273.x

Hodgson, J.G., Montserrat-Martí, G., Charles, M., Jones, G., Wilson, P., Shipley, B. et al. (2011) Is leaf dry matter content a better predictor of soil fertility than specific leaf area? *Annals of Botany*, 108, 1337–1345. https://doi.org/10.1093/aob/mcr225

José-María, L., Armengot, L., Blanco-Moreno, J.M., Bassa, M. & Sans, F.X. (2010) Effects of agricultural intensification on plant diversity in Mediterranean dryland cereal fields. *Journal of Applied Ecology*, 47, 832–840. https://doi.org/10.1111/j.1365-2664.2010.01822.x

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. https://doi.org/10.1111/gcb.14904

Kattge, J., Díaz, S., Lavorel, S., Prentice, I.C., Leadley, P., Bönisch, G. et al. (2011) TRY – a global database of plant traits. *Global Change Biology*, 17, 2905–2935. https://doi.org/10.1111/j.1365-2486.2011.02451.x

Krähmer, H., Andreasen, C., Economou-Antonaka, G., Holec, J., Kalivas, D., Kolářová, M. et al. (2020) Weed surveys and weed mapping in Europe: State of the art and future tasks. *Crop Protection*, 129, 105010. https://doi.org/10.1016/j.cropro.2019.105010

Lamanna, C., Blonder, B., Violle, C., Kraft, N.J.B., Sandel, B., Šímová, I. et al. (2014) Functional trait space and latitudinal diversity gradient. *Proceedings of the National Academy of Sciences of the United States of America*, 111, 13745–13750. https://doi.org/10.1073/pnas.1317722111

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. https://doi.org/10.1046/j.1365-2435.2002.00664.x

Lavorel, S., Grigulis, K., Lamarque, P., Colace, M.P., Garden, D., Girel, J. et al. (2011) Using plant functional traits to understand the landscape distribution of multiple ecosystem services. *Journal of Ecology*, 99, 135–147. https://doi.org/10.1111/j.1365-2745.2010.01753.x

Le Bas, C., King, D. & Daroussin, J. (1997) A tool for estimating soil water available for plants using the 1:1,000,000 scale Soil Geographical Data Base of Europe. In: Beek, K.J., De Bie, K.A. & Driessen, P.M. (Eds.), *Geo-information for sustainable land management*. (p. 10). Netherlands: Enschede.

Lichstein, J.W. (2007) Multiple regression on distance matrices: a multivariate spatial analysis tool. *Plant Ecology*, 188, 117–131. https://doi.org/10.1007/s11258-006-9126-3

Mahaut, L., Cheptou, P.-O., Fried, G., Munoz, F., Storkey, J., Vasseur, F. et al. (2020) Weeds: against the rules? *Trends in Plant Science*, 25, 1107–1116. https://doi.org/10.1016/j.tplants.2020.05.013

Mahaut, L., Fried, G. & Gaba, S. (2018) Patch dynamics and temporal dispersal partly shape annual plant communities in ephemeral habitat patches. *Oikos*, 127, 147–159. https://doi.org/10.1111/oik.04415

Mahn, E.-G. (1984) Structural changes of weed communities and populations. *Vegetatio*, 58, 79–85. https://doi.org/10.1007/BF00044931

Mahn, E.-G. & Kästner, A. (1985) Effects of herbicide stress on weed communities and soil nematodes in agroecosystems. *Oikos*, 44, 185–190. https://doi.org/10.2307/3544060

McGill, B.J. (2019) The what, how and why of doing macroecology. *Global Ecology and Biogeography*, 28, 6–17. https://doi.org/10.1111/geb.12855

McGill, B.J., Enquist, B.J., Weiher, E. & Westoby, M. (2006) Rebuilding community ecology from functional traits. *Trends in Ecology and Evolution*, 21, 178–185. https://doi.org/10.1016/j.tree.2006.02.002

McGill, B. J. (2019). The what, how and why of doing macroecology. *Global Ecol Biogeogr*, 28, 6–17. https://doi-org.acces.bibl.ulaval.ca/10.1111/geb.12855

Moles, A.T., Perkins, S.E., Laffan, S.W., Flores-Moreno, H., Awasthy, M., Tindall, M.L. et al. (2014) Which is a better predictor of plant traits: temperature or precipitation? *Journal of Vegetation Science*, 25, 1167–1180. https://doi.org/10.1111/jvs.12190

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D. et al. (2019) Vegan: community ecology package. Version 2.5-6.

Onoda, Y., Westoby, M., Adler, P.B., Choong, A.M., Clissold, F.J., Cornelissen, J.H. et al. (2011) Global patterns of leaf mechanical properties. *Ecology Letters*, 14, 301–312. https://doi.org/10.1111/j.1461-0248.2010.01582.x

Ordóñez, J.C., van Bodegom, P.M., Witte, J.-P.-M., Wright, I.J., Reich, P.B. & Aerts, R. (2009) A global study of relationships between leaf traits, climate and soil measures of nutrient fertility. *Global Ecology and Biogeography*, 18, 137–149. https://doi.org/10.1111/j.1466-8238.2008.00441.x

Pakeman, R.J., Eastwood, A. & Scobie, A. (2011) Leaf dry matter content as a predictor of grassland litter decomposition: a test of the 'mass ratio hypothesis'. *Plant and Soil*, 342, 49–57. https://doi.org/10.1007/s11104-010-0664-z

Perronne, R., Gaba, S., Cadet, E. & Le Corre, V. (2014) The interspecific and intraspecific variation of functional traits in weeds: diversified strategies within arable fields. *Acta Botanica Gallica*, 161, 243–252. https://doi.org/10.1080/12538078.2013.868320

Perronne, R., Le Corre, V., Moinard, B. & Gaba, S. (under review) A functional strategy similar to the crop maximises arable weed individual biomass production in presence and absence of winter wheat plants. *Weed Research*.

Perronne, R., Le Corre, V., Bretagnolle, V. & Gaba, S. (2015) Stochastic processes and crop type shape weed assembly in arable fields. *Journal of Vegetation Science*, 26, 348–359. https://doi.org/10.1111/jvs.12238

Piedallu, C. & Gégout, J.-C. (2008) Efficient assessment of topographic solar radiation to improve plant distribution models. *Agricultural and Forest Meteorology*, 148, 1696–1706. https://doi.org/10.1016/j.agrformet.2008.06.001

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. & Core, R. (2018) nlme: linear and nonlinear mixed effects models. R package version 2.1-137.

Pinke, G. & Gunton, R.M. (2014) Refining rare weed trait syndromes along arable intensification gradients. *Journal of Vegetation Science*, 25, 978–989. https://doi.org/10.1111/jvs.12151

Pontes, L.D.S., Soussane, J.F., Louault, F., Andueza, D. & Carrère, P. (2007) Leaf traits affect the above-ground productivity and quality of pasture grasses. *Functional Ecology*, 21, 844–853. https://doi.org/10.1111/j.1365-2435.2007.01316.x

R Core Team (2018) *R: a language and environment for statistical computing*. Vienna: The R Foundation for Statistical Computing.

Ramankutty, N., Evan, A.T., Monfreda, C. & Foley, J.A. (2008) Farming the planet: 1. Geographic distribution of global agricultural lands in the year 2000. *Global Biogeochemical Cycles*, 22, GB1003. https://doi.org/10.1029/2007GB002952

Read, Q.D., Moorhead, L.C., Swenson, N.G., Bailey, J.K. & Sanders, N.J. (2014) Convergent effects of elevation on functional leaf traits within and among species. *Functional Ecology*, 28, 37–45. https://doi.org/10.1111/1365-2435.12162

Reich, P.B. & Oleksyn, J. (2004) Global patterns of plant leaf N and P in relation to temperature and latitude. *Proceedings of the National Academy of Sciences of the United States of America*, 101, 11001–11006. https://doi.org/10.1073/pnas.0403588101

Sandel, B. (2019) Disequilibrium in trait–climate relationships of trees and birds. *Frontiers in Ecology and Evolution*, 7, 138. https://doi.org/10.3389/fevo.2019.00138

Sandel, B., Goldstein, L.J., Kraft, N.J., Okie, J.G., Shuldman, M.I., Ackerly, D.D. et al. (2010) Contrasting trait responses in plant communities to experimental and geographic variation in precipitation. *New Phytologist*, 188, 565–575. https://doi.org/10.1111/j.1469-8137.2010.03382.x

Shipley, B., De Bello, F., Cornelissen, J.H.C., Laliberté, E., Laughlin, D.C. & Reich, P.B. (2016) Reinforcing loose foundation stones in trait-based plant ecology. *Oecologia*, 180, 923–931. https://doi.org/10.1007/s00442-016-3549-x

Siefert, A., Fridley, J.D. & Ritchie, M.E. (2014) Community functional response to soil and climate at multiple scales: when does intraspecific variation matter? *PLoS One*, 9, e111189. https://doi.org/10.1371/journal.pone.0111189

Siefert, A., Violle, C., Chalmandrier, L., Albert, C.H., Taudiere, A., Fajardo, A. et al. (2015) A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. *Ecology Letters*, 18, 1406–1419. https://doi.org/10.1111/ele.12508

Šímová, I., Sandel, B., Enquist, B.J., Michaletz, S.T., Kattge, J., Violle, C. et al. (2019) The relationships of woody plant size and leaf nutrient content to large-scale productivity for forests across the Americas. *Journal of Ecology*, 107, 2278–2290. https://doi.org/10.1111/1365-2745.13163

Shipley, B., De Bello, F., & Cornelissen, J. H. C. (2016). Reinforcing loose foundation stones in trait-based plant ecology. *Oecologia*, 180, 923–931. https://doi.org/10.1007/s00442-016-3549-x

Šímová, I., Violle, C., Svenning, J.-C., Kattge, J., Engemann, K., Sandel, B. et al. (2018) Spatial patterns of major plant traits in the New World differ between woody and herbaceous species. *Journal of Biogeography*, 45, 815916. https://doi.org/10.1111/jbi.13171

Simpson, A.H., Richardson, S.J. & Laughlin, D.C. (2016) Soil–climate interactions explain variation in foliar, stem, root and reproductive traits across temperate forests. *Global Ecology and Biogeography*, 25, 964–978. https://doi.org/10.1111/geb.12457

Storkey, J., Moss, S., & Cussans, J. (2010). Using Assembly Theory to Explain Changes in a Weed Flora in Response to Agricultural Intensification. *Weed Science*, 58(1), 39–46. https://doi.org/10.1614/WS-09-096.1

Storkey, J. (2005) Modelling assimilation rates of 14 temperate arable weed species as a function of the environment and leaf traits. *Weed Research*, 46, 361–370. https://doi.org/10.1111/j.1365-3180.2005.00466.x

Turc, L. (1961) Évaluation de besoins en eau d'irrigation, évapotranspiration potentielle. *Annales Agronomiques*, 12, 13–49.

Violle, C., Choler, P., Borgy, B., Garnier, E., Amiaud, B., Debarros, G. et al. (2015) Vegetation ecology meets ecosystems science: permanent grasslands as a functional biogeography case study. *Science of the Total Environment*, 534, 43–51. https://doi.org/10.1016/j.scitotenv.2015.03.141

Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I. & et al. (2007) Let the concept of trait be functional!. *Oikos*, 116, 882–892. https://doi.org/10.1111/j.0030-1299.2007.15559.x

Violle, C., Reich, P.B., Pacala, S.W., Enquist, B.J. & Kattge, J. (2014) The emergence and promise of functional biogeography. *Proceedings of*

the National Academy of Sciences of the United States of America, 111, 13690–13696. https://doi.org/10.1073/pnas.1415442111

Wagner, M., Bullock, J.M., Hulmes, L., Hulmes, S. & Pywell, R.F. (2017) Cereal density and N-fertiliser effect on the flora and biodiversity value of arable headlands. *Biodiversity and Conservation*, 26, 85–102. https://doi.org/10.1007/s10531-016-1225-4

Walker, E.R. & Oliver, L.R. (2008) Weed seed production as influenced by glyphosate applications at flowering stage across a weed complex. *Weed Technology*, 22, 318–325. https://doi.org/10.1614/WT-07-118.1

Wang, Y.P., Lu, X.J., Wright, I.J., Dai, Y.J., Rayner, P.J. & Reich, P.B. (2012) Correlations among leaf traits provide a significant constraint on the estimate of global gross primary production. *Geophysical Research Letters*, 39, L19405. https://doi.org/10.1029/2012GL053461

Weiner, J., Andersen, S.B., Wille, W.-K.-M., Griepentrog, H.W. & Olsen, J.M. (2010) Evolutionary agroecology: the potential for cooperative, high density, weed-suppressing cereals. *Evolutionary Applications*, 3, 473–479. https://doi.org/10.1111/j.1752-4571.2010.00144.x

Wickham, H. (Ed.) (2016) *ggplot2: elegant graphics for data analysis*. New York: Springer-Verlag.

Wright, I.J., Dong, N., Maire, V., Prentice, I.C., Westoby, M., Díaz, S. et al. (2017) Global climatic drivers of leaf size. *Science*, 357, 917–921. https://doi.org/10.1126/science.aal4760

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. https://doi.org/10.1038/nature02403

Wright, I.J., Reich, P.B., Cornelissen, J.H.C., Falster, D.S., Groom, P.K., Hikosaka, K. et al. (2005) Modulation of leaf economic traits and trait relationships by climate. *Global Ecology and Biogeography*, 14, 411–421. https://doi.org/10.1111/j.1466-822x.2005.00172.x

Zanin, G., Otto, S., Riello, L. & Borin, M. (1997) Ecological interpretation of weed flora dynamics under different tillage systems. *Agriculture, Ecosystems and Environment*, 66, 177–188. https://doi.org/10.1016/S0167-8809(97)00081-9

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

Appendix S1 Statistics of cropland/grassland comparison

Appendix S2 Statistics of cropland/grassland comparison without growing season length accounting for both temperature and soil water limitations (GSL_{tw}) = 365 days

Appendix S3 Statistics of herbicide-free/herbicide-sprayed cropland comparison

Appendix S4 Statistics of herbicide-free/herbicide-sprayed cropland comparison without growing season length accounting for both temperature and soil water limitations (GSL_{tw}) = 365 days