



HAL
open science

Intraspecific trait variability mediates the response of subalpine grassland communities to extreme drought events

Vincent Jung, Cécile H. Albert, C. Violle, G. Kunstler, G. Loucougaray, T. Spiegelberger

► To cite this version:

Vincent Jung, Cécile H. Albert, C. Violle, G. Kunstler, G. Loucougaray, et al.. Intraspecific trait variability mediates the response of subalpine grassland communities to extreme drought events. *Journal of Ecology*, 2014, 102 (1), pp.45-53. 10.1111/1365-2745.12177 . hal-00949680

HAL Id: hal-00949680

<https://hal.science/hal-00949680>

Submitted on 24 Feb 2014

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

1 **Intraspecific trait variability mediates the response of subalpine grassland**
2 **communities to extreme drought events**

3

4 **Vincent Jung^{1,2*}, Cécile H. Albert^{3,4}, Cyrille Violle^{5,6}, Georges Kunstler^{1,7}, Grégory**
5 **Loucougaray¹ & Thomas Spiegelberger^{1,8}**

6

7 ¹ *Irstea, UR Mountain Ecosystems, St-Martin-d'Hères, France*

8 ² *CNRS UMR 6553, ECOBIO, Université de Rennes 1, Rennes, France*

9 ³ *Laboratoire d'Ecologie Alpine, CNRS UMR 5553, Université Joseph Fourier, Grenoble,*
10 *France*

11 ⁴ *Department of Biology, McGill University, Montreal, Quebec, Canada*

12 ⁵ *Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, USA*

13 ⁶ *Centre d'Ecologie Fonctionnelle et Evolutive, CNRS UMR 5175, Montpellier, France*

14 ⁷ *Department of Biological Sciences, Macquarie University, Sydney, NSW 2109, Australia*

15 ⁸ *Ecole Polytechnique Fédérale de Lausanne (EPFL), Laboratory of Ecological Systems*

16 *(ECOS) - Swiss Federal Institute for Forest, Snow and Landscape Research (WSL), Research*

17 *Group Restoration Ecology, station 2, CH-1015 Lausanne, Switzerland*

18 | ***Correspondence author. E-mail: vincent.jung@univ-rennes1.fr**

19

20 **Running headline:** Extreme droughts in subalpine grasslands

21

22

1 Summary

- 2 1. Climate change is expected to increase the magnitude and the frequency of extreme
3 climatic events such as droughts. Better understanding how plant communities will
4 respond to these droughts is a major challenge. We expect the response to be a shift in
5 functional trait values resulting from both species turnover and intraspecific trait
6 variability, but little research has addressed the relative contribution of both
7 components.
- 8 2. We analysed the short-term functional response of subalpine grassland communities to
9 a simulated drought by focusing on four leaf traits (LDMC: leaf dry matter content,
10 SLA: specific leaf area, LNC: leaf nitrogen concentration, LCC: leaf carbon
11 concentration). After evaluating species turnover and intraspecific variability
12 separately, we determined their relative contribution in the community functional
13 response to drought, reflected by changes in community weighted mean traits.
- 14 3. We found significant species turnover and intraspecific variability, as well as
15 significant changes in community weighted mean for most of **the** traits. The relative
16 contribution of intraspecific variability to the changes in community mean traits was
17 more important (42-99%) than the relative contribution of species turnover (1-58%).
18 Intraspecific variability either amplified (for LDMC, SLA and LCC) or dampened (for
19 LNC) the community functional response mediated by species turnover. We
20 demonstrated that the small contribution of species turnover to the changes in
21 community mean LDMC and LCC was explained by a lack of covariation between
22 species turnover **and** interspecific trait differences.
- 23 4. *Synthesis*. These results highlight the need for a better consideration of intraspecific
24 **variability** to understand and predict the effect of climate change on plant
25 communities. While both species turnover and intraspecific variability can be

1 expected following an extreme drought, we report new evidence that intraspecific
2 variability can be a more important driver of the sort-term functional response of plant
3 communities.

4

5 | **Key-words:** climate change experiments, community weighted mean traits, drought,
6 | grasslands, intraspecific variability, plant-climate interactions, plant functional traits

7

1 **Introduction**

2 Extreme weather events are projected to increase in magnitude and in frequency due to
3 climate change (Easterling *et al.* 2000; IPCC 2007), calling for a shift from 'trend-focused' to
4 'event-focused' climate change experiments (Jentsch *et al.* 2007). Summer droughts and in
5 particular extreme drought events are expected to be among the main consequences of climate
6 change (Meehl & Tebaldi 2004). Understanding the mechanisms that underlie the response of
7 communities to such droughts is a major challenge for predicting climate change effects on
8 biodiversity (Smith 2011). Plants, as sessile organisms, are likely to be particularly exposed to
9 an increasing frequency of extreme droughts.

10 Drought represents a strong abiotic filter (Chase 2007) that restricts trait range within
11 communities to a limited set of values (e.g. Cornwell & Ackerly 2009). The regulation of
12 water loss through leaves can be expressed by several key leaf functional traits (Wright *et al.*
13 2001; Ackerly 2004) and, for example, be reflected through higher leaf dry matter content
14 (LDMC) and/or lower specific leaf area (SLA) (Buckland *et al.* 1997; Volaire 2008; Poorter
15 *et al.* 2009). Therefore, drought events are expected to shift community trait composition. A
16 change in trait composition within a community through time can be caused by a change in
17 species composition and/or relative abundance ('species turnover' hereafter, used in a broad
18 sense including both qualitative and quantitative changes), by intraspecific trait variability
19 ('intraspecific variability' hereafter) or by any combinations of these factors (Lep *et al.* 2011;
20 Violle *et al.* 2012; Albert *et al.* 2012). Community functional response to drought can be
21 evaluated through the analysis of community weighted mean traits (i.e., the mean of trait
22 values weighted by the relative abundance of each species in the community, Garnier *et al.*
23 2004; Violle *et al.* 2007, 'community mean trait' hereafter), the variation of which is able to
24 capture trait shifts due to both species turnover and intraspecific variability. Up to now, while
25 dealing with the response of plant communities to climate changes, most studies have mostly

1 focused on species turnover (e.g. Evans *et al.* 2011; Kreyling *et al.* 2011) or on changes in
2 community mean traits driven by species turnover (e.g. Sandel *et al.* 2010). Intraspecific
3 variability in response to climate changes was investigated for many species individually (e.g.
4 Buckland *et al.* 1997; Hudson *et al.* 2011; Weißhuhn *et al.* 2011; West *et al.* 2012), but the
5 contribution of intraspecific variability in changes in community mean traits has been largely
6 overlooked. However, recent studies have started to shed some light on the importance of
7 intraspecific variability for community functional responses to environmental changes (Jung
8 *et al.* 2010; Andersen *et al.* 2012; Violle *et al.* 2012; Albert *et al.* 2012).

9 The relative contribution of intraspecific variability vs. species turnover in driving
10 community response to environmental change is likely to vary with the timescale under
11 scrutiny (Smith *et al.* 2009; Sandel *et al.* 2010). For instance short-term events such as
12 extreme droughts are likely to induce community functional responses mainly via
13 intraspecific variability through plastic adjustment of the resident plants (Helmuth *et al.*
14 2005), while long-term progressive changes are likely to impact communities mainly by
15 species turnover (Teurillat & Guisan 2001; Jump & Peñuelas 2005; Helmuth *et al.* 2005). For
16 the stability of plant communities in response to drought events, assessing the relative
17 contribution of intraspecific variability vs. species turnover to community functional
18 responses is thus a crucial question. However surprisingly few studies have explored this
19 question.

20 In this study, we address the question of the relative contribution of intraspecific
21 variability to community weighted mean traits by examining the short-term functional
22 response of subalpine grassland communities to a simulated drought. We focus on four key
23 functional leaf traits known to be related to species water use strategy (Wright *et al.* 2001;
24 Chaves *et al.* 2002; Ackerly 2004; Weih *et al.* 2011): specific leaf area, leaf dry matter
25 content, leaf nitrogen concentration and leaf carbon concentration. We address two main

- 1 questions: (i) how does drought modify species abundances and species trait values? (ii) what
- 2 is the relative contribution of species turnover and intraspecific variability in driving the
- 3 short-term community functional response to drought?
- 4
- 5

1 | **Materials and methods**

2

3 | *Study area*

4 | The study site (44°51' N, 5°28' E, 1500 m a.s.l.) is situated in the Hauts-Plateaux du Vercors
5 | Nature Reserve which is part of the Long-Term Socio-Ecological Research (LTSER) platform
6 | “Central French Alps”. The geological substrate consists of highly permeable karstic
7 | limestone. The vegetation is a mosaic of dry grasslands and woody patches of *Juniperus*
8 | *communis* (L.), *Picea abies* (L.) and *Pinus uncinata* (Ramond ex DC.). Grassland
9 | communities are species-rich and composed of perennial species, dominated by
10 | hemicryptophyte life forms (90% of the total abundance) with either persistent or summer
11 | green leaves (65% and 35% of the total abundance, respectively, Klotz *et al.* 2002). The
12 | dominant species are *Carex sempervirens* (Vill.), *Festuca laevigata* (Gaudin) and *Festuca*
13 | *nigrescens* (Lam.) (see Table S1 in Supporting Information). The studied subalpine grassland
14 | has been grazed by sheep since the Middle Ages. Currently it is extensively grazed each year
15 | by sheep during the plant growing season, from mid-June until the end of September. During
16 | the experiment, the study area was protected from grazing by fencing. The study area is
17 | covered by snow for approximately 5–6 months of the year (December–May).

18

19 | *Rainfall manipulation*

20 | An extreme drought event was simulated during peak vegetation growth in summer 2010 by
21 | exclusion of ambient rainfall through four semi-cylindrical rainout shelters. The shelters
22 | (length: 8 m; width: 4 m; height: 2.5 m, c. 30 m distant from each other) were covered with a
23 | transparent polyethylene roof with open sides to allow air circulation. Air moisture and
24 | temperature were not significantly altered by this system (EHT humidity/temperature sensor,

1 Decagon Devices, Pullman, Washington, USA, data not shown). Shelters were fenced to
2 prevent access to sheep during the experiment.

3 Rain shelters covered both drought and control plots. Six 0.60×0.60 m plots (three
4 control plots / three drought plots) were randomly located under each shelter (total 24 plots),
5 by ensuring at least 1.20 m spacing between plots and at least 60 cm spacing from the edge of
6 the shelter. In order to prevent rain water from accumulating at the edge of the shelters, rain
7 falling on the roof of the shelters was collected thanks to gutters connected to 300-L tanks and
8 was used to water the control plots. Control plots were watered twice a week following the
9 local June-July average rainfall over the 1952-2009 period (data: meteorological station of
10 Météo-France, La Chapelle en Vercors, c. 10km distant from the study area). Drought plots
11 were not watered from 7 June to 12 July 2010, corresponding to a rainfall deficit of 115 mm
12 (62%) from the June-July average rainfall (see Fig. S1). Drought with this intensity used to
13 correspond to a 30-years return period of the simulated drought based on the 1952-2009 data.
14 This return period is projected to decrease to 10 years for 2050-2100 under the B1 scenario
15 (IPCC 2007, climate projection simulations from the Hadley Centre model HADCM3, Fig.
16 S1). The average volumetric soil water content during the experiment was 6% (3% SD) in the
17 drought plots, against 17% (4% SD) in the control plots (ECH₂O soil moisture sensor,
18 Decagon Devices, Pullman, Washington, USA).

19

20 *Data collection*

21 Plant species were recorded twice, immediately before (3-4 June) and after (15-16 July) the
22 drought event. All species were recorded within each plot and the relative abundance of each
23 species was obtained by the "point-quadrat" sampling (Levy & Madden 1933), a suitable
24 method for the calculation of community-weighted mean traits (Lavorel *et al.* 2008). For a

1 given plot, the local abundance of each species was determined as the number of hits among
2 16 sampling points evenly distributed within the plot.

3 Leaf traits were measured in each plot for the most abundant species, i.e. species for
4 which the cumulated relative abundance reached at least 80% of the plot total abundance
5 (Pakeman & Quested 2007). Leaves were collected at the end of the drought event (8-16 July)
6 on three individuals of each species per plot. The youngest fully expanded leaf was sampled
7 for each individual. Specific leaf area (SLA, the ratio of fresh leaf area to leaf dry mass,
8 $\text{m}^2.\text{kg}^{-1}$) and leaf dry matter content (LDMC, the ratio of leaf dry mass to leaf fresh mass,
9 $\text{g}.\text{kg}^{-1}$) were measured after complete rehydration of leaves (Garnier *et al.* 2001a). Leaf
10 nitrogen concentration (LNC, the ratio of total nitrogen to leaf dry mass, $\text{g}.\text{kg}^{-1}$) and leaf
11 carbon concentration (LCC, the ratio of total carbon to leaf dry mass, $\text{g}.\text{kg}^{-1}$) were analysed
12 with FlashEA 1112 elemental analyzer (Thermo Fisher Scientific Inc., Milan, Italy). For a
13 given species, data were averaged per plot, thus accounting for intraspecific variability
14 between plots.

15

16 *Drought-induced species turnover and intraspecific variability*

17 Bray-Curtis dissimilarity in species composition between drought and control plots was used
18 to evaluate the species turnover due to drought. Species abundances were aggregated across
19 drought or control plots and then converted in relative abundance or presence/absence. The
20 Bray-Curtis dissimilarity between drought and control plots was calculated before and after
21 the drought event, from relative abundance and presence-absence data. We used the 'vegdist'
22 procedure in the vegan package of R version 2.11.1 (R Development Core Team 2010). To
23 identify which species contributed to species turnover we estimated the effect of drought on
24 each species by calculating the difference in relative abundance (Δ_{Ab}) between drought and
25 control plots. Statistical significances for Bray-Curtis dissimilarity and Δ_{Ab} were evaluated

1 using a permutation test (10000 permutations) wherein treatments (control/drought) were
2 randomly reassigned to plots separately within each shelter.

3 In order to compare the different sources of variability in raw trait values, we used
4 nested linear models to decompose the total variance of each trait into hierarchical
5 components, as described in Messier *et al.* (2010). For each trait, the total variance was
6 decomposed into three variance components: 'among species' (i.e. interspecific trait
7 differences), 'among treatments within species' (i.e. intraspecific variability explained by the
8 drought treatment) and 'among plots within treatments' (i.e. unexplained intraspecific
9 variability). We assessed the effect of drought on each trait over all species and for each
10 species independently by using mixed GLM including 'shelter' as a random effect.

11

12 *Community functional response to drought*

13 In order to capture the drought-induced community functional response, we calculated the
14 community mean for each trait and each plot, as the mean of trait values in the plot weighted
15 by the relative abundance of each species (Garnier *et al.* 2004; Violle *et al.* 2007). As changes
16 in community mean traits account for both species turnover and intraspecific variability, we
17 disentangled their relative contributions. We calculated community mean traits within each
18 plot from species relative abundances and trait values recorded in their respective plot. We
19 recalculated community mean traits in drought plots from species abundances in drought plots
20 but the trait values measured in control plots and averaged by species, i.e. under the
21 hypothesis of a lack of intraspecific variability. We quantified the contributions of species
22 turnover and intraspecific variability in the response of community mean traits to drought
23 (C_{Tum} and C_{Intra} , respectively), as:

$$24 \quad C_{\text{Tum}} = T_{\text{Dr}^*} - T_{\text{Ct}} \quad \text{eq. 1}$$

25 and

$$1 \quad C_{\text{Intra}} = T_{\text{Dr}} - T_{\text{Dr}^*} \quad \text{eq. 2}$$

2 where T_{Ct} and T_{Dr} are the observed community mean traits averaged by treatments
 3 (Control/Drought), and T_{Dr^*} is the average of community mean traits recalculated in drought
 4 plots by using species trait values in control plots. C_{Turn} and C_{Intra} represent the isolated effects
 5 of species turnover and intraspecific variability, respectively, in driving the response of
 6 community mean traits to drought. We used mixed GLMs with 'shelter' as random effect to
 7 test the significance of the drought-induced shift in the average community mean traits
 8 between control and drought plots (i.e., T_{Dr} vs. T_{Ct} and T_{Dr^*} vs. T_{Ct}), as well as the
 9 significance of the effects of intraspecific variability in the drought plots (i.e., T_{Dr^*} vs. T_{Dr}).

10 Finally, we determined the extent to which we could have expected C_{Turn} and C_{Intra} to
 11 be greater than we found, given the observed levels of species turnover and of intraspecific
 12 variability. In order to explore the way traits interact with species abundances to determine
 13 C_{Turn} and C_{Intra} , we generated random distributions of C_{Turn} and C_{Intra} from a dataset
 14 comprising, for each species and each trait, a pair of abundance values (i.e. the averages in the
 15 control treatment and in the drought treatment) and the corresponding pair of trait values.
 16 Pairs of trait values were randomly reallocated to pairs of abundance values, and each trait or
 17 abundance value within a pair was randomly reallocated to treatments. This procedure
 18 allowed us to randomize trait values with respect to abundance values while maintaining the
 19 magnitude of the observed inter- and intraspecific differences. For each trait we generated a
 20 random distribution of C_{Turn} and of C_{Intra} from 10000 permutations. We used these
 21 distributions to calculate the proportion of the simulated values of C_{Turn} or of C_{Intra} that is
 22 higher, in magnitude, than the observed value, as:

$$23 \quad P_{|\text{sim}|>|\text{obs}|} = N(|\text{sim}C_x| > |\text{obs}C_x|) / 10000 \quad \text{eq. 3}$$

24 where $N(|\text{sim}C_x| > |\text{obs}C_x|)$ is the number of time the magnitude of the simulated values of
 25 C_{Turn} (or of C_{Intra}) is higher than the observed value. For C_{Turn} , $P_{|\text{sim}|>|\text{obs}|}$ close to 0 indicates

- 1 that species turnover covaries with interspecific trait differences, leading to the highest
- 2 magnitude that C_{Turn} could potentially reach given the observed trait and abundance values.
- 3 For C_{Intra} , $P_{|\text{sim}|>|\text{obs}|}$ close to 0 indicates that intraspecific trait response covaries with species
- 4 abundances, leading to the highest magnitude that C_{Intra} could potentially reach.
- 5

1 **Results**

2

3 *Species turnover*

4 Before the drought event, we found no significant difference between drought and control
5 plots in terms of species composition (Bray-Curtis dissimilarity; Fig. 1a, b). Drought
6 significantly shifted species' relative abundance (Fig. 1a), but not species' presence-absence
7 (Fig. 1b). The relative abundance of *Festuca laevigata* and *Hieracium pilosella* (L.)
8 significantly increased due to drought, whereas the relative abundance of *Ranunculus*
9 *montanus* (Willd.), *Trifolium pratense* (L.), *Agrostis capillaris* (L.) and *Festuca nigrescens*
10 significantly decreased (Fig. 2).

11

12 *Intraspecific variability*

13 We performed a variance component analysis in order to examine the relative contribution of
14 species, treatment and plot identity to the total variance in raw trait values. This analysis
15 revealed that, on average, intraspecific variance accounted for 27% of the total trait variance
16 and that most of the trait variance (73%) was due to differences between species (Fig. 3).
17 Moreover, only 7% of the total trait variance was due to intraspecific variance between
18 treatments, while 20% was due to intraspecific variance within treatments.

19 We found a significant intraspecific trait response to drought among all species for all
20 traits except SLA (Fig. 4), as well as significant individual species responses in 12 species for
21 LDMC and in 4 species for SLA, LNC and LCC (Fig. 4). However, changes in individual
22 species responses did not show a unidirectional pattern. For example, five species showed a
23 significant decrease in LDMC, thus going against the prevailing trend.

24

25 *Community mean traits*

1 Community mean traits significantly increased in response to drought for LDMC (Fig. 5a)
2 and LCC (Fig. 5d), and significantly decreased for SLA (Fig. 5b). Intraspecific variability
3 significantly contributed to the changes in community mean LDMC, SLA and LCC, and
4 accounted for 48% to 99% of these changes; species turnover only contributed significantly to
5 the community response for SLA (Fig. 5b). The direction of intraspecific variability effects on
6 community mean traits were in accordance with the prevailing trends in trait responses
7 observed in Fig. 4. Community mean LNC was unaffected by drought through a
8 compensatory effect of intraspecific variability on species turnover (Fig. 5c).

9 The comparison of observed vs. simulated contributions of species turnover and of
10 intraspecific variability revealed that in many cases, the magnitude of the simulated
11 contributions largely exceeded the observed magnitude (Fig. 6). The amount by which the
12 magnitude of the simulated contributions exceeded the observed magnitude (i.e. $P_{|sim|>|obs|}$)
13 differed between traits and between species turnover and intraspecific variability. In
14 particular, for LDMC and LCC $P_{|sim|>|obs|}$ was higher for species turnover than for intraspecific
15 variability, whereas for SLA and LNC $P_{|sim|>|obs|}$ was higher for intraspecific variability.

16

1 **Discussion**

2 We have studied the immediate functional response of herbaceous communities to an extreme
3 drought event, in contrast to long-term experiments that addressed the impact of mean climate
4 change (e.g. Grime *et al.* 2008; Hudson *et al.* 2011). We particularly addressed the
5 contribution of intraspecific variability in mediating trait shifts within communities.

6 Intraspecific variability can result from genetic variability and phenotypic plasticity. Here we
7 evaluated the overall intraspecific variability induced by drought regardless of its underlying
8 cause. Given the short-term period under scrutiny, intraspecific variability recorded here is
9 probably mainly due to plastic physiological adjustments.

10

11 *Species turnover and intraspecific variability in response to drought*

12 Although drought induced a significant species turnover, this was due to changes in the
13 relative abundance of species rather than in the identity of species. This result is obviously
14 related to the short period of our experiment during which drastic compositional changes due
15 to species replacements were not likely to occur. However, this may also reflect the existence
16 of stabilizing processes such as reduced adult mortality that minimize the short-term effect of
17 drought on plant species composition (Lloret *et al.* 2012).

18 Whatever the trait under scrutiny, most of the variance in raw trait values was
19 explained by differences between species, in accordance with the general agreement that traits
20 vary more between than within species (Garnier *et al.* 2001b). Though intraspecific variance
21 accounted for a smaller part of the total variance, interestingly most of it occurred among
22 plots within treatments rather than between treatments. This corroborates the findings of
23 Albert *et al.* (2010) that the most important proportion of the intraspecific variance of LDMC
24 occurred at a fine spatial scale rather than between different locations along strong abiotic
25 gradients. The high level of intraspecific variance within treatments can be related to the high

1 fine-scale soil heterogeneity due to irregularities of the bedrock surface in the study area.
2 (Fridley *et al.* 2011). The low intraspecific variance between treatments suggests that the level
3 of intraspecific variability involved in the response to drought did not exceed the level that is
4 usually expressed in response to spatial environmental micro-heterogeneity.

5 The drought treatment induced significant intraspecific trait responses over all species.
6 The directions of these responses are consistent with expectations regarding plant drought
7 tolerance. High LDMC and LCC and low SLA are related to high investment in structural
8 tissues, which allows plants to maintain leaf turgor under drought stress (Niinemets 2001;
9 Chaves *et al.* 2002). However, the analysis of each species independently revealed that only
10 20% of the studied species showed significant intraspecific variability for SLA, LNC and
11 LCC in response to drought. This result is consistent with studies in which few or no
12 significant species responses were found in leaf traits following a simulated drought
13 (Weißhuhn *et al.* 2011). Moreover, the intraspecific trait responses varied in direction among
14 species. This between-species idiosyncratic pattern corroborates previous studies exploring
15 trait-environment relationships (Albert *et al.* 2010; Kichenin *et al.* 2013). It may arise from
16 two main different causes. First, this can be explained by the expression of different
17 functional trade-offs between traits. Indeed, species can combine trait responses in different
18 ways to cope with drought (Marks & Lechowicz 2006; West *et al.* 2012), which can result in
19 a lack of convergent responses of a given trait among species. Second, trait values, as
20 determinants of individual plant performances, may be used as a surrogate for species niche
21 (Violle & Jiang 2009; Kearney *et al.* 2010). According to this framework, trait values of a
22 given species are expected to follow a bell-shaped response curve along environmental
23 gradients (Violle *et al.* 2007). Therefore the intraspecific trait response to drought can vary
24 depending on whether drought moves species closer or away from their ecological optimum
25 (Albert *et al.* 2010).

1 *Community functional response to drought*

2 The variation in community mean traits revealed significant responses for LDMC, LCC and
3 SLA. Despite the low magnitude of intraspecific variability compared to interspecific trait
4 differences, intraspecific variability contributes significantly and sometimes much more than
5 species turnover to the community functional response to drought. For LDMC and SLA,
6 intraspecific variability amplified the community response mediated by species turnover, and
7 the response of community mean LDMC was significant only when accounting for
8 intraspecific variability. This result was even more marked for LCC, for which the increase in
9 community mean was entirely due to intraspecific variability.

10 Conversely, for LNC, the significant decrease in community mean trait mediated by
11 species turnover was dampened by the effect of intraspecific variability. Opposite
12 contributions of species turnover and intraspecific variability to community mean LNC have
13 been recently observed along an elevation gradient (Kichenin *et al.* 2013). In our study,
14 despite a significant intraspecific increase in LNC over all species, several low-LNC species
15 (e.g. *Festuca laevigata* or *Cerastium arvense*, L.) increased their relative abundance and high-
16 LNC species (e.g. *Trifolium pratense*, L.) decreased their relative abundance in response to
17 drought. The decrease in community mean LNC mediated by species turnover can be
18 interpreted as a filtering effect of drought that favours species with low resource acquisition
19 strategy (i.e. 'conservative' species, Reich *et al.* 1999). However, the intraspecific increase in
20 LNC suggests the existence of physiological mechanisms that allow plants to maintain
21 resource acquisition during drought (Weih *et al.* 2011). This result is consistent with previous
22 findings that phenotypic plasticity tends to maximize resource acquisition in the short term
23 (Ryser & Eek 2000), and supports the idea that phenotypic plasticity can differ from
24 genetically determined interspecific trait differences (Ryser & Eek 2000; Valladares &
25 Sánchez-Gómez 2006).

1 It is important to point out that the low and not significant contribution of species
2 turnover to the change in community mean LDMC and LCC cannot be explained by the fact
3 that the observed level of species turnover over the short time period of the experiment was
4 too low to make a more important contribution. Indeed, we demonstrated that given the
5 observed levels of species turnover and of interspecific trait differences, one might have
6 expected (with a probability of 0.60 and 0.90 for LDMC and LCC, respectively) a much
7 greater contribution of species turnover to the community functional response. The low
8 contribution of species turnover to the changes in community weighted mean is due to a lack
9 of covariation with interspecific trait differences (Lep *et al.* 2011). For example, the
10 increasing abundance of high-LDMC species (e.g. *Festuca laevigata*) was counterbalanced by
11 the increasing abundance of low-LDMC species (e.g. *Cerastium arvense*), resulting in
12 antagonist effects on community mean LDMC. Thus, the relative contribution of inter- and
13 intraspecific variability in the community response to drought depends on the way they are
14 distributed with respect to species abundances and turnover. This finding provides strong
15 support for the emerging view that whether intraspecific variability matters in community
16 ecology does not only depend on its intensity (Albert *et al.* 2012).

17 Our results report a key role of intraspecific variability to a short-term drought event,
18 thus providing more evidence for the importance of intraspecific variability in the functional
19 response of plant communities to spatial and temporal environmental heterogeneity. Such
20 strong effect of intraspecific variability has already been reported along a narrow spatial
21 gradient of flooding (Jung *et al.* 2010). On the other hand, several studies have shown that
22 trait shifts mediated by species turnover play a strong structuring role among communities
23 located along broad environmental gradients (Ackerly & Cornwell 2007; Kichenin *et al.*
24 2013). Intraspecific variability may thus play a dominant role at short spatial and temporal
25 scales. This would fit within a recent theoretical framework proposing a spatial scale-

1 dependence of the importance of intra- vs. interspecific trait variability (Albert *et al.* 2012).
2 Intra- and interspecific responses could thus play complementary roles through time and
3 space scales from the short-term changes to the long-term changes (Smith *et al.* 2009; Sandel
4 *et al.* 2010), illustrating the necessity to examine both components of community trait
5 variability in order to better understand the response of trait averages to environmental
6 variability (Lep *et al.* 2011). The high contribution of intraspecific variability in the temporal
7 changes in community mean traits suggests that intraspecific variability can provide the
8 potential for communities to respond rapidly and reversibly to drought events through plastic
9 adjustments. In this way, intraspecific variability can promote the short-term stability of plant
10 communities' species composition (Lloret *et al.* 2012) by leading to drought adjustment
11 without requiring a strong species turnover.

12

13 *Implications*

14 Increasing recurrence of extreme weather events is an important component of climate change
15 (Easterling *et al.* 2000; IPCC 2007). Most previous climate-changes studies using trait-based
16 approaches have ignored intraspecific variability, relying on the assumption that intraspecific
17 variability is much lower than between-species trait differences that underlie trait shifts due to
18 species turnover. Analysing changes in community mean traits without accounting for
19 intraspecific variability (e.g. by using species trait values provided by trait databases, e.g.
20 Kattge *et al.* 2011) can tremendously underestimate – or even wrongly estimate – the
21 response of communities to extreme drought events. We advocate for a better inclusion of
22 intraspecific variability into climate-change experiments that use functional traits to
23 understand the impact of extreme events on plant communities (Nicotra *et al.* 2011).
24 Modelling approaches making future projections (Scheiter & Higgins 2009; Kearney & Porter
25 2009; McMahon *et al.* 2011) could also benefit from more attention to intraspecific

1 variability. Indeed, changes in species composition under climate change can be
2 overestimated if models do not allow for species adjustment through intraspecific variability.

3 Our study underlines the role of intraspecific variability as a potentially stabilizing
4 process of plant communities after drought events. However, such stability of community
5 composition does not imply stability in ecosystem processes. Indeed, there is a growing
6 consensus that ecosystem processes are related to functional rather than species diversity
7 (Díaz & Cabido 2001). Therefore the effect of drought on ecosystem processes should be
8 more important than expected from the simple analyses of species turnover, as community
9 trait changes are mainly driven by intraspecific variability. Further studies are needed to
10 evaluate the extent to which drought would indirectly affect ecosystem processes through
11 community functional response mediated by intraspecific variability.

12

13

1 **Acknowledgments**

2 This research was conducted on the long term research site Zone Atelier Alpes, a member of
3 the ILTER-Europe network. ZAA publication n° xxx. We are grateful to P.-E. Biron and to B.
4 Fourgous for access to the study area, and to G. Consoli, C. Bernard-Brunet, G. Favier, N.
5 Daumergue and C. Arnoldi for field and laboratory assistance. We thank two anonymous
6 referees as well as the Handling Editor for constructive comments on the manuscript. Marie
7 Curie International Outgoing Fellowships within the 7th European Community Framework
8 Program were supporting C.H.A. (DYVERSE project, no. 272284) and G.K. (Demo- traits
9 project, no. 299340).

10

11 **SUPPORTING INFORMATION**

12 Additional supporting information may be found in the online version of this article:

13

14 **Table S1** Relative abundances of the studied species recorded in control plots and in drought
15 plots.

16 **Fig S1** Positioning of the simulated drought on the frequency distribution of the observed
17 (1952-2009) and projected (2050-2100) June-July cumulated precipitation in the study site.

18

19

20

1 **References**

- 2 Ackerly, D.D. (2004) Functional traits of chaparral shrubs in relation to seasonal water deficit
3 and disturbance. *Ecological Monographs*, **74**, 25-44.
- 4 Albert, C.H., Thuiller, W., Yoccoz, N.G., Soudan, A., Boucher, F., Saccone, P. & Lavorel, S.
5 (2010) Intraspecific functional variability: extent, structure and sources of variation within
6 an alpine valley. *Journal of Ecology*, **98**, 604-613.
- 7 Albert, C.H., de Bello, F., Boulangeat, I., Pellet, G., Lavorel, S. & Thuiller, W. (2012) On the
8 importance of intraspecific variability for the quantification of functional diversity. *Oikos*,
9 **121**, 116-126.
- 10 Andersen, K.M., Endara, M.J., Turner, B.L. & Dalling, J.W. (2012) Trait-based community
11 assembly of understory palms along a soil nutrient gradient in a lower montane tropical
12 forest. *Oecologia*, **168**, 519-531.
- 13 Buckland, S.M., Grime, J.P., Hodgson, J.G. & Thompson, K. (1997) A comparison of plant
14 responses to the extreme drought of 1995 in Northern England. *Journal of Ecology*, **85**,
15 875-882.
- 16 Chase, J.M. (2007) Drought mediates the importance of stochastic community assembly.
17 *Proceedings of the National Academy of Sciences USA*, **104**, 17430-17434.
- 18 Chaves, M.M., Pereira, J.S., Maroco, J., Rodrigues, M.L., Ricardo, C.P.P., Osorio, M.L.,
19 Carvalho, I., Faria, T. & Pinheiro, C. (2002) How plants cope with water stress in the
20 field: photosynthesis and growth. *Annals of Botany*, **89**, 907-916.
- 21 Cornwell, W.K. & Ackerly, D.D. (2009) Community assembly and shifts in the distribution
22 of functional traits values across an environmental gradient in coastal California.
23 *Ecological Monographs*, **79**, 109-126.
- 24 Díaz, S. & Cabido, M. (2001) Vive la difference: Plant functional diversity matters to
25 ecosystem processes. *Trends in Ecology and Evolution*, **16**, 646-655.

- 1 Easterling, D.R., Meehl, G.A., Parmesan, C., Changnon, S.A., Karl, T.R. & Mearns, L.O.
2 (2000) Climate extremes: observations, modeling, and impacts. *Science*, **289**, 2068-2074.
- 3 Evans, S.E., Byrne, K.M., Lauenroth, W.K. & Burke, I.C. (2011) Defining the limit to
4 resistance in a drought-tolerant grassland: long-term severe drought significantly reduces
5 the dominant species and increases ruderals. *Journal of Ecology*, **99**, 1500-1507.
- 6 Fridley, J.D., Grime, J.P., Askew, A.P., Moser, B. & Stevens, C.J. (2011) Soil heterogeneity
7 buffers community response to climate change in species-rich grassland. *Global Change*
8 *Biology*, **17**, 2002-2011.
- 9 Garnier, E., Shipley, B., Roumet, C. & Laurent, G. (2001a) A standardized protocol for the
10 determination of specific leaf area and leaf dry matter content. *Functional Ecology*, **15**,
11 688-695.
- 12 Garnier, E., Laurent, G., Bellmann, A., Debain, S., Berthelie, P., Ducout, B., Roumet, C. &
13 Navas, M.-L. (2001b) Consistency of species ranking based on functional leaf traits. *New*
14 *Phytologist*, **152**, 69-83.
- 15 Garnier, E., Cortez, J., Billès, G., Navas, M.-L., Roumet, C., Debussche, M., Laurent, G.,
16 Blanchard, A., Aubry, D., Bellmann A., Neill C. & Toussaint J.-P. (2004) Plant functional
17 markers capture ecosystem properties during secondary succession. *Ecology*, **85**, 2630-
18 2637.
- 19 Grime, J.P., Fridley, J.D., Askew, A.P., Thompson, K., Hodgson, J.G. & Bennett, C.R. (2008)
20 Long-term resistance to simulated climate change in an infertile grassland. *Proceedings of*
21 *the National Academy of Science*, **105**, 10028-10032.
- 22 Helmuth, B., Kingsolver, J.G. & Carrington, E. (2005) Biophysics, physiological ecology,
23 and climate change: does mechanism matter? *Annual Review of Physiology*, **67**, 177-201.

- 1 Hudson, J.M.G., Henry, G.R.H. & Cornwell, W.K. (2011) Taller and larger: shifts in Arctic
2 tundra leaf traits after 16 years of experimental warming. *Global Change Biology*, **17**,
3 1013-1021.
- 4 IPCC (2007) *Climate change 2007: The Physical Science Basis. Contribution of Working*
5 *Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate*
6 *Change*. Cambridge University Press, Cambridge, UK.
- 7 Jentsch, A., Kreyling, J. & Beierkuhnlein, C. (2007) A new generation of climate-change
8 experiments: Events, not trends. *Frontiers in Ecology and the Environment*, **5**, 365-374.
- 9 Jump, A.S. & Peñuelas, J. (2005) Running to stand still: adaptation and the response of plants
10 to rapid climate change. *Ecology Letters*, **8**, 1010-1020.
- 11 Jung, V., Violle, C., Mondy, C., Hoffmann, L. & Muller, S. (2010) Intraspecific variability
12 and trait-based community assembly. *Journal of Ecology*, **98**, 1134-1140.
- 13 Kattge, J., Díaz, S., Lavorel, S., Prentice, I.C., Leadley, P. *et al.* (2011) TRY – a global
14 database of plant traits. *Global Change Biology*, **17**, 2905-2935.
- 15 Kearney, M. & Porter, W. (2009) Mechanistic niche modelling: combining physiological and
16 spatial data to predict species' ranges. *Ecology Letters*, **12**, 334-350.
- 17 Kearney, M., Simpson, S.J., Raubenheimer, D. & Helmuth, B. (2010) Modelling the
18 ecological niche from functional traits. *Philosophical Transactions of the Royal Society B*,
19 **365**, 3469-3483.
- 20 Kichenin, E., Wardle, D.A., Peltzer, D.A., Morse, C.W. & Freschet, G.T. (2013) Contrasting
21 effects of plant inter- and intraspecific variation on community-level trait measures along
22 an environmental gradient. *Functional Ecology*, **27**, 1254-1261.
- 23 Klotz, S., Kühn, I. & Durka, W. (2002) BIOLFLOR – Eine Datenbank zu biologisch-
24 ökologischen Merkmalen der Gefäßpflanzen in Deutschland. *Schriftenreihe für*
25 *Vegetationskunde*, **38**. Bundesamt für Naturschutz, Bonn.

- 1 Kreyling, J., Jentsch, A. & Beierkuhnlein, C. (2011) Stochastic trajectories of succession
2 initiated by extreme climatic events. *Ecology Letters*, **14**, 758-764.
- 3 Lavorel, S., Grigulis, K., McIntyre, S., Garden, D., Williams, N., Dorrough, J., Berman, S.,
4 Quétier, F., Thébault, A., & Bonis, A. (2008) Assessing functional diversity in the field –
5 methodology matters! *Functional Ecology*, **22**, 134-147.
- 6 Lep , J., de Bello, F., milauer, P. & Dole al, J. (2011) Community trait response to
7 environment: disentangling species turnover vs intraspecific trait variability effects.
8 *Ecography*, **34**, 856-863.
- 9 Levy, E.B. & Madden, E.A. (1933) The point method of pasture analysis. *New Zealand*
10 *Journal of Agriculture*, **46**, 267-279.
- 11 Lloret, F., Escudero, A., Iriondo, J.M., Martínez-Vilalta, J. & Valladares, F. (2012) Extreme
12 climatic events and vegetation: the role of stabilizing processes. *Global Change Biology*,
13 **18**, 797-805.
- 14 Marks, C.O. & Lechowicz, M.J. (2006) Alternative designs and the evolution of functional
15 diversity. *American Naturalist*, **167**, 55-67.
- 16 McMahon, S.M., Harrison, S.P., Armbruster, W.S., Bartlein, P.J., Beale, C.M., Edwards,
17 M.E., Kattge, J., Midgley, G., Morin, X. & Prentice, I.C. (2011) Improving assessment
18 and modelling of climate change impacts on global terrestrial biodiversity. *Trends in*
19 *Ecology & Evolution*, **26**, 249-259.
- 20 Meehl, G.A. & Tebaldi, C. (2004) More intense, more frequent, and longer lasting heat waves
21 in the 21st century. *Science*, **305**, 994-997.
- 22 Messier, J., McGill, B.J. & Lechowicz, M.J. (2010) How do traits vary across ecological
23 scales? A case for trait-based ecology. *Ecology Letters*, **13**, 838-848.

- 1 Nicotra, A.B. , Atkin, O.K. , Bonser, S.P., Davidson, A.M., Finnegan, E.J., Mathesius, U.,
2 Poot, P., Purugganan, M.D., Richards C.L., Valladares F. & van Kleunen, M. (2011) Plant
3 phenotypic plasticity in a changing climate. *Trends in Plant Science*, 15, 684-692.
- 4 Niinemets, U. (2001) Global-scale climatic controls of leaf dry mass per area, density, and
5 thickness in trees and shrubs. *Ecology*, **82**, 453-469.
- 6 Pakeman, R.J. & Quested, H.M. (2007) Sampling plant functional traits: what proportion of
7 the species need to be measured? *Applied Vegetation Science*, **10**, 91-96.
- 8 Poorter, H., Niinemets, Ü., Poorter, L., Wright, I.J. & Villar, R. (2009) Causes and
9 consequences of variation in leaf mass per area (LMA): a meta-analysis. *New Phytologist*,
10 **182**, 565-588.
- 11 R Development Core Team (2010) *R: A Language and Environment for Statistical*
12 *Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- 13 Reich, P.B., Ellsworth, D.S., Walters, M.B., Vose, J.M., Gresham, C., Volin, J.C. & Bowman,
14 W.D. (1999) Generality of leaf trait relationships: a test across six biomes. *Ecology*, **80**,
15 1955-1969.
- 16 Ryser, P. & Eek, L. (2000) Consequences of phenotypic plasticity vs. interspecific differences
17 in leaf and root traits for acquisition of aboveground and belowground resources.
18 *American Journal of Botany*, **87**, 402-411.
- 19 Sandel, B., Goldstein, L.J., Kraft, N.J.B., Okie, J.G., Shuldman, M.I., Ackerly, D.D., Cleland,
20 E.E. & Suding, K.N. (2010) Contrasting trait responses in plant communities to
21 experimental and geographic variation in precipitation. *New Phytologist*, **188**, 565-575.
- 22 Scheiter, S. & Higgins, S.I. (2009) Impacts of climate change on the vegetation of Africa: an
23 adaptive dynamic vegetation modelling approach. *Global Change Biology*, **15**, 2224-
24 2246.

- 1 Smith, M.D. (2011) The ecological role of climate extremes: current understanding and future
2 prospects. *Journal of Ecology*, **99**, 651-655.
- 3 Smith, M.D., Knapp, A.K. & Collins, S.L. (2009) A framework for assessing ecosystem
4 dynamics in response to chronic resource alterations induced by global change. *Ecology*,
5 **90**, 3279-3289.
- 6 Theurillat, J.-P. & Guisan, A. (2001) Potential impact of climate change on vegetation in the
7 European Alps: a review. *Climatic Change*, **50**, 77-109.
- 8 Valladares, F. & Sánchez-Gómez, D. (2006) Ecophysiological traits associated with drought
9 in Mediterranean tree seedlings: Individual responses versus interspecific trends in eleven
10 species, *Plant Biology*, **8**, 688-697.
- 11 Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I. & Garnier, E.
12 (2007) Let the concept of trait be functional! *Oikos*, **116**, 882-892.
- 13 Violle, C. & Jiang, L. (2009) Towards a trait-based quantification of species niche. *Journal of*
14 *Plant Ecology*, **2**, 87-93.
- 15 Violle, C., Enquist, B.J., McGill, B.J., Jiang, L., Albert, C.H., Hulshof, C., Jung, V. &
16 Messier, J. (2012) The return of the variance: intraspecific variability in community
17 ecology. *Trends in Ecology and Evolution*, **27**, 244-252.
- 18 Volaire, F. (2008) Plant traits and functional types to characterise drought survival of pluri-
19 specific perennial herbaceous swards in Mediterranean areas. *European Journal of*
20 *Agronomy*, **29**, 116-124.
- 21 Weih, M., Bonosi, L., Ghelardini, L. & Rönnerberg-Wästljung, A.C. (2011) Optimizing
22 nitrogen economy under drought: increased leaf nitrogen is an acclimation to water stress
23 in willow (*Salix* spp.). *Annals of Botany*, **108**, 1347-1353.
- 24 Weißhuhn, K., Auge, H. & Prati, D. (2011) Geographic variation in the response to drought in
25 nine grassland species. *Basic and Applied Ecology*, **12**, 21-28.

- 1 West, A.G., Dawson, T.E., February, E.C., Midgley, G.F., Bond, W.J. & Aston, T.L. (2012)
2 Diverse functional responses to drought in a mediterranean-type shrubland in South
3 Africa. *New Phytologist*, **195**, 396-407.
- 4 Wright, I.J., Reich, P.B. & Westoby, M. (2001) Strategy shifts in leaf physiology, structure
5 and nutrient content between species of high- and low-rainfall and high- and low-nutrient
6 habitats. *Functional Ecology*, **15**, 423-434.
- 7

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21

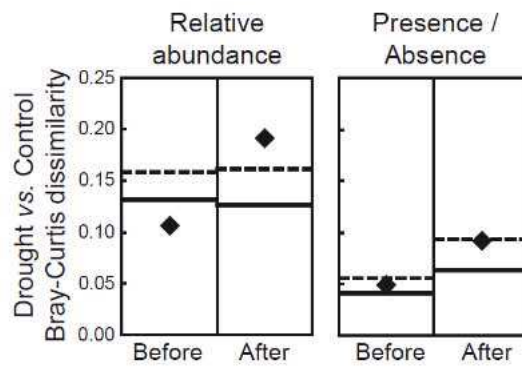


Fig 1 Bray-Curtis dissimilarity between drought plots and control plots before and after the simulated drought event, calculated from relative abundance data (left) and from presence/absence (right). Diamonds indicate observed Bray-Curtis dissimilarity values; solid and dotted lines indicate respectively the median and the 95% percentile of a null distribution obtained from 10000 permutations.

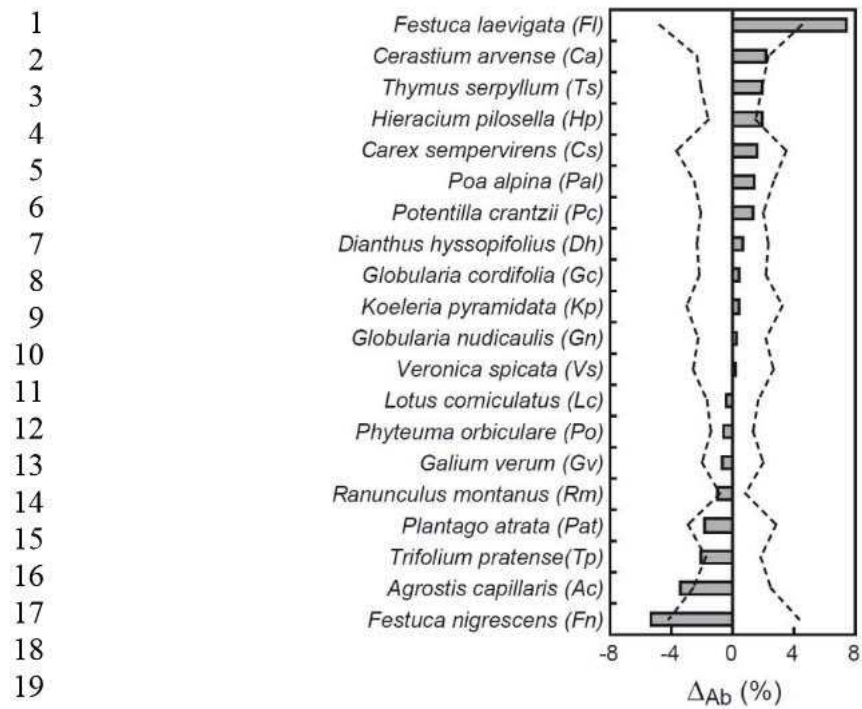


Fig 2 Difference in the relative abundance (ΔAb) of each species in control vs. drought plots. Bars indicate the observed differences and dotted lines indicate the 2.5% and 97.5% percentiles of a null distribution obtained from 10000 permutations. Species are ordered according to their change in relative abundance. Only the 20 most abundant species are shown, i.e. the species on which leaf traits were measured.

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17

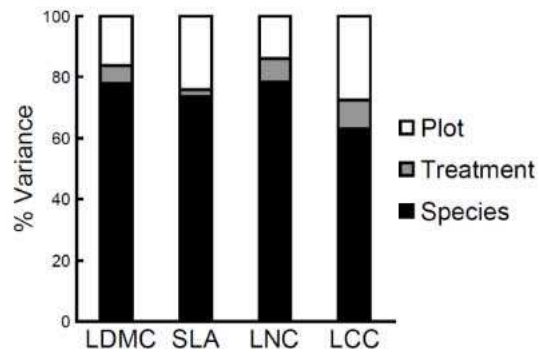


Fig 3 Relative variance decomposition of leaf dry matter content (LDMC), specific leaf area (SLA), leaf nitrogen concentration (LNC) and leaf carbon concentration (LCC) at the plot (i.e. intraspecific trait variability within treatments), treatment (i.e. intraspecific trait variability between treatments) and species (i.e. between-species trait variability) levels.

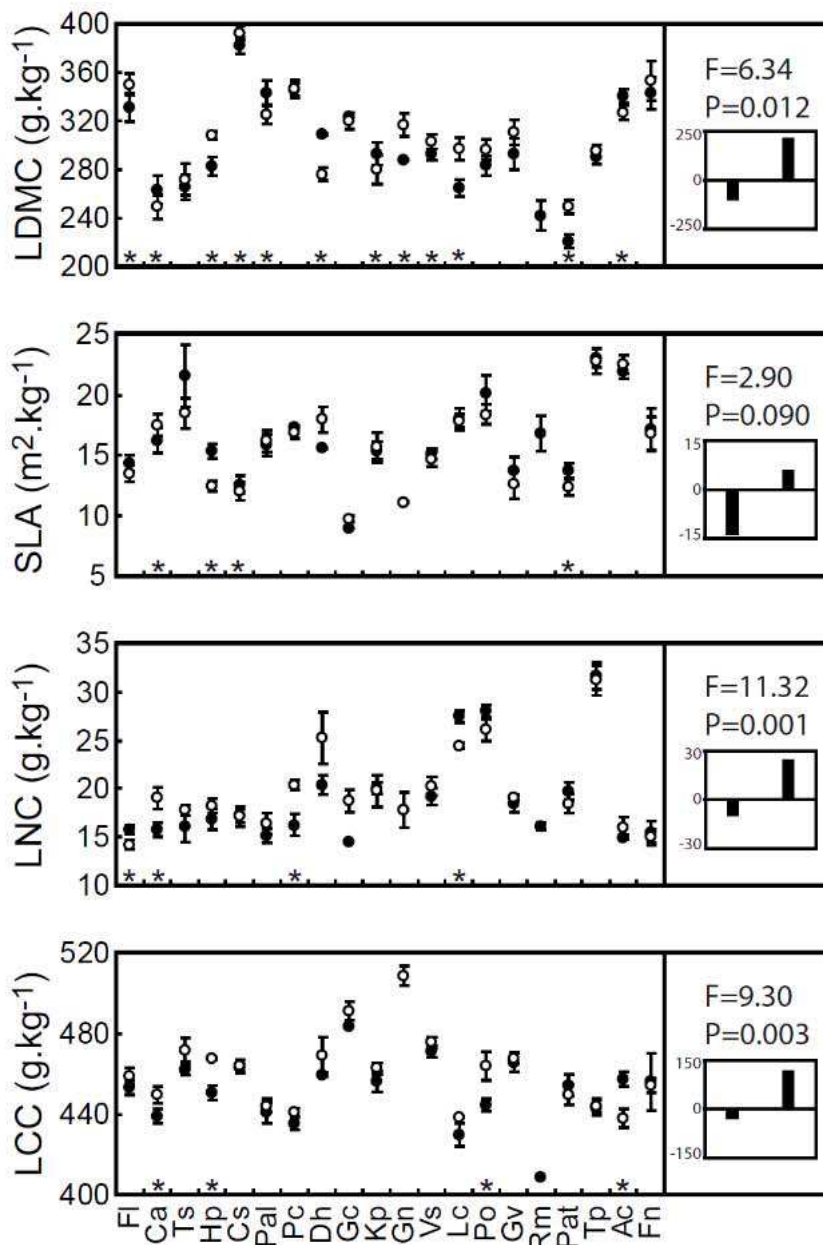


Fig 4 Leaf trait responses to drought for each species. Data are means \pm standard deviations of leaf dry matter content (LDMC), specific leaf area (SLA), leaf nitrogen concentration (LNC) and leaf carbon concentration (LCC) in control plots (closed symbols) and in drought plots (open symbols). Species are ordered in the same way as in Fig. 2, i.e. in decreasing order of their change in relative abundance (see Fig. 2 for species names). Asterisks indicates significant differences between drought plots and control plots ($P < 0.05$) for each species. Insets at the right of each graph represent the cumulated decrease (left bar) and increase (right bar) of trait values over all species in response to drought, and therefore indicate the prevailing trends of trait responses. The statistical results for the effect of drought over all species are given above the insets.

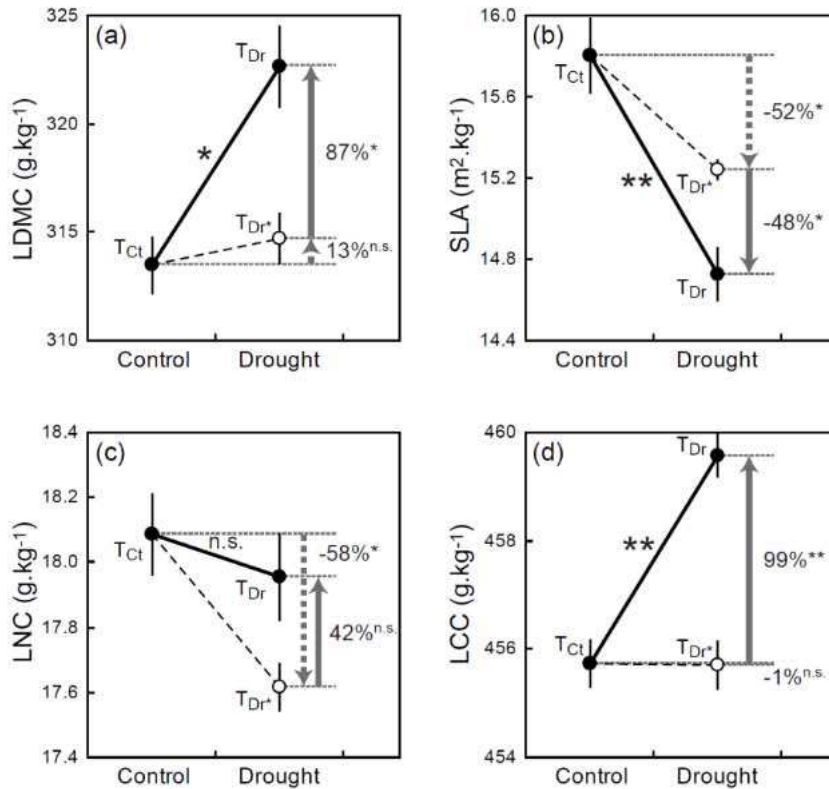
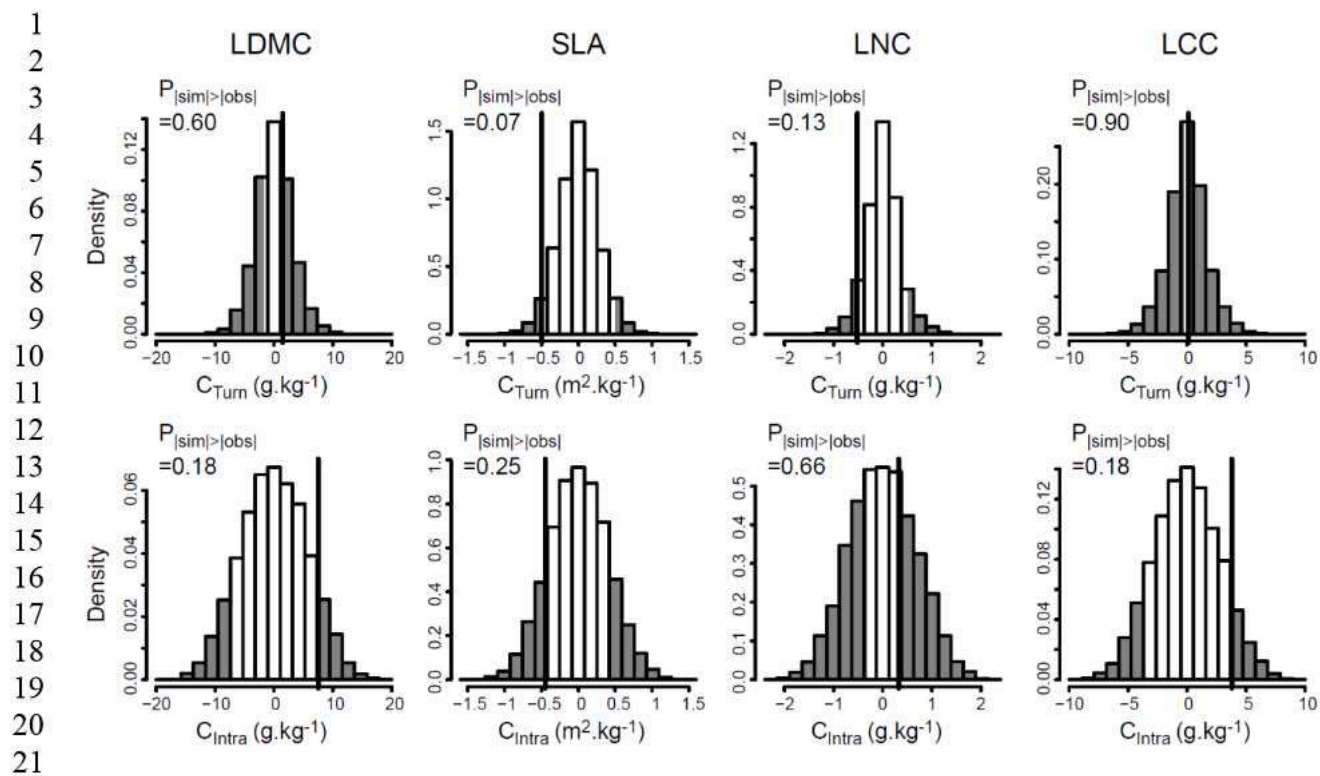


Fig 5 Changes in community weighted mean trait values due to both species turnover and intraspecific variability (solid line) and due to species turnover only (dashed line). T_{Ct} and T_{Dr} correspond to the observed community mean traits in control plots and in drought plots; T_{Dr}^* corresponds to the community mean trait in drought plots recalculated from trait values measured in control plots. Data are means \pm standard errors of community means of LDMC (a), SLA (b), LNC (c) and LCC (d). Arrows indicate the contributions of species turnover (C_{Turn} ; dashed-line arrows) and of intraspecific variability (C_{Intra} ; solid-line arrows) to the changes in community mean traits. C_{Turn} and C_{Intra} are expressed as percentages of their cumulative magnitude (Significance levels: * $P < 0.05$, ** $P < 0.01$, n.s. not significant).



22 **Fig 6** Observed vs. simulated contribution of species turnover (C_{Turn}) and of intraspecific
 23 variability (C_{Intra}) to the change in community mean LDMC, SLA, LNC and LCC in response
 24 to drought. Each histogram represents the distribution of 10000 simulated values of C_{Turn} or of
 25 C_{Intra} , resulting from random reallocations of species traits to species abundances. Thick lines
 26 indicate the observed contributions of turnover or of intraspecific variability. For each graph,
 27 the shaded area (and the associated proportion $P_{|sim|>|obs|}$) indicates the portion of the
 28 distribution where the simulated contributions are higher, in magnitude, than the observed
 29 contribution.

30

Figure S1

Positioning of the simulated drought on the frequency distribution of the observed (1952-2009) and projected (2050-2100) June-July cumulated precipitation in the study site.

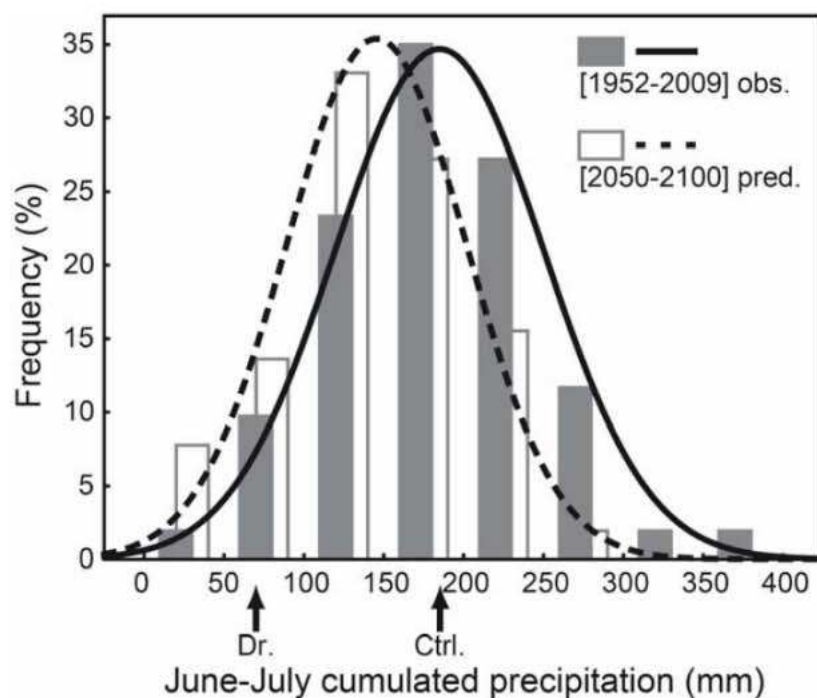


Figure S1 Frequency distribution of the observed June-July cumulated precipitation in the study site observed over the 1952-2009 period (data: Météo-France, grey) and predicted for the 2050-2100 period under the B1 scenario (Hadley Centre model HADCM3, white). Curves correspond to fitted normal distributions. Precipitations simulated in the control (Ctrl.) and the dry (Dr.) treatments are indicated on the x axis.

Table S1

Relative abundances of the studied species recorded in control plots and in drought plots.

Table S1 Relative abundances of the species sampled for trait measurements, in control plots and in drought plots during the second survey (15-16 July 2010, after the simulated drought event).

Species	Relative abundance (%)	
	Control	Drought
<i>Carex sempervirens</i>	14,0	15,0
<i>Festuca laevigata</i>	12,9	19,9
<i>Festuca nigrescens</i>	12,1	6,1
<i>Plantago atrata</i>	9,3	7,0
<i>Koeleria pyramidata</i>	7,4	7,6
<i>Veronica spicata</i>	6,9	6,7
<i>Agrostis capillaris</i>	6,5	2,7
<i>Galium verum</i>	4,7	3,7
<i>Cerastium arvense</i>	4,0	6,1
<i>Trifolium pratense</i>	3,9	1,7
<i>Potentilla crantzii</i>	3,3	4,6
<i>Poa alpina</i>	3,2	4,5
<i>Lotus corniculatus</i>	2,6	2,0
<i>Dianthus hyssopifolius</i>	2,0	2,6
<i>Phyteuma orbiculare</i>	1,6	1,0
<i>Thymus serpyllum</i>	1,6	3,5
<i>Globularia cordifolia</i>	1,2	1,6
<i>Globularia nudicaulis</i>	1,2	1,3
<i>Ranunculus montanus</i>	1,1	0,0
<i>Hieracium pilosella</i>	0,5	2,4