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RESEARCH ARTICLE

Species stress tolerance and community competitive effects drive differences in species composition between calcareous and siliceous plant communities

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Abstract

1. Both chemical and physical properties of soils have been used for two centuries for explaining differences in species composition and diversity between plant communities from calcareous and siliceous soils. Here, we examine the prediction from the 'physical hypothesis', which proposes that species from siliceous soils are absent from calcareous soils because of high drought stress, while species from calcareous soils are absent from siliceous soils because of high competition due to higher water availability. This hypothesis therefore predicts a trade-off between stress tolerance and competitive response that allows calcareous and siliceous species to dominate their respective communities. There has been no attempt to experimentally assess these predictions.
2. We cross-transplanted with and without neighbours using a removal experiment, two dominant species from calcareous soils (*Bromus erectus* and *Brachypodium sylvaticum*) and two species from siliceous soils (*Pseudarrhenatherum longifolium* and *Deschampsia flexuosa*) in herbaceous communities from the two soils types. We repeated the experiment 4 years, taking advantage of inter-annual climatic variability to test the interplay between year quality (dry vs. wet years) and soil types on survival responses with and without neighbours. We quantified species stress tolerances, their competitive responses and the competitive effect of the two community types.
3. In the absence of neighbours, species from siliceous soils had much lower survival than species from calcareous soils during dry years, in particular on calcareous soils. It indicates a lower stress tolerance of siliceous species and a higher level of stress occurring on calcareous soils. Competition strongly reduced the survival of calcareous but not siliceous species, indicating a greater competitive response of the latter and competition was more important on siliceous soils than on calcareous soils during wet years. However, we found that species stress tolerances were more important than competitive effect of neighbours in driving differences in species composition.
4. *Synthesis*. The contrasting responses found for dominant species from calcareous and siliceous soils support the trade-off between stress tolerance and competitive

response proposed by the physical hypothesis. Our results bring additional evidence that differences in water availability and stress between the two soil types are driving species responses to bedrock types.

KEYWORDS

calcareous soils, climate variability, competitive effects, competitive responses, drought stress, siliceous soils, stress tolerance

1 | INTRODUCTION

Edaphic factors (e.g. water and nutrient availability, soil chemistry, soil texture, etc.) related to substrate types are known to be strongly correlated with community composition and species distribution, although causal relationships are not always identified (Austin & Smith, 1989; Whittaker, 1956). For example, Chauvier et al. (2021) showed that the contribution of soil and land cover on species distribution in the European Alps was as large as climate. However, since edaphic factors are known to interact with other complex environmental variables such as climate (e.g. Chaieb et al., 2020; Liancourt et al., 2013), they are likely to amplify or buffer the effect of climate. Thus, identifying the mechanisms by which edaphic factors interact with climate is therefore necessary for addressing the role of soils and substrate type for community composition.

Contrasting species composition of plant communities occurring on soils derived from calcareous and siliceous substrates has raised the attention of botanists, physiologists and ecologists, in particular in Europe, for almost 200 years (Bothe, 2015; Braun-Blanquet, 1964; Ellenberg, 1958; Gigon, 1987; Kinzel, 1983; Lee, 1999; Michalet et al., 2002; Thurmann, 1849; Unger, 1836). The work of Braun-Blanquet and Jenny (1926) has largely contributed to the wide acceptance of the idea among European scientists that this difference in species composition was mainly due to differences is soil chemistry. This is particularly the case for alpine communities due to the high correlation existing between pH, calcium and aluminium contents in soils and bedrock types (Duchaufour, 1997; Gensac, 1990; Reisigl & Keller, 1987).

This chemical hypothesis was further developed by Duchaufour (1989, 1997) in the context of the wet climate of the north-east of France. Briefly, he argued that soils derived from siliceous bedrocks have low pH (acidic) and clay content. These soil characteristics, leading to slow organic matter decomposition, low nutrient and high exchangeable aluminium contents, are considered as unfavourable for species from calcareous and neutral soils (Pinto & Gégout, 2005; Rameau et al., 1989).

However, the chemical hypothesis fails at fully explaining several empirical observations. For instance, the basis of the chemical hypothesis, the differences in organic matter decomposition between acidic and neutral soils, is not consistent with overwhelming evidence that have shown that litter quality and climate (and not soil chemistry) are the most important drivers of litter decay in terrestrial ecosystems (Cornwell et al., 2008; Coûteaux et al., 1995). It suggests that pH is more likely the consequence of organic matter accumulation than its driver (Michalet et al., 2001). Moreover, species pH optima and amplitudes have been shown to vary geographically (Coudun & Gégout, 2005; Diekmann & Lawesson, 1999; Pakeman et al., 2008; Petřik & Bruelheide, 2006; Szymura et al., 2014), and the aforementioned tolerance to toxicity may only partly explain the pattern in the field. The interactions between soil moisture and pH have also been highlighted (Le Bagousse-Pinguet et al., 2017; Pakeman et al., 2008), suggesting that physical factors related to substrate types (such as water availability) may also drive differences in species and functional composition between communities occurring on siliceous and calcareous bedrocks.

The alternative 'physical hypothesis', first proposed by Thurmann (1849), posits that the physical structure of the substrate drives water percolation beneath the soil profile and soil moisture availability, which in turn determines community composition. Several authors have highlighted that climate and substrate type are complex factors both driving water availability (e.g. Gigon, 1987; Grime & Curtis, 1976), in particular for deep-rooted tree and shrub species that may benefit from the water flow existing at bedrock–soil interface. Although, there could be strong differences in physical structure within either calcareous or siliceous rocks, calcareous soils are overall drier than siliceous soils because of the higher porosity of calcareous bedrocks that induces rapid water percolation within the substrate (Michalet et al., 2001, 2002; Rolland et al., 1998).

Michalet et al. (2002) found at the subalpine belt of the French Alps that water stress on calcareous soils and competition on siliceous soils (due to lower drought stress) were the direct driving factors of richness, composition and structure of both community types. The more 'stress-tolerant' calcareous species may be favoured over 'intolerant to stress' siliceous species on calcareous soils, whereas calcareous species may be excluded in siliceous environments with dense vegetation due to the competitive effects of siliceous species (Gigon, 1971; Michalet et al., 2002; Thurmann, 1849). The existence of a trade-off between responses to stress and competition has important implication in ecological plant theory and has already been shown in contrasting conditions of water and light availability (Liancourt, Callaway, et al., 2005; Smith & Huston, 1989). Such trade-off has also been highlighted for other organisms than plants, such as animals and microbes (Connell, 1978; Dean & Connell, 1987; Garland, 2014; Peterson, 1991; Wissinger et al., 1999; Wood et al., 2018). However, to our knowledge, the implication of such trade-off in driving differences in species composition and diversity

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between calcareous and siliceous communities has never been tested experimentally.

Our main objective in this study is to experimentally disentangle the relative contribution of stress tolerance and competition in determining the differences in plant composition between calcareous and siliceous communities by focusing on the responses of their dominant species. We set-up a field competition experiment in the south-west of France, cross-transplanting with and without neighbours two dominant species from calcareous origin and two dominant species from siliceous origin in two grasslands from the two soils types. For quantifying competition, we used the 'importance of competition index' together with the 'intensity of competition index' (Brooker et al., 2005; Seifan et al., 2010). The former index is particularly adapted to address our question, since it quantifies the relative importance of competition for a target species as compared to other environmental constraints, in particular stress. The latter only quantifies the effect of neighbours on the target species, independent of other environmental effects (Brooker et al., 2005; Corcket et al., 2003; Welden & Slauson, 1986). This experiment was repeated 4 years (2016, 2018, 2019 and 2020) to take advantage of the year-to-year variation in precipitation and evaluate the responses of our target species on the two soil types under 'wet' and 'dry' year conditions. We tested the two main predictions of the physical hypothesis:

1. Calcareous species are more tolerant to stress and less tolerant to competition than siliceous species, and, thus, both species types should respond differently to meteorological variations.
2. Competition is stronger on siliceous than on calcareous soils.

Finally, we expected that species stress tolerance and the difference in competitive effects between the two communities explain equal species distribution on their respective soil type.

2 | MATERIALS AND METHODS

2.1 | Study sites and target species

The study was conducted in the Gironde department, south-west of France. The climate is temperate oceanic with 931 mm of annual precipitation. As for other oceanic climates, winter is the rainiest season and temperatures are mild (the average seasonal winter temperature is 7.1°C; Michalet et al., 2021). Summer is less rainy but not dry (the average seasonal summer temperature is 20.7°C). The Gironde department is particularly adapted to answer our questions since it includes, in similar conditions of climate and topography, two lands having different soils types. The two lands occur at short distance on the two sides of the Garonne River, allowing the replication of soil type treatment in different blocks.

The ecosystems with calcareous soils are located on the Entre-Deux-Mers land, on the east bank of the Garonne River. The land is formed of small hills of less than a 100 m of elevation on a tertiary calcareous bedrock. Soils are deep and fine-textured if topography is not too convex. Soil pH varied between 6 and 7.5, thus not acidic, due to the high content of exchangeable calcium and calcareous sands (between 50% and 60% of $CaCO_3$ in the upper soil horizon). The ecosystems with siliceous soils are located in the Graves land, on the west bank of the Garonne River. The land is at sea level and on flat quaternary terraces of siliceous deposits originating from the weathering of Pyrenean and Central Massif mountain ranges. Soils have a coarse sandy texture with lots of gravel. They are unfertile and acidic with pH lower than 4 (Wang et al., 2020). We selected two community types (one in each of the two soil types) occurring on poorly managed old fields with very low disturbance to avoid the confounding effects of grazing or mowing.

The community type on calcareous soil is a herbaceous shrubland dominated by *Erica scoparia* and *Brachypodium pinnatum*. Other common species are the shrubs *Prunus spinosa*, *Cornus sanguinea* and *Rosa rubiginosa*, and the grass *Bromus erectus*. Species richness is high (up to 25 species per m^2) and community composition is the characteristic of a 'calcareous' vegetation (Rameau et al., 1989). The community type on siliceous soil is a shrubland dominated by *Ericaceae* species (*Erica scoparia*, *Erica arborea*, *Erica cinerea*, *Calluna vulgaris*), the fern *Pteridium aquilinum* and the grass *Pseudarrenatherum elatius*. The average species richness is lower and community composition is the characteristic of a 'siliceous' vegetation (Rameau et al., 1989). We selected four perennial grass species as targets that are common dominant species of either calcareous or siliceous communities from western Europe '*Bromus erectus* (Huds.) Fourr.' and '*Brachypodium sylvaticum* (Huds.) Beauv.' for the former and '*Pseudarrhenatherum longifolium* (Thore.) Rouy.' and '*Deschampsia flexuosa* (L.) Trin.' for the latter. *Bromus erectus* and *Pseudarrhenatherum elatius* are dominant herbaceous species of calcareous and siliceous grasslands and heathlands, respectively, whereas *Brachypodium sylvaticum* and *Deschampsia flexuosa* are dominant herbaceous species of calcareous and siliceous forest understories and hedgerows respectively (Corcket et al., 2003; Michalet et al., 2015; Pagès & Michalet, 2006; Wang et al., 2020).

2.2 | Experimental design

Our field experiment was conducted from early March to late August and was repeated 4 years (2016, 2018, 2019 and 2020). The experimental design included soil type as main plot treatment (calcareous or siliceous soil), and vegetation removal (with or without neighbouring vegetation) and species origin (calcareous or siliceous species) as subplot treatments. Four blocks spaced 10 km apart were placed from upstream to downstream of the Garonne river between Langon (located 50 km south-east of Bordeaux, 44°33′23″N, 0°14′41″W) and Bordeaux (44°48′51″N, 0°32′37″W). Within each of the four blocks, one main plot was located to the east of the river on calcareous soil, and the second main plot was located to the west of the river on siliceous soil. Each year within each main plot, we randomly selected six circular subplots of 1 m^2 for the vegetation

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removal treatment. Above-ground vegetation of half of the subplots was removed by hand. These subplots with no neighbours were kept free from vegetation during the experiment. Each year, we re-established new plots and applied the removal treatment at a slightly different location within each main plot to ensure that removal treatment did not affect our results on the long term (e.g. modification of nutrient dynamics, root decomposition). Tillers of the four target species were harvested in their own communities before transplantation. Finally, three replicates of individuals of each of the four target species originating from calcareous or siliceous soils were transplanted each year in all subplots (with or without neighbours). Each tiller of transplanted individual of the four species had from 2 to 10 leaves. All target individuals were tagged with metal wire and placed at a distance of at least 50 cm from each other within each subplot. In total, 768 transplants were performed in the experiment (4 blocks × 2 soil types × 2 neighbouring conditions × 4 target species × 3 replicates × 4 years).

2.3 | Data collection and analysis

Each year, the survival of all target individuals was determined at the end of the experimental period (August). Survival rate was calculated at the block level in all combinations, per species and neighbour treatments. We did not analyse biomass because survival was too low in some treatments. We took advantage of the 4 years with different meteorological conditions to test the effect of different weather conditions (e.g. precipitation and temperature) on the performance and the outcome of plant–plant interactions in the two soil type conditions and for the species of the two origins. We used a drought index (the Standardized Precipitation Evaporation Index—hereafter 'SPEI') in the central location of our study (44.72N, −0.41W) to characterize meteorological conditions during the study. This drought index is based on the balance between precipitation and potential evapotranspiration and is more suitable than an index based on precipitation only to detect drought episodes compared to an historical background (Vicente-Serrano et al., 2010). The index allows estimates of how dry or wet a month is in comparison to the same month for other years. Corresponding climatic data were obtained on the ClimateDT web tool available at https://ibbr.cnr.it//climate-dt/. ClimateDT downscales historical monthly, seasonal and annual climate variables for any location in the Globe from a 1-km grid dynamically (see Marchi et al., 2020) for the European climate. Additionally, in order to characterize the 4 years as wet or dry climatic years, we calculated for each target species *i* growing without neighbours, per soil type *j*, per year *k* and per block *l* the survival anomaly as follows:

$$\text{Survival anomaly}_{i,j,k,l} = (\text{target}_i\text{survival}_{(\text{Soil type } j\times\text{block } l\times\text{Year } k)} - \text{average target}_i\text{survival}_{(\text{Soil type } j\times\text{block } l,\text{ all years})})/\text{average target}_i\text{survival}_{(\text{Soil type } j\times\text{block } l,\text{ all years})}, \quad (1)$$

For a given species in a given soil type treatment and in a given block, a positive anomaly indicates that the observed survival in the corresponding year is higher than the average of all years considered, while a negative anomaly indicates that survival is lower than the average.

We computed two indices to characterize the intensity (RII) and the importance (Iimp) of plant–plant interactions. To analyse the variation in competition intensity between treatments, we used the relative interaction index 'RII' (Armas et al., 2004). This index is based on the comparison of target performance with and without neighbours:

$$\text{RII} = \frac{P_{+\text{neighbour}} - P_{-\text{neighbour}}}{P_{+\text{neighbour}} + P_{-\text{neighbour}}}. \quad (2)$$

where $P_{+\text{neighbour}}$ and $P_{-\text{neighbour}}$ represent target performances (survival) in the presence and absence of neighbouring vegetation respectively. Values of RII vary between −1 and 1, with negative values stand for competition and positive ones for facilitation.

Competition importance measures the difference in an organism's performance in the presence of neighbours relative to the impact of other factors such as abiotic environment factors (Brooker et al., 2005; Welden & Slauson, 1986). We calculated the importance of interactions using 'Seifan et al., 2010' index 'Iimp', in which the maximum value of plant performance is the highest average survival for each species in all the experiment treatments, in the four blocks and in all the year considered.

$$\text{Thus the importance of competition index is computed as: Iimp} = \frac{N_{\text{imp}}}{|N_{\text{imp}}| + |E_{\text{imp}}|}, \quad (3)$$

where N_{imp} and E_{imp} are the neighbours and environmental contributions to plant performance, respectively, with: $N_{\text{imp}} = P_{+\text{neighbour}} - P_{-\text{neighbour}}$ and $E_{\text{imp}} = P_{-neighbour} + P_{max\pm N}$, where $P_{\max\pm N}$ is the maximum value of plant performance (survival).

2.4 | Statistical analyses

All statistical analyses were done using R software (R Core Team, 2016). Mixed modelling with 'Year nested within Blocks' as a random factor was used in all cases. Dependent variables and model residuals were systematically checked for normality to respect the assumption of linear modelling.

Survival anomalies were compared using a linear mixed-effects model with 'Year', 'Soil type' and 'Origin' and their interactions as fixed factors. We also used one-sample *t*-tests to detect significant deviation of anomaly values from zero. Since results clearly showed that the 4 years of our experiment largely differed in their effects on plant survival (see the results section and Figure 1), 'Year quality' was therefore considered as a factor in the subsequent analyses where 2016 and 2018 were pooled and considered as favourable years ('wet'), and 2019 and 2020 as unfavourable ('dry').

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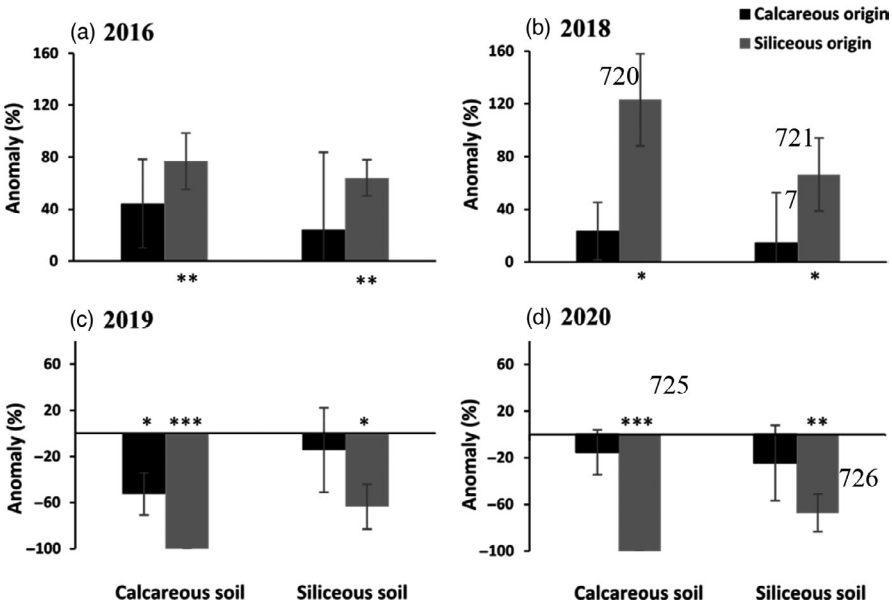

FIGURE 1 Survival anomalies (mean ± *SE*, *n* = 8 – two species for each origin × 4 blocks) for the species of the two origins for the 4 years on calcareous and siliceous soils. Black and grey bars represent species from calcareous and siliceous origin respectively. Results of one-sample *t*-tests are shown above or below bars when significant. (*), $p < 0.1$; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$

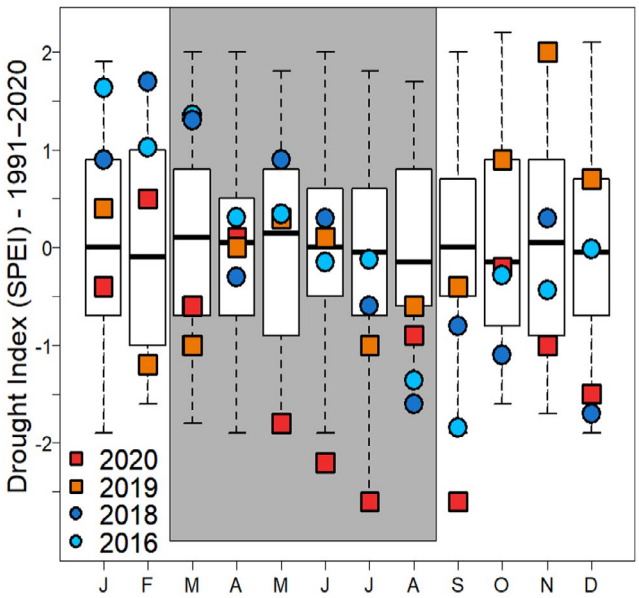

FIGURE 2 Boxplots for Monthly SPEI (Monthly drought index) for the period 1990–2020 in the central location of the study area (44.72N, −0.41W). SPEI values indicate how much dry (negative value) or wet (positive value) a month is compared to the same month during a reference period (1961–1990 on the ClimateDT Tools) considering the balance P-PET. Data for the years of the study are shown (2016: light blue circles; 2018: dark blue circles; 2019: orange squares; and 2020: red squares). Grey area from March to August indicate monitoring period (form initial plant transplantation to final harvest)

We then assessed the effect of the abiotic conditions ('Soil type' and 'Year quality'), alone, that is on the survival of target species growing without neighbours, originating from calcareous and siliceous soils ('Origin'), using a general linear mixed-effects model with a logit link function for binomial distribution. Additionally, planned comparisons among 'Year quality', 'Soil type' and 'Origin' combinations were made using differences in least squares means.

We analysed RII and Iimp separately using linear mixed-effects models (followed by Tukey tests when necessary) with 'Year quality', 'Soil type', 'Origin' and their interactions as fixed factors. We used one-sample *t*-tests to detect significant deviation of RII and Iimp values from zero.

3 | RESULTS

3.1 | Wet and dry years

'Year' had a highly significant effect on survival anomaly, with positive anomalies in 2016 and 2018, and negative in 2019 and 2020 ($p < 0.001$, Tukey results: a, 2016, 52.4 ± 17.8%, a, 2018, 56.9 ± 17.1%, b, 2019, −57.6 ± 12.1%, b, 2020, −51.7 ± 11.5%, Figure 1). SPEI drought index for the 4 years of the study (Figure 2) showed: (a) an important water deficit in February and March in 2019, that is at the time of target transplantation, and a similar water deficit in March 2020 (however less pronounced than in 2019). This was mainly due to a deficit in precipitation (Appendix S1); (b) the end of spring–early summer 2020 (May to July) was the driest of the last 30 years in the area (Figure 2); and (c) spring and early summer (from March to July) in 2016 and 2018 were wetter or close to the median of SPEI drought index of the last 30 years. Thus, the differences in survival anomalies over the 4 years delineating contrasting 'wet' and 'dry' years were likely to be explained by these differences in meteorological conditions. Additionally, there was a significant Year × Origin interaction regarding anomaly responses ($p < 0.01$), because species from siliceous origin were more sensitive to the negative effect of dry years than species from calcareous origin (Tukey results: siliceous origin: a, for 2016, 70.6 ± 12.5% and 2018, 94.8 ± 23.8%, and b, for 2019, −81.8 ± 10.5% and 2020, −83.6 ± 8.84%, calcareous

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origin, a, the 4 years, 2016, 34.2 ± 33.2%, 2018, 19.1 ± 21.3%, 2019, −33.4 ± 20.4%, 2020, −19.85 ± 18.2%, Figure 1). Finally, the one-sample *t*-tests showed that the negative anomalies of species from siliceous origin were higher and more significant on calcareous than on siliceous soils. This shows a tendency for species from siliceous origin to have more negative survival anomalies in the dry years on calcareous than on siliceous soils, although there was no significant Year × Origin × Soil type interaction.

3.2 | Survival without neighbours

Year quality and Soil type had a significant effect on survival without neighbours (Table 1). Survival was three times higher during wet than dry years ($p < 0.001$, Tukey results: a, 58 ± 4.27% for 2016 and 2018, and b, 19.1 ± 3.52% for 2019 and 2020, Figure 3) and on average higher on calcareous than on siliceous soil ($p = 0.012$; 42 ± 4.82% and 35.2 ± 4.37% respectively). There was also a significant Origin × Soil type interaction, indicating that species from calcareous origin survived better on calcareous soil, whereas there was a tendency for species from siliceous origin to survive better on siliceous soil ($p = 0.032$; calcareous soils: a, 51.8 ± 6.51% for calcareous origin, and b, 32.1 ± 6.76% for siliceous origin, siliceous soils: b, 27.9 ± 5.98% for calcareous origin and ab, 42.4 ± 6.20% for siliceous origin). Additionally, the Origin × Year quality interaction was also significant, because survival was much higher for calcareous species than siliceous ones during dry years, whereas there was no difference due to species origin during wet years ($p < 0.01$; wet years: ab, 49.8 ± 6.86% for calcareous origin and a, 66.3 ± 4.76% for siliceous origin, dry years: b, 30 ± 5.83% for calcareous origin and c, 8.25 ± 2.96% for siliceous origin). Survival for species from the two origins was reduced on both soils during dry years, resulting in no significant Origin × Soil type × Year quality interaction (Table 1). However, planned comparisons revealed that survival was equally high for the two origins during wet years on calcareous soil and equally low on siliceous soil during dry years ($p > 0.05$), whereas survival on siliceous soil was greater for species from siliceous origin during wet years ($p < 0.001$), and only the species from calcareous origin survived on calcareous soil during dry years ($p < 0.001$).

TABLE 1 Results of generalized linear mixed-effects models (GLMM) for the effects of the Soil type, Origin, Year quality treatments and their interactions on survival without neighbours. Significant ($p < 0.05$) effects are indicated in bold

		Survival	
Effects	***df***	X^2	***p***
Origin	1	1.77	0.182
Soil type	1	6.27	**0.012**
Year quality	1	23.03	**<0.001**
Origin × Soil type	1	4.56	**0.032**
Origin × Year quality	1	7.27	**0.007**
Soil type × Year quality	1	0.43	0.507
Origin × Soil type × Year quality	1	0.01	0.911

3.3 | Intensity and importance of competition

RII survival results showed a significant Origin × Year quality interaction, indicating that competition was always intense for species from calcareous origin, whereas competition was intense only during wet years for species from siliceous origin ($p = 0.010$, Table 2; wet years: ab, −0.19 ± 0.09 for calcareous origin and ab, −0.29 ± 0.08 for siliceous origin, dry years: a, −0.34 ± 0.1 for calcareous origin and b, −0.01 ± 0.07 for siliceous origin, Figure 4a). The effect of soil type was also marginally significant ($p = 0.058$) indicating a tendency for more intense competition on siliceous soil (RII: −0.29 ± 0.06 vs. −0.13 ± 0.05) in agreement with the results from one-sample *t*-tests (Figure 4a).

Results of Imp survival also showed a significant Origin × Year quality interaction, indicating that competition was always important for the species from calcareous origin, but important only during wet years for species from siliceous origin ($p = 0.011$, Table 2, wet years: ab, −0.21 ± 0.09 for calcareous origin and ab, −0.26 ± 0.09 for siliceous origin, dry years: a, −0.31 ± 0.06 for calcareous origin and b, 0.01 ± 0.04 for siliceous origin, Figure 4b). In addition, there was a significant Soil type × Year quality interaction, indicating that competition was more important on siliceous than on calcareous soils during wet years, whereas competition was as important on both soils during dry years ($p = 0.025$; Table 2; Figure 4b, wet years: a, −0.09 ± 0.105 for calcareous soil and b, −0.37 ± 0.07 for siliceous soil, dry years: ab, −0.17 ± 0.06 for calcareous soil and ab, −0.12 ± 0.06 for siliceous soil). The results of one-sample *t*-tests were consistent with these two two-way interactions, showing that the importance of competition was always significant for species for calcareous origin, except the wet years on calcareous soils, and significant for siliceous species only the wet years on siliceous soils.

4 | DISCUSSION

The strong inter-annual variability of meteorological conditions during this study revealed important differences in stress tolerance and competitive response between both species types. Consistent with our first hypothesis, calcareous species were much more tolerant to dry climatic years than siliceous species, but suffered the most from competition. Consistent with our second hypothesis, competition on siliceous soils was stronger than that on calcareous soils, highlighting differences in competitive effects of the two communities. However, competitive effects of neighbours appeared to be less important than target species tolerance to stress for explaining differences in species distribution on both soil types. Overall, our results support the physical hypothesis, and highlight in particular

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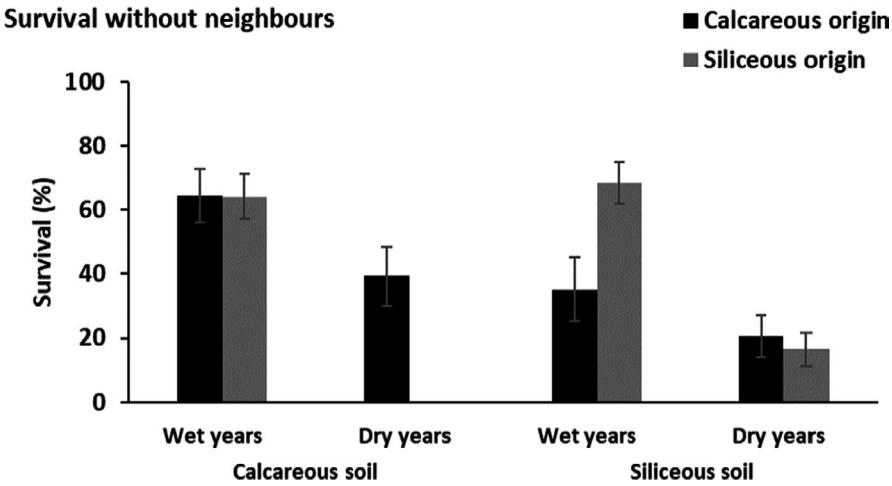

FIGURE 3 Survival (mean ± *SE*, $n = 16$) of the species of the two origins during dry and wet years on calcareous and siliceous soils. Black and grey bars represent species from calcareous and siliceous origin respectively

TABLE 2 Results of linear mixed-effects models for the effects of the Soil type, Origin, Year quality treatments and their interactions on RII and Iimp. Significant ($p < 0.05$) effects are indicated in bold and marginally significant are indicated in italic

		RII		Iimp	
Effects	***df***	***F***	***p***	***F***	***p***
Origin	1	1.77	0.185	3.01	*0.085*
Soil type	1	3.66	*0.058*	2.52	0.114
Year quality	1	0.29	0.593	0.71	0.413
Origin × Soil type	1	0.46	0.498	0.44	0.505
Origin × Year quality	1	6.81	**0.010**	6.57	**0.011**
Soil type × Year quality	1	1.24	0.266	5.12	**0.025**
Origin × Soil type × Year quality	1	0.13	0.714	0.04	0.841
Residual error	120				

the importance of species drought tolerance for explaining the difference in species composition and diversity between calcareous and siliceous soils.

4.1 | Species with contrasting stress tolerance and response to competition respond to variations in environmental conditions differently

Several of our results support the trade-off for stress tolerance and response to competition between calcareous and siliceous species. First, unlike calcareous species, siliceous species were prone to year-to-year fluctuations, as their survival anomalies shifted from significantly positive during wet years (higher than the average survival) to significantly negative during dry years (2019 and 2020). Second, calcareous species had higher survival than siliceous species during dry years. These findings indicate that calcareous species were better able to cope with stress when environmental conditions became severe. The greater stress tolerance ability found in calcareous species is consistent with the physical hypothesis and the overall lower water availability of calcareous soils compared to siliceous soils (Michalet et al., 2002; Rolland et al., 1998; Thurmann, 1849). Consistently, Contran et al. (2013) and Hu et al. (2013) showed that oak species/populations from calcareous bedrocks were more adapted to drought stress than oak species/populations from siliceous soils. Third, the higher stress tolerance abilities of the calcareous species that were used in our study appeared to decrease their capacity to cope with competition, confirming the occurrence of a trade-off. Calcareous species suffered from intense and important competition during wet and dry years, whereas for siliceous species, competition was intense and important during wet years only. This trade-off between stress tolerance and response to competition has been reported and recognized in a large number of studies (e.g. Forey et al., 2010; Liancourt, Callaway, et al., 2005; Lind et al., 2013; Qi et al., 2018; Suding et al., 2003).

4.2 | The relationship between community competitive effects and substrate type

In accordance with our second hypothesis, competition by neighbouring plants was both more intense and more important on siliceous soils than that on calcareous soils during the wet years. A possible explanation would be a greater availability of water on siliceous substrate than on calcareous substrate (Gigon, 1987; Thurmann, 1849), inducing a higher competition on siliceous soils, the least stressful habitat (Grime, 1973, 1974). This is also consistent with the study by Michalet et al. (2002) showing a higher biomass and lower species richness found on siliceous bedrocks. Similarly, Nicklas et al. (2021) have observed in the Alps, on siliceous bedrocks

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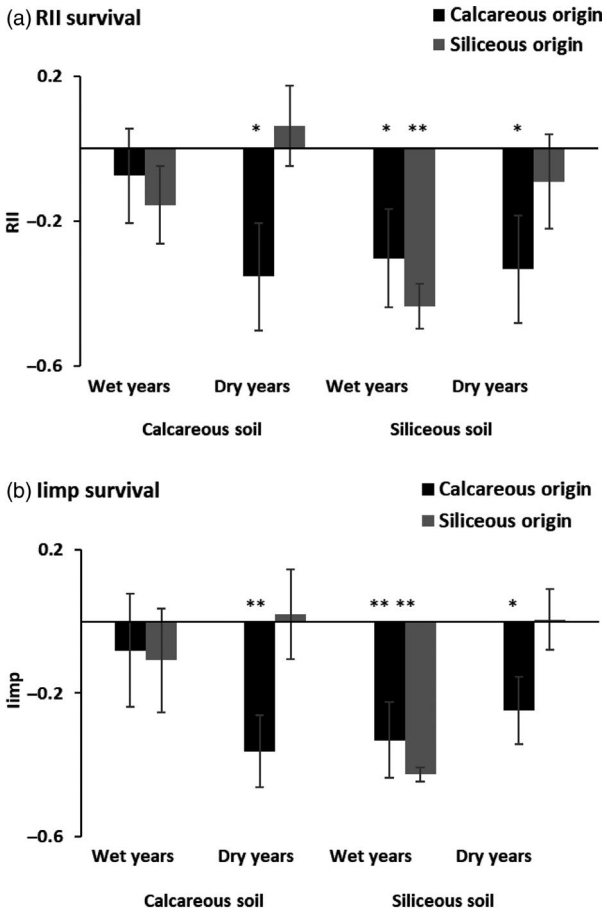

FIGURE 4 Means (±*SE*, $n = 16$) of Relative Interaction Index (RII survival) (a) and Competition importance index (Iimp survival) for survival (b) for the species from the two origins on calcareous and siliceous soils during wet and dry years. Black and grey bars represent species from calcareous and siliceous origin respectively. Results of one-sample *t*-tests are shown below bars when significant. (*), $p < 0.1$; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$

only, an increase in plant richness, related to a decrease in vegetation cover with increasing drought stress with climate change, suggesting a higher importance of competition on siliceous than on calcareous substrate. Strong competition on acidic siliceous soil has also been regularly reported in studies conducted in European heathlands (Aerts et al., 1991; Delerue et al., 2018).

Interestingly, Grime (1979) proposed two humped back model (HBM) of biomass/species richness relationships, one for calcareous regions with higher species richness and the other for siliceous regions with lower species richness, arguing that differences in species richness between both community types should be explained by differences in species pools related to different evolutionary history. Thus, he was considering himself that his CSR strategy model could not explain differences in species richness between the two community types. Nicklas et al. (2021) also proposed two separate HBMs for each substrate type. Instead, Michalet et al. (2002) proposed only one HBM merging the two community types, with calcareous communities on the stressful side and siliceous communities on the high-biomass side of the unimodal curve. Our results provide additional support to this more synthetic view, with stress tolerance and competition being the two main drivers of differences in diversity between the two community types.

4.3 | The relative contribution of stress tolerance and community competitive effects in the physical hypothesis

Both higher stress tolerance of calcareous species and higher competitive effects in siliceous communities were observed in our experiment, but their relative importance was not equal. Stressful conditions on calcareous soils during the dry years lead to the almost complete exclusion of siliceous species only. Additionally, calcareous species during dry years suffered more from competition by neighbours than siliceous species as shown by RII and Imp results. However, competition never led to their complete exclusion from siliceous communities, unlike the effect of stress on siliceous species on calcareous soils. Thus, in our study, stress tolerance ability was more important than competitive effect for explaining contrasts in species composition between the two soil types. To our knowledge, no study before has attempted to disentangle the relative importance of the response to stress and the effect of competition in driving differences in species composition between calcareous and siliceous plant communities. Finally, our results support previous works that stressed the importance to distinguish competitive responses and effects, the latter being more important for understanding the patterns of composition and diversity in plant communities (Goldberg, 1990; Liancourt, Corcket, et al., 2005; Liancourt & Tielbörger, 2009).

Finally, concerning the two alternative hypotheses explaining differences in species composition and richness between communities from both bedrock types, the chemical hypothesis (greater availability of nutrients found on calcareous soils compared to siliceous soils) should have led to a more important competitive exclusion on calcareous soils (Grime, 1973, 1977) and a higher plant diversity on siliceous soils. This is in contradiction with the well-known higher diversity of calcareous grasslands (Michalet et al., 2002; Nicklas et al., 2021; Thurmann, 1849). Additionally, there should be reciprocal toxicity between the two soils and the two types of species. If the chemical hypothesis was true, more plants from siliceous communities would have died on calcareous soils (with and without neighbours), and more plants from calcareous communities would have died on siliceous soils (with and without neighbours). Thus, our results provide strong additional support to the physical hypothesis.

5 | CONCLUSIONS

By assessing the relative importance of stress tolerance and response to competition of calcareous and siliceous dominant species on the two types of soils during 4 years with contrasting climate conditions, our study clearly showed a trade-off between these two components.

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However, stress tolerance had a greater effect than competitive effect of neighbours in the ability of the different species to develop in both communities. Additionally, our results add support to the physical hypothesis of the ecological determinism of difference in species composition and diversity between calcareous and siliceous soils. Our results have also important implications for studies forecasting how environmental factors influence plant species distributions in the context of climate change. They suggest that future modelling approaches focusing on plant responses to climate change should consider ecological interactions between biotic interactions and physical abiotic factors related to substrate types in order to improve their predictions.

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CONFLICT OF INTEREST

None of the authors have a conflict of interest.

AUTHORS' CONTRIBUTIONS

R.M. conceived the design and made field experiments during the 4 years; D.N. made field experiments during the fourth year and conducted statistical analyses with P.L. and H.R.; D.N. and P.L. wrote the first draft of the manuscript and F.D., P.L., H.R. and R.M. contributed critically to the writing.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.6q573n609 (Nemer et al., 2021).

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