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Home-field advantage effects in litter decomposition is largely linked to litter quality

Francisco I. Pugnaire [a,*], Karoline H. Aares [b], Mohamed Alifriqui [c], Kari Anne Bråthen [b], Christian Kindler [a], Christian Schöb [d,e], Esteban Manrique [f]

[a] Estación Experimental de Zonas Áridas, Consejo Superior de Investigaciones Científicas (EEZA-CSIC), Carretera de Sacramento s/n, E-04120 La Cañada, Almería, Spain
[b] Department of Arctic and Marin Biology, UiT-Arctic University of Norway, N-9037 Tromsø, Norway
[c] Biology Department, Cadi Ayyad University, BP 2390, 40001 Marrakech, Morocco
[d] Institute of Agricultural Sciences, ETH Zurich, Universitätstrasse 2, 8092 Zurich, Switzerland
[e] Área de Biodiversidad y Conservación, Universidad Rey Juan Carlos, Calle Tulipán s/n, E-28933 Móstoles, Spain
[f] Real Jardín Botánico, Consejo Superior de Investigaciones Científicas (RJB-CSIC), Plaza de Murillo 2, E-28014 Madrid, Spain

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ABSTRACT

Climate change and associated environmental alterations affect plant communities, potentially decoupling links between plants and their associated soil microbial communities. This may in turn affect processes like litter decomposition, an important function that controls nutrient and carbon cycling as well as many other ecosystem processes. Microbial decomposers have been proposed to specialize, being able to easier decompose litter from its 'home' community than litter from other communities, in what is termed the *home field advantage* (HFA) hypothesis. We report a litter decomposition experiment including four alpine meadow communities spread along a geographical gradient that ranged from the Atlas in Morocco to the Iberian Peninsula to the Swiss Alps. We tested whether litter decomposition rate would differ depending on litter and soil origin, expecting interactions between litter and soil microbial communities to be at the core of responses. We expected to find HFA in all four alpine communities. HFA ranged from very negative to neutral to positive along our geographical gradient, in a variation that could be attributed to the interaction of microbial communities with soil and plant traits, and linked to the relative abundance of microbial groups performing specific functions. Litter decomposition depended on litter quality and on the fungal community, which seemed adapted to deal with poor-quality, recalcitrant litter, leading to HFA. Climate plays a role as well, indirectly through plant community composition. Phyllosphere communities competed with soil communities when in interaction, a fact that may have blurred results of some previous HFA experiments. In summary, there is a clear HFA in systems with low-quality litter that requires a specialised fungal community to maximize decomposition. By contrast, high-quality, easy to decompose litter would be dealt with by any decomposer community, not showing evidence of HFA.

1. Introduction

The ongoing climate change and associated environmental alterations affect plant communities, potentially decoupling links between plants and their associated soil microbial communities (Berg et al., 2010; Morriën et al., 2010). This has consequences for ecosystem processes that can modify ecosystem functioning (Veen et al., 2015). Plants are affected directly by climate change, but also through modification of the abundance and structure of soil microbial communities (Allison et al., 2013), influencing ecosystem processes governed by microbes (Schimel, 1995). Although climate exerts direct effects on decomposition, it also affects litter quality, which is determinant for decomposition rate (Gholz et al., 2000; Ayres et al., 2009). This is relevant as there seems to be a specialization of decomposer communities to the substrate they thrive on (Ayres et al., 2006; Strickland et al., 2009; Arnoldi et al., 2020), evidenced by a strong coordination between the chemical stoichiometry of litter and their decomposer community (Parton et al., 2007; Manzoni et al., 2010; Freschet et al., 2012). In fact, there is experimental evidence suggesting that microbial communities specialize in breaking down litter from the plant community they live on (Vivanco and Austin, 2008;

* Corresponding author.
E-mail address: fip@eeza.csic.es (F.I. Pugnaire).

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Strickland et al., 2009). A consequence of this specialization is that litter would decompose faster in their own soil than in a foreign soil, a phenomenon termed the '*home-field advantage*' (HFA) hypothesis (Bocock et al., 1960; Hunt et al., 1988; Gholz et al., 2000, Negrete-Yankelevich et al., 2008). This hypothesis is gaining relevance as climate change evolves because of the potential decoupling of below- and above-ground communities and the potential consequences thereof. However, the occurrence of HFA is highly variable and context-dependent (Prescott et al., 2000; Ayres et al., 2006; Chapman and Koch, 2007; Freschet et al., 2012) for yet little-understood reasons (Veen et al., 2015), which has hindered its widespread acceptance into ecological theory (Freschet et al., 2012). HFA is not always evident (Prescott et al., 2000; Chapman and Koch, 2007; Li et al., 2015; Bani et al., 2019; Song et al., 2019), and the magnitude and direction of its effects are quite variable, with as many cases in which HFA does and does not occur (Allison et al., 2009, Ayres et al., 2009, Freschet et al., 2012; Veen et al., 2015, 2019).

Most reported HFA involved reciprocal litter transplants between rather disparate systems (Bocock et al., 1960; Hunt et al., 1988; de Toledo Castanho and de Oliveira, 2008) or of highly contrasted litter quality (Hunt et al., 1988; Gholz et al., 2000; Strickland et al., 2009; Jacob et al., 2010; Elias et al., 2020). However, when litter was of similar quality (Ayres et al., 2006) HFA did not appear, which led Veen et al. (2015) to argue that the probability of finding HFA would be higher with increasing differences between '*home*' and '*away*' plant communities. In addition, HFA has often been found in ecosystems dominated by single (Hunt et al., 1988; Vivanco and Austin, 2008; Ayres et al., 2009) rather than by multiple plant species (Prescott et al., 2000; Chapman and Koch, 2007). Overall, plant community type, elevation, plant traits or soil properties do not explain HFA, even though these factors are major drivers of litter decomposition (Veen et al., 2015). HFA seems to be more frequent where litter is hard to decompose (Elias et al., 2020; Zhang et al., 2021), and depends strongly on water availability (Fraser and Hockin, 2013; Lam et al., 2021) and other interacting factors that may affect decomposition, often leading to inconsistent outcomes (Rawat et al., 2021).

Despite such inconclusive results, increased understanding of the factors driving HFA is highly relevant in the context of global change, as HFA can be modified by increased stress caused by climate (Wang et al., 2020), and in response to changes in microbial community selection and adaptation (Morella et al., 2020). Temperature and precipitation are crucial drivers of litter decomposition at large spatial scales (Coûteaux et al., 1995; Liski et al., 2003), being climatic controls on litter decomposition quantitatively more important than factors like species or site of origin (Portillo-Estrada et al., 2016). Decomposition rates are overall higher in warmer and wetter sites than in colder and drier sites as soil biota activity depends on these factors (Portillo-Estrada et al., 2016). However, temperature seems to have a stronger influence than humidity on litter decomposition (Berg and McClaugherty, 2020), likely making HFA linked to climate gradients.

Here we report a litter decomposition experiment including four alpine meadow communities selected across a large geographical and climatic gradient, from the Atlas in Morocco to Sierra Nevada in Spain, the French Pyrenees, and the Swiss Alps. Although belowground biomass in alpine meadows is by far higher than aboveground biomass (Becker et al., 2015; Sun et al., 2017), litterfall is still one of the major pathways connecting above- and below-ground processes (Becker et al., 2015) and decomposition rates are higher in the surface than in buried litter due to differences in soil microbial activity (Lee et al., 2014; Fan et al., 2021; Su et al., 2021). In addition, global warming effects are stronger in high-elevation environments than elsewhere (Giorgi and Lionello, 2008; Lenoir and Svenning, 2015; Pugnaire et al., 2021), and getting data on plant-soil feedbacks in these environments may contribute to anticipate the impacts of climate change on these processes. We tested whether litter decomposition rate would differ depending on litter and soil origin, expecting to find HFA in all four alpine meadows, overall sharing climate patterns and plant physiognomy; we also assumed interactions between microbial communities of litter and soil to be at the core of responses, decomposition rate being dependent on microbial community size. Finally, and because of climate effects on litter decomposition, we expected HFA to change along the climate gradient.

2. Materials and methods

2.1. Sites description and experimental procedures

We selected four ecosystems along an N–S gradient of alpine meadows in the Atlas (Oukaimeden, Morocco), Sierra Nevada (Granada, Spain), the Pyrenees (St. Lary-Soulan, France), and the Alps (Flüelapass, Switzerland). We focused on these systems trying to keep environmental variability to a minimum by choosing habitats with similar physiognomy and ecological functions. Although community composition along such a large gradient would differ, we expected climate to be a main driver of potential differences affecting plant-soil feedbacks. Our field sites spread over a gradient of high-elevation grasslands between North Africa and Western Europe, all within the 2,300–2,800 m elevation range (Table 1). They had similar traits, like low pH and high OM content, but differed in other soil and climate variables as, for instance, mean annual temperature and rainfall (Table 1, Table S1). Soils were generally in hydromorphic systems, showing a histic horizon with high organic matter, low pH and high C:N ratio (Table 2).

At each site, we selected five plots 10–300 m apart from each other and within each plot we established six subplots where we sampled the top 5 cm of soil along several 5 m long transects, totalling 30 samples per site. Senesced leaves were picked along the same transects from the surface, gleaning through the green leaves, and sorted out by colour to make sure it was fresh-fallen litter. Litter from different subplots was homogenised by blending samples in a large bag in a process gentle enough to avoid breaking the senesced leaves into smaller pieces. When collecting soil, we cleansed tools with towel paper and 70% ethanol between samples to prevent cross-contamination. We collected 5–10 g of litter in each subplot, intended to represent the community rather than individual species. Because of the high variability in the composition of individual samples and the small amount collected, all five subplots in a plot were combined to get a more representative sample of the community. Soil samples were air-dried at room temperature, stored, and sent to the lab, where they were analyzed for physical and chemical properties and DNA quantification. Litter samples were also air-dried at room temperature and stored at 5 °C until analysis.

To assess plant cover and community structure, five 5 m-long transects were randomly laid out in each subplot, and plant cover was recorded as the proportion covered by each species in the transect using the point intercept method.

The decomposition experiment was set up in a growth chamber at 18 °C and ~70% air humidity, with a 16/8 h light/dark regime. Soil from four subplots per plot and site (4 × 5 × 4) were randomly selected, and 200 g of soil from each selected sample were sieved to 2 mm and placed on 20 × 8 cm, 3 cm deep aluminium trays, adding another 20 trays filled with sterilized vermiculite as control. Sieves were cleaned with 70% ethanol between samples. On each tray, we spread dry litter (~2 g) collected from every plot in each site with a factorial design,

Table 1
Location and main data of the four field sites along a gradient N–S, including mean annual precipitation (MAP), mean annual temperature (MAT), and the standardised precipitation-evapotranspiration index (SPEI).

Site	SPEI	Latitude	Longitude	Elevation	MAP	MAT
Atlas	−1.7	31.05	−7.90	2700	450	6.5
Sierra Nevada	−1.8	37.08	−3.39	2800	690	3.9
Pyrenees	−0.3	42.61	1.47	2400	916	9.6
Alps	1.2	46.75	9.95	2300	1022	3.5

Table 2
Soil traits, including pH, soil carbon (C), C:N ratio, and bacterial and fungi DNA amplicon copy number (qPCR) in soils of four alpine grasslands spreading along a N–S gradient.

	pH	C (g/kg)	C:N	Bacteria (copies/100 g)	Fungi (copies/100 g)
Atlas	5.90 ± 0.05	40.08 ± 0.76	12.78 ± 0.24	7.7E+09 ± 3.0E+08	1.9E+06 ± 2.3E+05
Sierra Nevada	4.93 ± 0.04	42.86 ± 0.42	15.31 ± 0.37	5.7E+09 ± 7.0E+08	1.2E+06 ± 1.9E+05
Pyrenees	5.19 ± 0.04	43.98 ± 0.30	11.97 ± 0.31	6.0E+09 ± 4.3E+08	1.1E+06 ± 1.7E+05
Alps	4.73 ± 0.06	42.14 ± 0.59	13.25 ± 0.39	5.6E+09 ± 3.5E+08	2.6E+06 ± 4.3E+05

totalling 20 trays per site and 80 trays in total, plus 20 control trays. Soils were kept nearly at saturation (as in their original systems) by watering with deionized water twice a week. After 18 weeks, litter samples were carefully recovered, cleansed of soil particles, dried at 60 °C for 48 h, and weighted. Decomposition was assessed by differences in dry mass between initial and final values.

Climate data were collected from official Met offices, either local or state-level. As a synthetic, simple measurement of climate stress, we used the Standardized Precipitation Index (SPEI) since our field sites spread over a strong gradient of temperature and rainfall. SPEI is a multi-scale drought index calculated from monthly difference between precipitation and potential evapotranspiration (PET) that takes into account the main impact of temperature on water demand (Vicente-Serrano et al., 2010).

Soil nutrients were determined at the CEBAS-CSIC ionomics lab (Murcia, Spain), including total C and N content using a C/N analyser (LECO Truspec, St. Joseph, MI, USA) and organic C after removal of inorganic carbon with HCl 2N (Schumacher, 2002); anion phosphate (PO_4^{3-}) and sulphate (SO_4^{2-}) concentrations in water extracts (1:5 soil: water, w:v) were analyzed by HPLC (Metrohm, HE, Switzerland). Soil nitrate (NO_3^-) and ammonium (NH_4^+) were extracted with potassium chloride (KCl 2M) and their contents determined with an automatic continuous segmented flow analyser (model SAN++, Skalar Analytical B.V., Breda, The Netherlands). Other elements were determined after acid digestion with an inductively coupled plasma (ICP) emission spectrometer (ICAP 6500 DUO; Thermo Scientific, Wilmington, DE, USA). pH was measured with a pH-meter (Crison, Spain) in a 1:2.5 (w:v) water solution, and organic matter by dry combustion at 430 °C for 24 h.

2.2. DNA extraction and quantitative PCR

DNA was extracted from 250 mg of soil using the DNeasy Powersoil® Kit (Qiagen, Inc., Venlo, Netherlands), following manufacturer's protocol. DNA concentration was estimated using a Qubit Fluorometric Quantification (Thermo Scientific, USA) and samples were stored at −80 °C. Quantitative PCR (qPCR) analyses were performed in soil DNA extracts to determine the abundance of microbial marker genes for bacteria and fungi. The primer pairs used for the qPCR analyses were 515f (5′-GTGYCAGCMGCCGCGGTAA-3′) and 806r (5′-GGACTACNVGGGTWTCTAAT-3′) for prokaryote (Walters et al., 2015), and ITS1 (5′-TCCGTAGGTGAACCTGCGG-3' [Gardes and Bruns, 1993];) and ITS5.8S (5′-CGC TGC GTT CTT CAT CG-3' [Vilgalys and Hester, 1990];) for fungi, respectively. Amplifications were performed by using a SYBR® Green (Sigma-Aldrich, USA) based qPCR method in a CFX96 ™ Real-Time PCR Detection System (BioRad Laboratories, USA). Standard curves were prepared in every assay using 10-fold serial dilutions of stock solutions containing the target DNA molecules. The reaction mixture contained 10 μl of 2X PowerUp™ SYBR™ Green Master Mix (Applied Biosystems, USA), 1 μl of each primer (20 μM), 10–100 ng of template DNA and nuclease free water (Ambion Thermofisher) up to 20 μl of final volume. Amplification conditions were as follows: 95 °C for 10 min, bacteria: 35 cycles of 10 s at 95 °C, 30 s at 57 °C and 30 s at 72 °C, fungi: 40 cycles of 15 s at 95 °C, 30 s at 53 °C and 1 min at 72 °C, followed by melt curve from 60 °C to 95 °C at 0.5 °C increment. Triplicate reactions were performed for each DNA extract, standard curve, and negative control. PCR efficiency for different assays ranged between 75% and 95% with $R^2 > 0.9$. The specificity of amplified products was verified by melting curves and agarose gel electrophoresis analysis.

2.3. HFA calculations

Following Ayres et al. (2009), we quantified HFA effects using a method originally developed to assess HFA in sports (Clarke and Norman 1995). This method allows obtaining an HFA value for each sample involved in an experiment including home and away soils and litter. We calculated the home-field advantage using the following set of equations

$$HDDH = \sum_{i=1}^{3}(DHh - DAih)$$

$$ADD_H = \sum_{i=1}^{3}(D_{Hai} - D_{Aiai})$$

where H is home soil, h is home litter, A is away soil, and a is away litter; thus, there were 3 away sites for any given home site (i). D is a measure of decomposition (e.g., mass loss of litter from the different sites on the different soils with a factorial design) and HDD and ADD represent *home* and *away* decomposition differences, respectively; capital case subindices denote soil and lower case show litter from the Atlas (ATL), Sierra Nevada (SN), Pyrenees (PYR), and Alps (ALP).

H is the HFA mean effect for all sites combined, and N is the number of sites

$H = (HDD_{ATL} + HDD_{SN} + HDD_{PYR} + HDD_{ALP})/N$

ADH is the additional decomposition at home

$ADH_I = HDD_I - ADD_I - H$

If $ADH_I > 0$, litter in site *I* decomposes at home faster than expected (i.e., there is positive HFA); if $ADH_I = 0$, litter decomposition at home in site *I* did occur at the expected rate (i.e., no HFA), and whenever $ADH_I < 0$, litter decomposition in site *I* occurred at home slower than expected (i.e., there is home-field disadvantage).

We calculated ADH values of litter from each community decomposing on soil from every other field site.

2.4. Statistical analysis

Linear mixed models (LMM) were performed for determining significant differences in soil nutrients and microbial abundance (qPCR data) between sites including soil and litter origin as fixed factors and plot as random factor. Decomposition, ADH and other variables were tested through ANOVA. We also carried out a partial least squares regression (PLS) to show how environmental properties related to ADH across sites. We used PLS because we had more variables than observations and because of the high collinearity between variables. We used t-tests to assess significance of mean differences, as well as linear regression analysis between variables. Normality of residuals and homogeneity of variance were assessed by graphical inspection of residuals; when these assumptions were not met, we used a model correction for heterogeneity of variance (varIdent). Post hoc differences were tested with Fisher least significant difference tests. Statistical analyses were performed with R (R Development Core Team, 2020) version 4.1.2.A using the InfoStat statistical package (Di Rienzo et al., 2020).

3. Results

Our selected grasslands spread over a large range of environmental variables, mostly linked to latitude. Drought stress played a main role, differing notably along the gradient, as SPEI evidenced, with important consequences for plant community composition, soil nutrient availability, and other soil characteristic (Table 2). Overall, soils were acidic, with pH ranging 4.73–5.90, and with high percentage of OM, which ranged from 15.01% in the Pyrenees to 29.5% in the Atlas (Table 2).

Plant cover was well over 100% in all four sites and plant community composition showed differences between sites, both in the number of species (e.g., 18 in Sierra Nevada, 41 in the Pyrenees) and number of endemic species (50% of genera in the Atlas and Sierra Nevada, vs 38% in the Pyrenees and 20% in the Alps). Standing biomass also varied, ranging between 1.6 kg m^{-2} in Sierra Nevada to 9.6 kg m^{-2} in the Pyrenees, with the remaining two sites in between. Biomass data, which differed widely between sites, could be influenced by herbivory pressure, which also differed widely among them. Only a few genera were present in all four sites, including *Carex*, *Euphrasia, Festuca*, and *Ranunculus*. Six other genera were shared by 3 sites, while some of them were exclusive of just one site. Dominant species were also quite different, with forbs being the main functional group in the Atlas and decreasing toward the north, while grasses increased their presence at increasing latitudes, being overwhelmingly dominant in the Alps (Table 3). There were significant differences in plant litter quality. Atlas litter had significantly more nutrients than Alps litter, with the two other sites in between, showing a marked geographical pattern of nutrient content of litter, which increased toward the South (Table S1). Overall, nutrients in litter from the two southernmost sites was at least 50% higher than in the two northernmost sites, perhaps due to the dominance of forbs.

Decomposition during the 4.5 months span of our experiment averaged 46.90 ± 1.33%, although with huge differences regarding soil and plant communities. For instance, in control (vermiculite) substrate, mean litter decomposition was 55.20 ± 2.22% while in all other treatments combined it was 44.74 ± 1.48%. The decomposition rate, being higher in control (vermiculite) than in any other soil, suggests a strong competition between soil microbial communities and the foreign microbiota introduced *via* litter (Fig. 1). Litter decomposition in control (vermiculite) differed among sites, with significant differences ($p < 0.05$) between decomposition of Atlas (65.97 ± 1.59%) and Pyrenees litter (46.23 ± 3.82%). Litter from the two Mediterranean sites, i.e., the Atlas and Sierra Nevada, were easier to decompose than litter from the two more temperate climates, i.e., the Alps and Pyrenees (in both, control vs all other soils, Fig. 2). Decomposition rate was related to the soil C:N ratio ($p = 0.007$), which ranged 12.7–15.4, but was only marginally related to the litter C:N ratio, which ranged from 26.3 in the Atlas to 38.8 in the Alps (Table S1), showing a trend to decreasing decomposition as C:N increases ($F = 2.4$; $p = 0.12$, ANOVA).

All four sites differed in the effects of *home* soil on litter decomposition following a geographical pattern that ranged from very negative effects in the Atlas and Sierra Nevada to no effect in the Pyrenees and quite positive effects in the Alps (Fig. 3). In other words, there seems to be a trend to home field *disadvantage* in the southern, dry Mediterranean sites and home-field *advantage* in the northernmost site, the Alps. The

Table 3
Number of plant species, dry mass, and growth form cover in four alpine grasslands spreading along a N–S gradient.

	Species	Biomass	Forbs	Graminoids
	#	g/m^2	%	%
Atlas	23	5,823 ± 337	65.35 ± 2.39	35.26 ± 0.50
Sierra Nevada	18	1,599 ± 125	43.24 ± 0.32	56.43 ± 2.06
Pyrenees	41	9,583 ± 512	31.52 ± 0.11	68.45 ± 0.55
Alps	28	2,665 ± 258	15.43 ± 0.10	83.65 ± 1.24

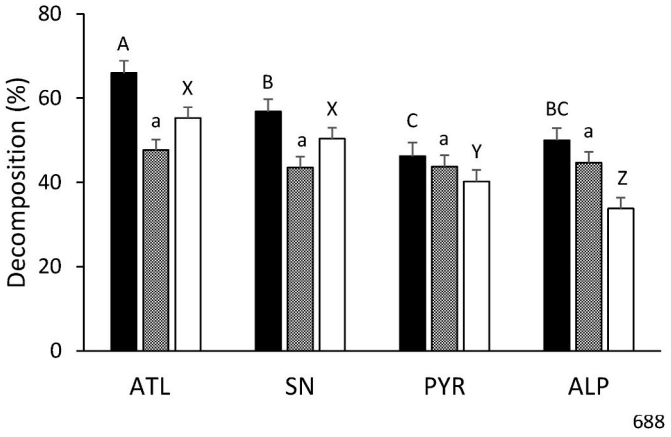

Fig. 1. Mean decomposition rate of litter from the Atlas (ATL), Sierra Nevada (SN), Pyrenees (PYR) and Alps (ALP) on sterilized vermiculite (black bars), on average of all soils combined (grey), and on average per site, using all litter samples combined (clear bars). Data are mean ± 1 SE. Same superscript letters within the same treatment show non-significant differences between sites ($p < 0.05$, LMM).

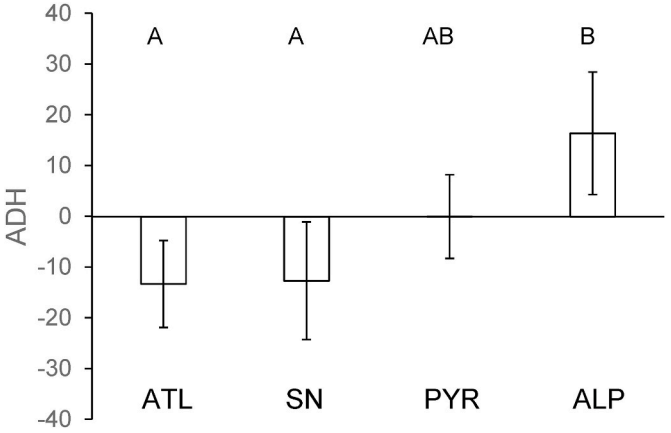

Fig. 2. Additional decomposition at home (ADH) (=*home field advantage*) effects of litter from the Atlas, Sierra Nevada, Pyrenees and Swiss Alps. Negative values show home field disadvantage while positive values mean advantage. Data are mean ± 1 SE. Same superscript letters show non-significant differences between sites ($p < 0.05$, ANOVA).

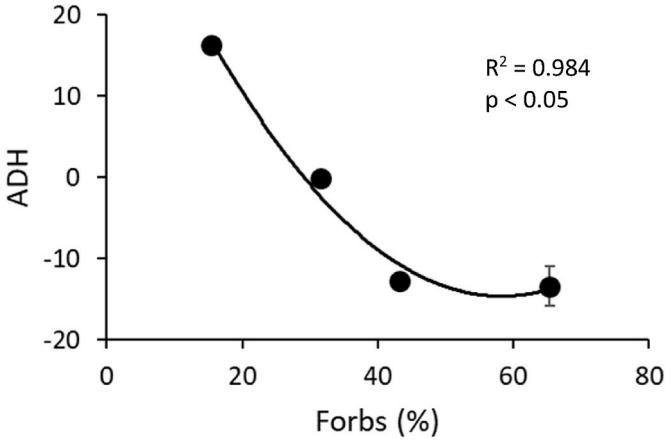

Fig. 3. Relationship between additional decomposition at home (ADH) and percent of forbs in the different field sites. Data are mean ± 1 SE. SE shown when larger than symbol.

fact that ADH increased with SPEI (Fig. 4) also suggests that this pattern would be linked to drought, and most likely through the proportion of forbs in the community. *Home* decomposition differences (HDD) were closely related to fungal abundance (Fig. 4), pointing also to a link between decomposition and drought. However, the high variability led to little significant differences in HFA effects (ANOVA $p = 0.339$; $n = 5$).

Soil bacterial abundance, in terms of marker gene abundance assessed by qPCR, did not show significant variation among sites. By contrast, soil fungal DNA amplicon copy number, overall three orders of magnitude lower than bacteria, was higher at the two ends of the gradient. ADH was uncorrelated with microbial DNA amplicon copy number (data not shown) but the PLS analysis showed that ADH was linked on to higher fungal abundance and soil K and to lower soil N and P and pH (Fig. 5). The PLS test clearly differentiated sites along Factor 1, being positive in southern sites and negative in northern sites (Fig. 5), with statistically significant differences (ttest; $p = 0.04$).

4. Discussion

While testing the *home field advantage* hypothesis we found responses that ranged from home field *disadvantage* to neutral to home field *advantage* along our N–S geographical gradient. Such variation could not be attributed to the dominance of one species (Vivanco and Austin 2008; Ayres et al., 2009), as all sites were rather diverse; the contrasting traits of the species involved (Prescott et al., 2000; Chapman and Koch, 2007), which were forbs and grasses in all four sites; nor to strong differences between systems (Ayres et al., 2009; Veen et al., 2015), because they shared climate type and plant physiognomy, but rather to the interaction between microbial communities with soil and plant traits, linked to the relative abundance of specific microbial groups, like fungi (Veen et al., 2018). In addition, competition between soil microbial communities and those in the phyllosphere introduced *via* litter was determinant for decomposition rate and, ultimately, for any *home field* effect. Since a pre-established microbial community is largely resistant to distress by later comers (Carlström et al., 2019; Gong and Xin, 2021), the specific contribution of the phyllosphere to decomposition is still poorly understood and likely underestimated (Fanin et al., 2021). However, by introducing a confounding factor such as the phyllosphere in experimental manipulations, microbial competition might have contributed to blur the real effects of previous local adaptation experiments.

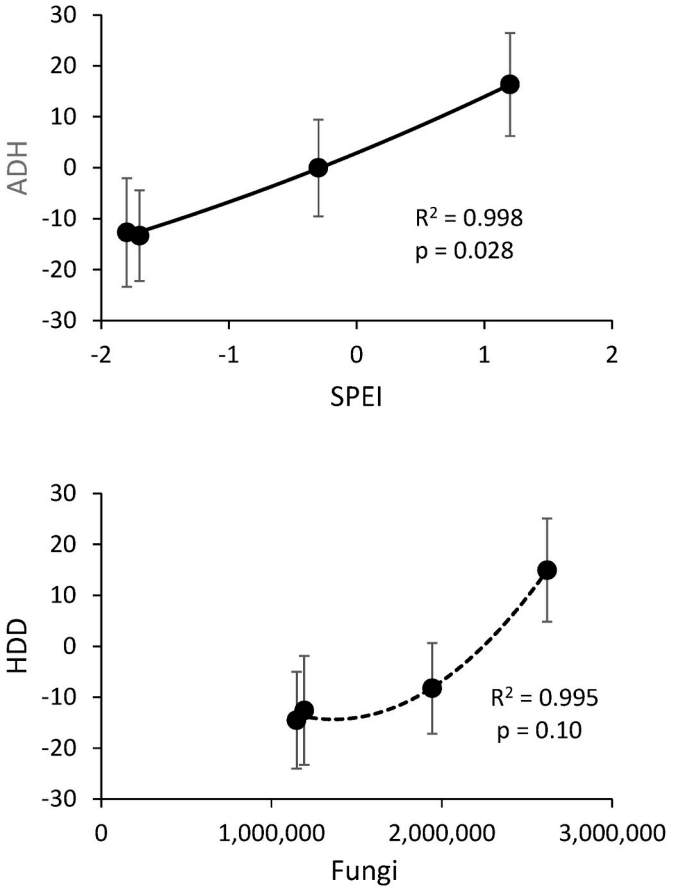

Fig. 4. Regression of additional decomposition at home (ADH) with SPEI (upper panel) and of home decomposition differences (HDD) with fungal abundance (DNA copies per g of soil; lower panel). Data are mean ± 1 SE.

Opposite to our expectations, *home* soil effects on litter decomposition ranged from very negative in the drier Atlas and Sierra Nevada mountains (i.e., there was in fact a home field *disadvantage*) to no effect in the Pyrenees to quite positive in the wettest site, the Alps (i.e., there was a home field *advantage*), showing that local factors influence HFA.

Some plant species produce easy to decompose, high-quality litter that requires no specialization of the soil decomposer community, as in the Atlas and Sierra Nevada sites. In such cases, most soil communities will contain biota capable of quickly dealing with litter, resulting in little or no HFA; in other words, there is no special ability of the local soil community to decompose this high-quality litter. In our experiment, the Atlas and Sierra Nevada systems produced the most decomposable litter because of the higher proportion of nutrient-rich forbs, and the proportion of this functional group in the community shows an inverse relationship with HFA (Fig. 3). By contrast, there are plant species that produce litter with highly recalcitrant or toxic compounds, and only locally-adapted soil communities would contain biota capable of degrading such compounds. In those plant communities, the presence of a specialised soil community would enable the decomposition of this recalcitrant litter, showing HFA. The plant community thus drives soil microbial community structure through litter production and quality, and such plant-soil feedbacks are critical processes governing the co-evolution of above- and belowground communities (Bever 1994; Bever et al., 2010; Pugnaire et al., 2019).

Contrary to our expectations, microbial numbers were unrelated to decomposition rate and to most measured abiotic variables (except pH for bacteria). Populations of soil microorganisms did show large variation among sites (Table 2) and bacterial DNA was overall orders of magnitude higher than fungal DNA, being more abundant in Sierra Nevada and less abundant in the Atlas and Alps. However, the high C:N ratios in our four systems suggest that fungal communities control decomposition processes in these alpine grasslands. Although microbial abundance and composition in soils play an important role in litter decomposition (e.g., Allison et al., 2013), and a link between HFA and litter quality has been recently evidenced (Elias et al., 2020; Zhang et al., 2021), only fungal abundance somehow influenced HDD in our dataset (Fig. 4). The high C:N ratio in our four alpine sites points to processes driven by fungi rather than bacteria, as fungi show lower metabolic demand (Danger et al., 2016) and more enzymatic capabilities than bacteria, which allow them to decompose low-quality leaf litter (Güsewell and Gessner, 2009). The microbial role in litter decomposition may be linked to species turnover rather than to microbial numbers (Voříšková and Baldrian, 2013; Veen et al., 2018). In fact, soil community composition differs in areas occupied by different plant species (Griffiths et al., 1992; Grayston et al., 1998; Priha et al., 1999; Porazinska et al., 2003; Bardgett and Walker, 2004; Hortal et al., 2015) as happens in our high-elevation sites.

Climate plays a significant role on litter decomposition (explaining 64–72% in the global teabag experiment [Djukic et al., 2018]), affecting decomposition at the global and regional scales through differences in temperature and precipitation (Powers et al., 2009; Austin et al., 2014; Zhang and Wang, 2015; Althuizen et al., 2018). It has been reported that increasing temperatures enhance litter decomposition while increasing precipitation usually decreases decomposition (Lv et al., 2020). In the alpine belt, extreme soil temperatures may override soil moisture effects

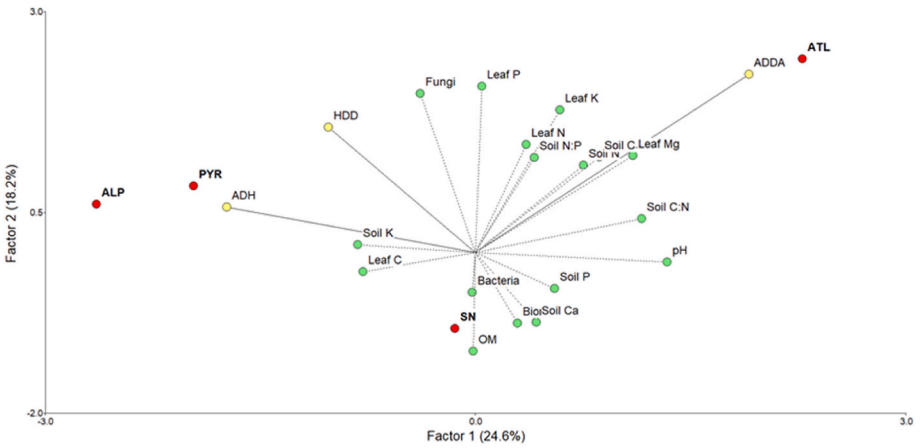

Fig. 5. Partial least squares analysis of environmental variables and decomposition indices across sites.

on decomposition, in a process that depends on the sensitivity of the different litter fractions to temperature and precipitation (Lv et al., 2020). This evidence suggests that climate change-induced alterations in precipitation regimes can substantially impact litter decomposition and affect carbon and nutrient cycling in terrestrial ecosystems (Su et al., 2023), which in our southernmost sites could lead to a decrease in litter quality as plant communities experience changes in composition.

Litter nutrient status is key for decomposition, which also depends on the local environmental context (Zhou et al., 2020). In our experiment, litter samples with higher nutrient content (Atlas and Sierra Nevada; Table S1) decomposed faster than litter from the two other sites, with significantly lower nutrients. Mineral nutrients in litter depend on nutrient resorption, a fundamental process through which plants withdraw nutrients from leaves before abscission (Reed et al., 2012) to support new growth. Resorption rates are quite variable, but could reach 62.1% of N and 64.9% of P, but these values decrease with increasing soil nutrient levels (Vergutz et al., 2012; Veneklaas, 2022). Resorption depends on mean annual temperature and precipitation (Reed et al., 2012) and, overall, remains poorly understood (Vergutz et al., 2012). Plants recover most nutrients except those in recalcitrant structures, so that litter tends to have a similar composition within similar functional groups (Zhang et al., 2021). Because of lower nitrogen resorption at higher temperatures (most likely related to water limitation), N in leaf litter is linked to latitude (Xie et al., 2021) which may be the reason why N is higher in litter from the Atlas and Sierra Nevada. Thus, differences in litter decomposition in the absence of climatic differences reflect the effects of litter chemistry and microorganisms in decomposition (Heemsbergen et al., 2004; Wall et al., 2008; Cornwell et al., 2008; Strickland et al., 2009), highlighting the importance of the decomposer community and its regional variation (Fierer et al., 2012).

Interestingly, forbs dominated in the Atlas and Sierra Nevada while grasses did in the Pyrenees and Alps. Forbs have higher nutrient content than grasses and less structural components like silica (Bråthen et al., 2021) being easier to decompose (Zhang et al., 2022). Litter quality has been shown to be the predominant factor controlling decomposition (Ayres et al., 2009; Murúa and Gaxiola, 2023), explaining >60% of the variability in decomposition rate at a global scale (Djukic et al., 2018). Therefore, communities with higher proportion of forbs, like the Atlas and Sierra Nevada, should have less recalcitrant litter (Bråthen et al., 2021), easier to decompose than in the Alps and Pyrenees. Indeed, there was no HFA in the two Mediterranean systems while there was HFA in the Alps, pointing to specialised decomposers in this latter system.

Climate also influences plant community composition, and the increase of ADH with increasing SPEI (Fig. 4A) indirectly shows the link between climate and HFA. However, the high rates of litter decomposition in *away* soils and the high variability of results weakened the significance of HFA differences (Fig. 2). Decomposition rate and additional decomposition at home (ADH) were more similar among plots from the Atlas and Sierra Nevada and among plots from the Alps and Pyrenees, as reflected by the PLS. Especially soil and litter variables related to nitrogen availability, along with soil pH, seemed to have a strong effect on ADH.

5. Conclusions

In summary, litter decomposition depended on litter nutrient status and on the fungal community, which seemed adapted to handle poor-quality, recalcitrant litter leading to HFA in our northernmost site, the Alps, but not elsewhere. Phyllosphere communities competed with soil communities when in contact, a fact that may have blurred results of previous HFA experiments. Our results suggest HFA in systems with low-quality litter requiring a specialised fungal community to deal with it. Opposite, high-quality, easy to decompose litter will not show HFA because it is largely dealt with by any decomposer community. Temperature and rainfall directly influence litter decomposition but climate, by modulating plant species composition, indirectly influences decomposition rate as well, hence HFA. Further research on feedbacks between soil communities and litter quality would increase our understanding of factors driving litter decomposition across large geographical scales, and to improve predictions on how environmental changes will influence C dynamics in terrestrial ecosystems.

Author contributions

FIP and EM designed the experiment. FIP wrote the first draft and made statistical analyses. All co-authors carried out field work and contributed to the writing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.soilbio.2023.109069.

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