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RESEARCH ARTICLE

Bridging the gap between microclimate and microrefugia: A bottom-up approach reveals strong climatic and biological offsets

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Abstract

In the context of global warming, a clear understanding of microrefugia—microsites enabling the survival of species populations outside their main range limits—is crucial. Several studies have identified forcing factors that are thought to favor the existence of microrefugia. However, there is a lack of evidence to conclude whether, and to what extent, the climate encountered within existing microrefugia differs from the surrounding climate. To investigate this, we adopt a "bottom-up" approach, linking marginal disconnected populations to microclimate. We used the southernmost disconnected and abyssal populations of the circumboreal herbaceous plant *Oxalis acetosella* in Southern France to study whether populations in sites matching the definition of "microrefugia" occur in particularly favorable climatic conditions compared to neighboring control plots located at distances of between 50 to 100 m. Temperatures were recorded in putative microrefugia and in neighboring plots for approximately 2 years to quantify their thermal offsets. Vascular plant inventories were carried out to test whether plant communities also reflect microclimatic offsets. We found that current microclimatic dynamics are genuinely at stake in microrefugia. Microrefugia climates are systematically colder compared to those found in neighboring control plots. This pattern was more noticeable during the summer months. Abyssal populations showed stronger offsets compared to neighboring plots than the putative microrefugia occurring at higher altitudes. Plant communities demonstrate this strong spatial climatic variability, even at such a microscale approach, as species compositions systematically differed between the two plots, with species more adapted to colder and moister conditions in microrefugia compared to the surrounding area.

KEYWORDS
global warming, marginal populations, Mediterranean region, *Oxalis acetosella*, Pignatti indicator values, temperatures

1 | INTRODUCTION

Plant species are thought to respond to climate change by adapting to new local environmental conditions, by migrating in the landscape to track their physiological requirements, or by going extinct if they fail to adapt or to migrate sufficiently rapidly (Corlett & Westcott, 2013; Editorial, 2020; Parmesan & Hanley, 2015). Alternatively, evidence from palaeoecological and phylogeographical studies of species distribution during the Last Glacial Maximum (c. 20 Ky) shows that some populations of warm-adapted species have subsisted locally far outside their main distribution range, even during episodes of drastically unfavorable climatic conditions (Clark et al., 1998; Hewitt, 1999; Parducci et al., 2012; Pearson, 2006). Sites enabling the subsistence of such populations have been termed microrefugia (Ashcroft, 2010; Rull, 2010).

Microrefugia are defined as small areas where conditions remain favorable for the persistence of populations outside their main species range limits (Ashcroft, 2010; Rull, 2010). This definition holds regardless of the time period considered, although geographical locations of glacial refugia certainly differ from current and future microrefugia (Hannah et al., 2014). In the context of global warming, understanding the functioning of microrefugia is crucial because they may allow some species unable to migrate upward or northward to subsist locally (Hannah et al., 2014; Lenoir et al., 2017; Pearson, 2006), and such sites could accumulate and conserve cool-adapted species efficiently (Nadeau et al., 2022). However, the available literature is concerned more with the characterization of microclimates than the climatic regime and the biological structure of microrefugia per se. Indeed, a classic approach to studying microrefugia consists in investigating microclimate heterogeneity across a landscape and identifying landscape forms and forcing factors that favor disconnected and stable microclimatic regimes and thus the emergence of microrefugia (Baker et al., 2021; Lembrechts & Lenoir, 2020; Meineri & Hylander, 2017). Hereafter, we call this type of study the "top-down" approach. In contrast, "bottom-up" studies investigating sites that resemble or match the definition of microrefugia are still very scarce (but see Bátori et al., 2019; García et al., 2020; Słowińska et al., 2022). Such studies are necessary to examine the link between the microclimatic variations highlighted by top-down studies and the emergence of microrefugia. In this paper, we study current microrefugia inferred from plant distribution patterns to assess whether these sites show a different fine-scale climate compared to the immediate surroundings, and whether this goes hand in hand with floristic changes.

In the current context, an efficient microrefugium would be a microsite with cooler temperatures and moister conditions that would lead to a lower vapor pressure mitigating heat waves and desiccation especially during the summer (Ashcroft & Gollan, 2013; Lenoir et al., 2017), and probably warmer and more stable minimum temperatures, protecting against frost events during the winter (De Frenne et al., 2021; Dobrowski, 2011; Hannah et al., 2014). Top-down studies indicate that concave relief patterns such as valley bottoms and sites near water bodies, provide such cooler, moister and more stable microclimatic conditions, although winter minimums may be lower compared to the surrounding area due to cool air pooling (Dobrowski, 2011; Meineri et al., 2015; Scherrer & Körner, 2011). Other studies show that forests have a strong buffering capacity for sub-canopy temperatures: the denser the vegetation cover is, the greater the forest can buffer regional warming and mitigate extreme heat, but also extreme frost during the winter (De Frenne et al., 2021; Greiser et al., 2018; Zellweger et al., 2020). Determining the main drivers of current microrefugia microclimates can address the question of the long-term sustainability of microrefugia. On the one hand, if we consider that microrefugia microclimates are mainly generated by topographic parameters, they could better withstand disturbances and protect the community within. On the other hand, if generated mainly by the canopy cover, disturbances affecting the biota, such as fire, biological invasions or human exploitation, might weaken the cooling capacity of such sites considerably. By specifically studying microrefugia characteristics, our approach tests these previous studies of microclimate forcing factors, and provides a better understanding of what makes putative microrefugia unique in the landscape, and insight into their capacity for persistence facing global climatic changes and other disturbances.

The aim of this study is to bridge the gap between microclimates and microrefugia by adopting a bottom-up approach, focusing on current putative microrefugia within the Mediterranean region. The putative microrefugia used in this study are identified using the southernmost disconnected and abyssal populations of *Oxalis acetosella* (Oxalidaceae), a circumboreal herbaceous plant attaining its southernmost limit in Southern France. The locations of these populations match the definition of microrefugia: "small areas where conditions remain favorable for the persistence of populations outside their main species range limits" (Ashcroft, 2010; Rull, 2010). The Mediterranean region is especially interesting in this context because of its remarkable topographic complexity (Harrison & Noss, 2017), and because it is particularly concerned by climate change impacts on biodiversity (Benito et al., 2014; Cramer et al., 2018; Giorgi, 2006; Thuiller et al., 2005). Due to this particular regional context of increasing temperatures and drier climatic conditions in Mediterranean biomes (Ali et al., 2022; Deitch et al., 2017), we consider microrefugia microclimates to be increasingly favorable for the persistence of species if colder mean and maximum temperatures were to be observed: if experiencing colder temperatures compared to the surroundings, populations persisting in such microrefugia would be less affected by a high vapor pressure deficit which peaks during periods of summer heatwaves and droughts (Grossiord et al., 2020). While we use a single species to identify sites that can be understood as microrefugia, our study assesses general interactions between landscape shape, forest type, microclimate and community composition and therefore can be generalized to other ecological models and regions. Specifically, we examine if and why there are systematic microclimatic and biological differences between putative microrefugia and their near surrounding landscape (50 to 100 m in distance) systematically located higher up on north facing slopes as a conservative choice to avoid forcing warmer climate. By doing so, we test the hypotheses that: (i) microrefugia microclimates are colder, remarkably different from the immediate surroundings, (ii) plant communities respond to these fine-scale climatic offsets and (iii) these offsets are enabled by a combination of topographic and forest forcing factors.

2 | MATERIALS AND METHODS

2.1 | Study area

Our study sites are located within the French Mediterranean region, more precisely in its eastern part, the *Provence-Alpes-Côte-d'Azur* (PACA-Sud) region This region spans over 31,400 km^2 and is comprised of 51% forest, dominated equally by deciduous trees and conifers (ONF, 2019). It is characterized by a large diversity of landscapes with highly heterogenous topographic conditions. Mountain barriers in the North protect the region from major cold air influx, and the Mediterranean Sea brings warmth during the winter. Summer and winter climates are highly differentiated, with strong solar radiation throughout the year. Precipitations usually vary from 500 to 2000 mm per year, along a considerable east-western gradient (GREC-SUD, 2016). Elevation ranges from sea level to a maximum of 4100 m (mean = 829 m). Furthermore, this region is known for its rugged topography with deep canyons such as the "Gorges du Verdon" (700 m in depth) or the "Gorges du Daluis" (900 m in depth) and 1000–2000 m high mountain ranges rising directly from the coast in the south eastern part of the region. The remarkable topography creates strong microclimatic gradients and contributed to a complex biogeographical history suggesting numerous past glacial refugia for Mediterranean as well as Alpine plants (Médail & Diadema, 2009; Noble & Diadema, 2011). Species richness and the level of endemism are very high and the region is qualified as both a climatic and a biodiversity hotspot (Médail & Quezel, 1997; Thompson, 2020). The complex physiography, together with the long history of human land-use has also resulted in a highly diverse matrix of anthropic and semi-natural habitats where Mediterranean scrublands, evergreen oak and pine forests contrast with broad-leaf forests dominated by beech or mountainous coniferous forests over very short distances (Médail & Diadema, 2006; Quézel & Médail, 2003).

2.2 | Microrefugia identification

We used the southernmost disconnected and abyssal populations of *O. acetosella* L. (Oxalidaceae) to identify a set of putative microrefugia. *O. acetosella* is a forest herbaceous plant (hemicryptophyte or geophyte sensu Raunkiaer) with a circumpolar distribution, adapted to temperate and boreal biomes (Rameau et al., 1989). While it can be found over a large part of Europe in temperate to boreal climates, it becomes rare in the Mediterranean region, where it attains its warm-edge limits at high altitudes. It occurs mainly between 1200 and 2000 m, and prefers shaded habitats covered by a dense tree canopy, with low luminosity and fairly moist soils (Kuusipalo, 1987; Rameau et al., 1989). Its physiological requirements do not correspond to the Mediterranean climate, due to low the precipitation rate and strong insolation. Populations of *O. acetosella* were identified based on occurrences within the SILENE-Flore database (CBNMed & CBNA, 2019). The list was narrowed down to precise records (10 m around GPS coordinates) beginning in 1960. We first selected the southernmost populations isolated from the main range. To do so, we represented the main range of the species by a juxtaposition of a 5 km buffer zone created around each record. We identified "disjunct microrefugia" as occurrences that were not comprised in the buffer continuum. Additionally, we identified "abyssal microrefugia" as species occurrences where the elevation was below the 5th percentile of *O. acetosella* altitudinal range (<1018 m) and its nearest neighbor was at least 500 horizontal and vertical meters away. From these abyssal occurrences, we kept only the southernmost populations. In total, we identified 5 disjunct and 9 abyssal microrefugia (Figure 1). The selection of populations was carried out using ArcMap (ESRI, 2020). By using disconnected plant populations to identify microrefugia, we aimed at testing if localizations of plant microrefugia were concordant with expectations stated in top-down studies, such as relief forms of canyons and valley bottoms and we purposely did not choose to study microrefugia populations based on specific landscape features or vegetation-pattern excepted occurences of *O. acetosella*.

2.3 | Microclimate measurements

Within each putative microrefugium, we installed Thermologgers developed by TOMST Ltd. measuring temperature at c. 5 cm soil depth and at 1.5 m for near surface air temperatures. Loggers recorded every 15 min for approximately 2 years in the center of the microrefugium, from June 2019 to May 2021, a period characterized by above-average monthly temperatures compared to the 20th century average (NOAA National Centers for Environmental Information, 2022). The same protocol was repeated in neighboring control plots, to determine whether they are warmer and less climatically stable than microrefugia. We selected neighboring control plots located about 50 m away from the upper limit of microrefugia, delimited by the absence of *O. acetosella*. We chose control plots systematically higher up and on more northerly slopes. This conservative choice was made to detect colder climatic conditions of microrefugia that are not due to regular variations with altitude and exposition during warmer periods. Since the choice of localization of microrefugia and control plots was only based on the presence and absence of *O. acetosella*, we were able to test if canopy cover may have varied between the paired-study sites and caused differences in local temperatures.

Due to accessibility and size of microrefugia, the distance between a microrefugium and its neighbor plot varied between 35 and 119 m (detail in Table 1). Based on logger data, we computed daily mean temperatures (T_{Mean}), the 5th percentile of daily minimum

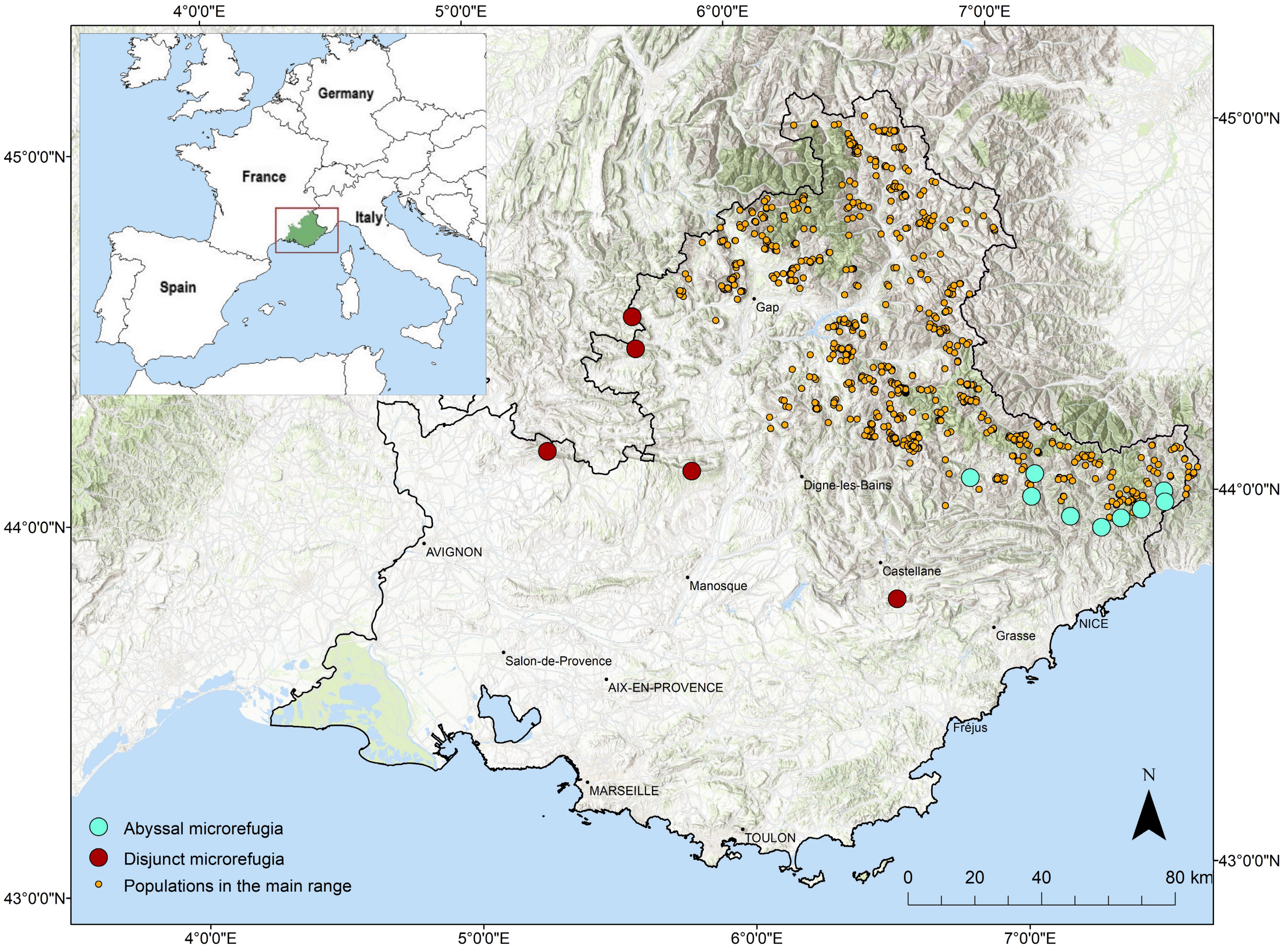

FIGURE 1 Occurrences of *Oxalis acetosella* populations in South-Eastern France, extracted from SILENE-Flore database (CBNMed & CBNA, 2019). Map lines delineate study areas and do not necessarily depict accepted national boundaries. Credits for map bases: World Topo Base: Esri, HERE, DeLorme, increment P Corp., NPS, NRCan, Ordnance Survey, © OpenStreetMap contributors, USGS, NGA, NASA, CGIAR, N Robinson, NCEAS, NLS, OS, NMA, Geodatastyrelsen, Rijkswaterstaat, GSA, Geoland, FEMA, Intermap and the GIS user community. World Hillshade: Esri, Airbus DS, USGS, NGA, NASA, CGIAR, N Robinson, NCEAS, NLS, OS, NMA, Geodatastyrelsen, Rijkswaterstaat, GSA, Geoland, FEMA, Intermap and the GIS user community.

temperatures (T_{Min}), the 95th percentile of daily maximum temperatures (T_{Max}) and the daily thermal amplitude calculated as the difference between daily maximum and minimum temperature (T_{Ampl}) for each site, resulting in four different response variables (Finocchiaro et al., 2022). Soil temperatures were not used for the final analysis, since loggers were often dredged to the surface due to high precipitations or animal disturbances at multiple sites.

2.4 | Characterization of plant communities

To determine if and why there is a variation in species composition between microrefugia and neighbor plots, we considered the percentage cover of species as well as potential forcing factors related to topography, luminosity and humidity (listed below) in each plot. First, we classified the tree layer in terms of foliage cover to calculate the ratio of evergreen to deciduous species (E:D) for each plot, as a proxy for shade conditions and evapotranspiration processes: a higher E:D ratio would indicate higher insolation during the summer due to evergreen tree characteristics compared to deciduous, and vice versa. Then, we used a 5 m grain digital elevation model (BD ALTI, Institut national de l'information géographique et forestière) to extract the variables below as proxies for solar radiation, cold-air drainage and soil relative humidity (Daly et al., 2010; Dobrowski, 2011; Keppel et al., 2012; Pepin & Lundquist, 2008; Pepin & Norris, 2005). First was the Heat Load Index, which is a direct proxy for incident radiation (HLI; McCune & Keon, 2002); then, the Topographic Wetness Index (TWI) following the method of Beven and Kirkby (1979), which gives information on flow accumulation and soil moisture; lastly, the longitudinal curvature of the slope (CURVE), which provides relative information about the shape of the landscape, as a more concave curvature would describe a valley bottom where cold air accumulates as well as shaded sites from the surrounding topography. Microclimate studies usually use relative elevation as a proxy for cold air drainage, however the very short

TABLE 1 Distance between plots and respective altitude

Site name (abbreviation)	Beginning of monitoring	Type of population	Altitude (m)	Distance between microrefugium and neighbor (m)
MOULINET (Mo)	2019-07-18	Abyssal	759	35
FONTAN (F)	2019-10-14	Abyssal	736	43
LUCERAM (L)	2019-07-17	Abyssal	961	47
GUILLAUMES (G)	2019-06-06	Abyssal	774	48
MARTRE (M)	2019-06-25	Disjunct	969	50
SIGOTTIER (Si)	2019-05-28	Disjunct	1309	52
SAORGE (Sa)	2019-08-28	Abyssal	513	53
ILONSE (I)	2019-06-07	Abyssal	884	54
CRUIS (C)	2019-05-27	Disjunct	1584	59
SAINT-SAUVEUR (S)	2019-05-24	Abyssal	656	61
BREIL-SUR-ROYA (Br)	2019-08-29	Abyssal	728	73
LA BEAUME (B)	2019-05-28	Disjunct	1498	83
UTELLE (U)	2019-05-23	Abyssal	749	96
VENTOUX (V)	2019-06-20	Disjunct	1407	119

distance between putative microrefugia and control sites made it non-relevant in this study, and also because it would vary systematically by the design of our study. Finally, we calculated the distance of each site to water (DWAT) as the distance of each cell to the nearest stream sections (BD TOPO Hydrography 2019; IGN) to account for the buffering capacity of water. All computations were done in ArcMap (ESRI, 2020). The toolbox Spatial Analyst and Geomorphometry & Gradient Metrics (Evans et al., 2014) was used for estimating TWI and HLI.

We characterized plant community composition associated with microrefugia and neighbor plots using botanical inventories carried out over a 100 m^2 surface. For each vascular plant identified, we associated a visual percentage cover (%). Then, we considered the plant's optimums of temperature and humidity indicated by ecological indicator values (EIV). The accuracy of EIVs to represent in situ conditions has been demonstrated, with strong suitability between community preferences described by EIVs and climatic measured data (Lenoir et al., 2013; Scherrer & Körner, 2011). For each species, we extracted Pignatti's EIV values of temperature (*T*) and humidity (*U*; Pignatti et al., 2005). Pignatti's EIVs were evaluated for the Italian flora, which reflects the environmental characteristics encountered in our study area very well. The range of indicator values for both variables extends from 1 to 12. For each plot (microrefugium and neighbor) and each indicator, we calculated average EIVs weighted by the percentage cover of each species (EIV community weighed means).

2.5 | Statistical analysis

To test if the climate inside microrefugia was colder compared to each paired neighbor plot, we performed linear mixed models on daily temperatures and amplitudes, with plot type (microrefugium vs. neighbor), type of site (abyssal vs. disjunct) and seasons as predictor variables. Sites were used as a random effect to account for spatial correlation. Models were followed by Tukey's post-hoc test to assess the significance of desired offsets.

We used non-metric multidimensional scaling (NMDS) based on the Bray–Curtis dissimilarity index, in order to visualize variations of plant community composition for both disjunct and abyssal sites, with respect to the forcing factors enumerated above. The significance of community differentiation was obtained by a permutational multivariate analysis of variance (PERMANOVA) using distance matrices (permutations = 999).

To assess whether ecological community optima differed between microrefugia and neighbor plots, we fitted linear mixed models on EIVs community weighted means with type of plot (microrefugia vs. neighbor) as predictor variables, for herbaceous, tree and all strata respectively, so as to specifically ask if the same optimums were observed between the understory vegetation and the tree layer. Again, sites were used as a random effect, to estimate differences in mean EIVs of temperature and humidity within each pair of microrefugium and neighbor plot.

All analyses were carried out in R (version 4.1.1). The package lmerTest (Kuznetsova et al., 2017) was used to fit mixed effect models. The package emmeans (Russell, 2021) was used to extract Tukey's post hoc tests. The package *vegan* (Oksanen et al., 2020) was used to performed NDMS, to fit environmental variables onto the ordination, and to run PERMANOVA.

3 | RESULTS

3.1 | Temperature offsets between microrefugia and neighbor control sites

The 2-year records from paired data-loggers show very distinct climatic dynamics between abyssal and disjunct microrefugia.

Abyssal microrefugia exhibit systematically colder temperatures than their neighbors. When considering all records (regardless of season), mixed effect models, followed by Tukey tests, establish that daily mean temperatures in abyssal microrefugia are 1.1°C colder (Figure 2a; $p < .001$) and that daily maxima are 1.4°C colder (Figure 2b; $p < .001$) compared to neighbor plots (Table 2). These patterns hold for every single abyssal site and season. The strongest buffering effect is detected during summer, with a climatic gap reaching 1.5°C for mean temperatures (Figure 2a; $p < .001$), and 1.6°C for maximum temperatures (Figure 2b; $p < .001$). Overall, minimum temperatures are lower in microrefugia by 0.6°C (Figure 2c; $p < .001$), and this offset is consistent throughout the seasons (Table 2). Thermal amplitudes are smaller in putative abyssal microrefugia for the whole study period, especially in autumn, summer and winter (Figure 2d; $p < .001$).

Disjunct putative microrefugia are also colder than their neighbor plots (Figure 2), but to a lesser extent than abyssal microrefugia. Both daily mean and minimal temperatures are lower in disjunct microrefugia by 0.3°C for the whole study period ($p = .003$ and $p < .001$ respectively), and these contrasts are also more pronounced for mean summer temperatures by 0.7°C ($p < .001$; Table 2). However, responses are neither homogeneous for all study sites, nor for all

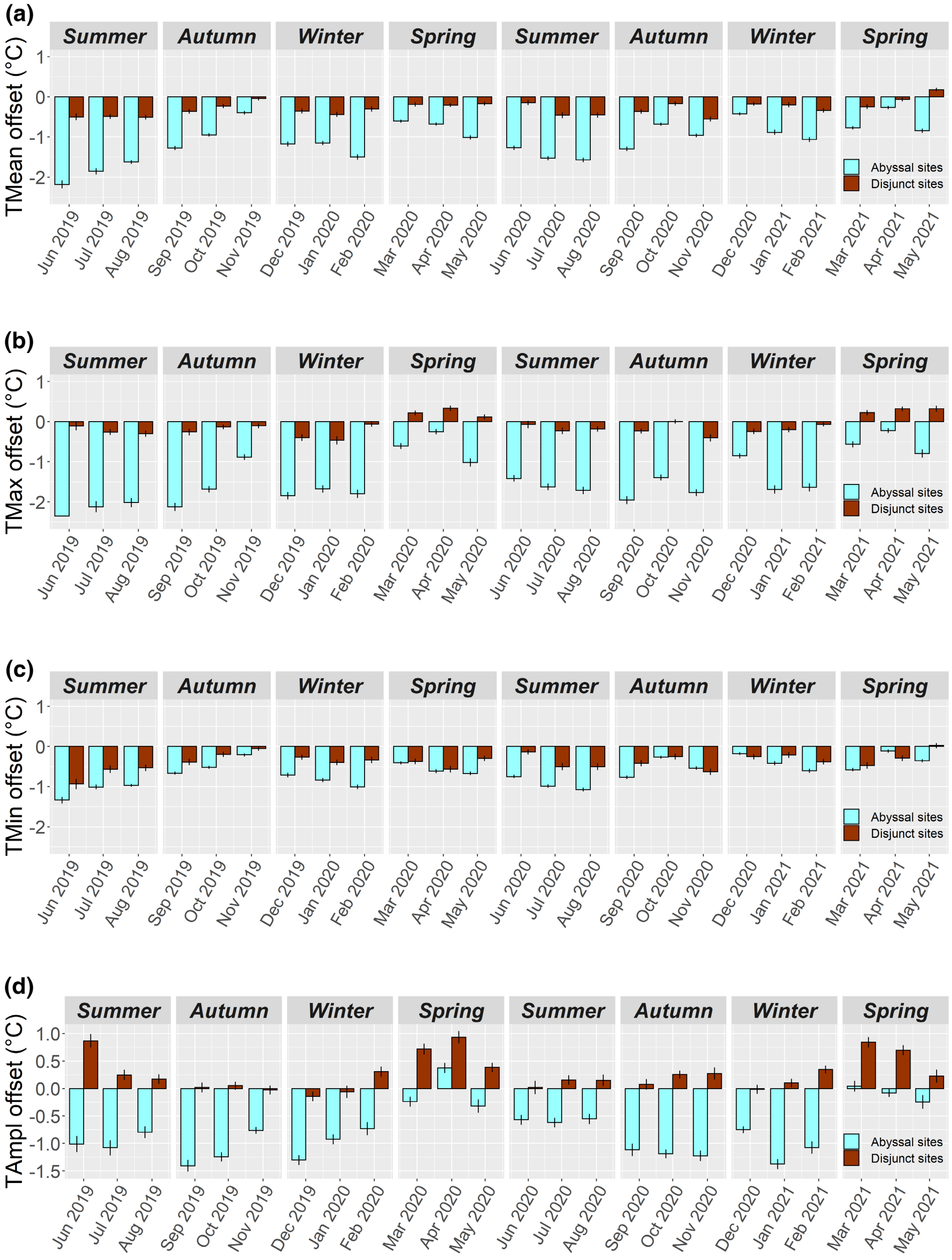

FIGURE 2 Temperature offsets between microrefugia and neighbors in abyssal (blue) and disjunct (red) sites throughout the whole study period calculated as the difference between microrefugia and neighbors for (a) mean (T_{Mean}), (b) maximum (T_{Max}), (c) minimum (T_{Min}) and (d) thermal amplitude (T_{Ampl}).

TABLE 2 Estimated offsets of temperatures between microrefugia and neighbor sites, extracted from Tukey posthoc tests carried out on linear mixed models of (1) ΔT_{Mean}, (2) ΔT_{Min}, (3) ΔT_{Max} and (4) ΔAmplitude as a function of type of plot (microrefugia vs. neighbor), type of sites (abyssal vs. disjunct) and seasons. Bold values denote statistical significance at the $p < .05$ level.

	Annual		Summer		Spring		Autumn		Winter	
	Estimate	*p*	Estimate	*p*	Estimate	*p*	Estimate	*p*	Estimate	*p*
Mean temperature										
Abyssal populations	−1.093	**<.001**	−1.486	**<.001**	−.8043	**<.0001**	−.9989	**<.0001**	−1.0828	**<.0001**
Disjunct populations	−.263	**.003**	−.659	**<.0001**	.0258	.8462	−.1688	.1961	−.2527	.0530
Maximum temperature										
Abyssal populations	−1.381	**<.001**	−1.647	**<.001**	−.721	**<.0001**	−1.574	**<.0001**	−1.579	**<.0001**
Disjunct populations	−.0514	.6275	−.318	.0406	.608	**.0001**	−.245	.1133	−.250	.1057
Minimum temperature										
Abyssal populations	−.616	**<.0001**	−.855	**<.0001**	−.502	**<.0001**	−.512	**<.0001**	−.595	**<.0001**
Disjunct populations	−.338	.0001	−.577	**<.0001**	−.224	.0754	−.234	.0581	−.317	**.0104**
Thermal amplitude										
Abyssal populations	−.763	**<.0001**	−.7911	**<.0001**	−.2178	**.0082**	−1.0604	**<.0001**	−.9831	**<.0001**
Disjunct populations	.287	**<.0001**	.2587	**.0036**	.8320	**<.0001**	−.0107	.9040	.0667	.4502

seasons, and no significant buffering of maximum temperatures in microrefugia can be detected (Table 2). Finally, disjunct putative microrefugia are characterized by a larger thermal amplitude than that of their neighbors ($p < .001$). However, the seasonal analyses show that this difference is significant during summer ($p = .003$) and spring ($p < .001$) only.

3.2 | Plant community differentiation

The results of the PERMANOVA show no difference between plant communities of microrefugia and neighbors in disjunct sites (Adonis $R^2 = .082$; $p = .738$), but a significant distinction for abyssal communities (Adonis $R^2 = .097$; $p = .043$), which means consistent NMDS can be carried out for this group only (stress value = 0.178; Figure 3).

Plant communities in abyssal microrefugia and neighbor plots are mainly differentiated by the TWI and relief curvature (CURVE), indicating a higher degree of humidity in microrefugia, but also a more concave landscape leading to cold air pooling and a greater protection against direct solar radiation compared to neighbor plots. This is consistent with the presence in these microrefugia of *Asplenium scolopendrium*, *Petasites albus*, *Brachypodium sylvaticum*, *Ilex aquifolium* and *Daphne laureola*, which require shade and a humid environment. In comparison, plant communities inside neighbor plots include species more adapted to warmer and drier conditions, such as *Quercus pubescens*, *Pinus sylvestris* or *Asplenium trichomanes*. The ratio E:D, which is the ratio of evergreen to deciduous species, also explains the distinction of plant communities between microrefugia and neighbor plots, showing a higher proportion of deciduous trees inside microrefugia. The variable HLI identifies abyssal microrefugia as sites with lower incoming radiations compared to neighbor plots. The proximity to a watercourse (DWAT) does not satisfactorily explain community repartition in the ordination.

3.3 | Plant community optima reflect fine-scale climatic offsets in abyssal microrefugia

The results of linear mixed models suggest that plant species observed inside putative abyssal microrefugia are characterized by colder temperature ($p > .01$) and wetter moisture requirements ($p > .01$) than those of neighbor plots according to the community weighed means of Pignatti EIVs (Figure 4a,b). This significant contrast is driven by the herbaceous layer for temperature optimum ($p > .01$; Figure 4c), as we find no significant difference in community temperature optima between microrefugia and neighbor plots for the tree layer ($p = .32$; Figure 4b). Inversely, even if only marginally significant ($p = .07$), moisture contrast is stronger for the tree layer (Figure 4e) compared to the herbaceous layer (Figure 4f), which results in a wetter optimum for microrefugia communities compared to neighbor communities, all layers considered (Figure 4d).

4 | DISCUSSION

Our bottom-up approach established a very clear link between putative microrefugia and microclimate at a very fine scale. We showed that microrefugia, especially the abyssal ones, benefit from colder and more stable microclimatic conditions that are reflected in plant community composition when compared to immediate surrounding plots located only 50 to 100 m away. These offsets are strong and systematic, even though we chose to locate neighbor plots at higher altitude compared to putative microrefugia and on northern slopes. Our study also enables isolating and often confirming microclimatic forcing factors playing a key role for the emergence of microrefugia. In particular, this study confirms that sites situated in depressions with concave surfaces are really good candidates for long-lasting microrefugia (Aalto et al., 2017; Dobrowski, 2011; Harrison & Noss, 2017). These results

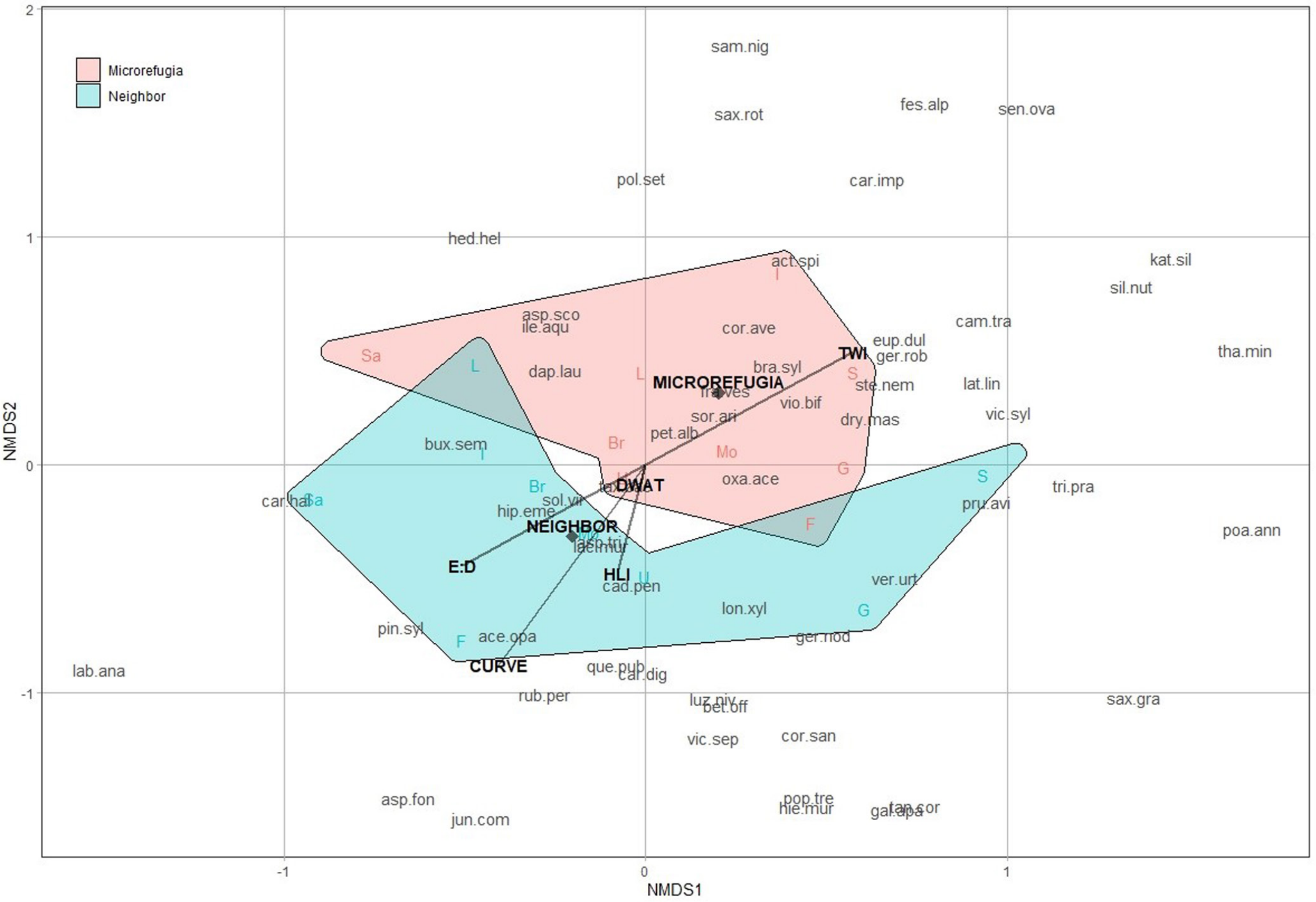

FIGURE 3 Non-metric multidimensional scaling (NMDS) ordination graph of species abundance in microrefugia and neighbor communities of abyssal sites, with potential forcing factors used as supplementary, and projection of sites (site abbreviations are given in Table 1). To avoid overlapping, species are primarily displayed according to Pearson correlation coefficients (higher than .45) on the two dimensions (species abbreviations are given in Table S3). CURVE, curvature index; DWAT, distance to nearest water body; E:D, ratio of evergreen over deciduous trees; HLI, Heat Load Index; TWI, Topographic Wetness Index.

are concordant with those of Bátori et al. (2019), which posit enclosed depressions as key habitat with colder and moister conditions for diverse taxa, including strong contrasts with surrounding south facing slopes and plateau in northern Hungary. Our results also suggest that canopy cover is a key explanatory factor for the presence of microrefugia, which is consistent with previous studies that showed the buffering effect of forest on mean and extreme temperatures (Haesen et al., 2021; Keppel et al., 2017; Zellweger et al., 2020). We could not separate clearly whether putative microrefugia were unique due to their particular physiographical parameters, or because of the composition and density of canopy cover. However, we can speculate that both actively participate in reducing temperatures experienced by the understory vegetation, so that their combined effect can increase the buffering capacity of microrefugia.

4.1 | Microrefugia are linked to microclimates

Records of free-air temperatures over a 2-year period showed that microrefugia have colder temperatures than immediate neighbors. These climatic contrasts are especially interesting during summer seasons if considering that mean and maximum temperatures are supposed to decrease with elevation, and that control plots are specifically positioned higher-up on the north facing slope. Still, thermal dynamics were not homogenous between all microrefugia monitored in our study, which may reflect different levels of sensitivity to warming and thus different chances of species persistence across time.

Temperature offsets between microrefugia and neighboring control plots were especially strong for abyssal microrefugia, which are sites where isolated populations are sustained at extremely low elevation. This holds for mean, minimum and maximum temperatures, and these offsets were stronger during the summer. This is of primordial importance since summer represents the most crucial period for the survival of plants in Mediterranean regions as water stress increases (Ali et al., 2022). Here, plant communities in such abyssal sites are less exposed to such extreme heat. For winter minimum temperatures, observing colder temperatures in microrefugia is less astonishing because abyssal microrefugia are most often located at lower relative elevations in concave valley bottoms, frequently

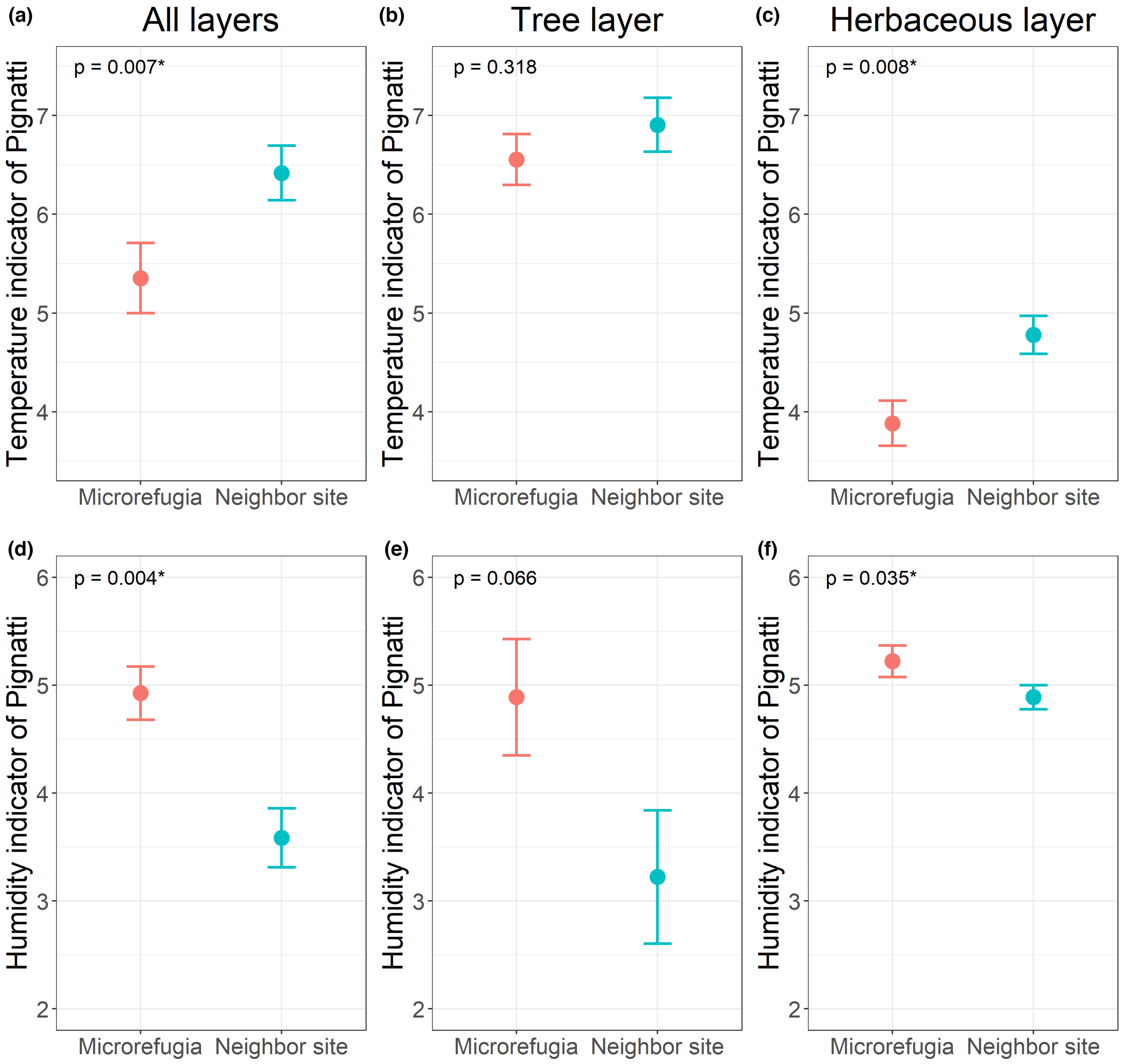

FIGURE 4 Estimated differences of Pignatti ecological indicator values in abyssal sites for (a–c) temperature and (d–f) humidity between microrefugia (pink) and neighbors (blue), for (a–d) all vegetation strata, (b–e) tree layer and (c–f) herbaceous layer (results of linear mixed models are indicated by *p*-values). Asterisks denote statistical significance at the $p < .05$ level.

facing temperature inversions (Ashcroft & Gollan, 2012; Meineri et al., 2015). However, placing putative microrefugia in concave landscapes such as valley bottoms was not chosen, as these were sites with occurrences of *O. acetosella* that were abnormally low in altitude. These results confirm that abyssal microrefugia are subject to specific microclimatic conditions, and acknowledge and reinforce the determinant role of top-down studies in studying microclimate forcing factors to, in the long term, predict the localization of future microrefugia. These results were meant to be completed with soil temperature measurements, giving us precious information about moisture levels in microrefugia (Ashcroft & Gollan, 2013), hypothesized to be higher than in neighbor sites, however soil temperature data turned out to be unreliable since too many soil loggers were dredged out by animals during the study period.

The NMDS results suggest differences in canopy composition and in particular landform between abyssal microrefugia and neighbors. The higher proportion of deciduous trees in microrefugia may provide shadier habitats during the summer, thanks to their horizontal geometry, as opposed to neighbor plots that contain a higher proportion of evergreen trees which allow more radiation to reach the soil surface (De Frenne et al., 2021; von Arx et al., 2013; Zellweger et al., 2019). A higher proportion of deciduous trees can also participate in an increase of air moisture in microrefugia, which in turn, is known to exacerbate the buffering effect of extreme temperatures under the canopy (Grimmond et al., 2000). The curvature index shows a higher degree of concavity in microrefugia compared to the neighbor sites. Due to their geometry, concave sites are likely to be subject to cool air pooling, a process that can cause temperature inversion where lower temperatures are sustained in sheltered sites and topographic depressions (Meineri et al., 2015; Pastore et al., 2022). Furthermore, the variable TWI revealed that water tends to flow into microrefugia. This, once more, indicates that abyssal microrefugia are systematically located at the bottom of topographic depressions (Daly et al., 2010; Dobrowski, 2011; Pepin & Lundquist, 2008). Therefore, we hypothesized that cool air pooling is among the most important drivers for the emergence of microrefugia (Pastore et al., 2022; Patsiou et al., 2017). Cool air pooling is suspected to favor decoupled microclimates that is to say a relative independence between the evolution of the macroclimate and the microclimate of microrefugia over time. We did not study such a process here but acknowledge that this should be the next step, as it would assess whether sites with similar landscape forms can serve as long-lasting microrefugia, where threatened flora in Mediterranean environments would be preserved (Médail & Diadema, 2009). Since respective thermal amplitudes also revealed a higher stability of temperatures in abyssal microrefugia, it would be interesting to see if these thermal offsets are stable or even amplified through time, preserving plant communities in microrefugia where conditions may be increasingly disconnected from macroclimatic fluctuations (De Frenne et al., 2021; Dobrowski, 2011; Lenoir et al., 2017). Still, since the increase of maximum temperatures is expected to be the greater compared to means and minima (Ali et al., 2022), it is clear that the greater offset of maximum temperature between microrefugia and neighbors is an advantage for the plant communities encountered in putative microrefugia, specifically in a region where climatic conditions are already hot and dry and will be even harsher in upcoming years.

Disjunct microrefugia, which in this paper simply represent sites with southernmost disconnected populations, also experienced colder annual mean temperatures compared to neighbors throughout the 2-year records, but with a magnitude four times lower than abyssal microrefugia (Table S1). However, no significant buffering of maximum temperatures was detected and thermal amplitude was significantly higher than in neighbor plots. This seriously questioned the qualification of these sites as putative microrefugia in the long term. The populations of these disjunct sites are systematically established on north-facing slopes at a relatively high elevation, where they can still fulfill their physiologic prerequisites. This distribution matches the "geo-ecological law of distribution" (Boyko, 1947) which posits that at its warm-edges, populations are mainly restrained to pole-facing slopes since they are cool locations protected from high insolation. Nevertheless, as pointed out by Ackerly et al. (2020), the expected warming will increasingly threaten north-facing slope communities, expected to decline and to be replaced by species adapted to warmer and drier conditions. The so-called thermophilization phenomenon (De Frenne et al., 2013; Pauli et al., 2012) is especially at stake in high-elevation landscapes (McCullough et al., 2016). Moreover, due to their exposure and their high elevation, these disjunct microrefugia are more exposed to wind flux coming from the North, particularly strong in the region, which may lead to increasingly drier conditions. As such, these disjunct north-exposed high-altitude sites may not be relevant in the light of the microclimatic definition of microrefugia: In such configurations, temperatures will probably follow closely the warming tendency expected in the Mediterranean region, and consequently, cold-adapted populations might not persist in the long-term facing a warmer and drier climate.

4.2 | Plant community dissimilarities responding to microclimatic variations

Beyond the sole study of a single species, *O. acetosella*, in unfavorable warm and dry surroundings, we wanted to determine whether species sharing the same habitat were also cold-adapted species beneficiating from these localized climatic shelters, in accordance with their physiological requirements. While underlining the link between microrefugia and microclimatic processes, Pignatti's EIVs also indicate that microrefugia plant communities are also characterized by low temperature and high moisture optimums in abyssal microrefugia. Analyzing EIVs for each vegetation stratum separately distinguished strong differences between the tree layer which appears to be greatly influenced by moisture, and the herbaceous layer which is more sensitively driven by temperature. This result might highlight the buffering capacity of canopy cover over temperatures experienced by understory species (De Frenne et al., 2021). We can reasonably argue that the presence of species with colder optima in the herbaceous layer is facilitated by the presence of trees, protecting the understory from direct solar radiation and preventing air mixing with warmer flux issuing from open areas (Greiser et al., 2018; Zellweger et al., 2020). Moreover, temperature and humidity can be seen as parts of a feedback loop below the canopy, where moist soils, beneficial to seedling establishment and the persistence of trees, lower temperatures, which are then favorable to the survival of cold-adapted species (von Arx et al., 2013). Importantly, it acknowledges that plant communities actively respond to microclimatic contrasts at a very fine-scale.

While providing precious information about microrefugia, our paired-study design is necessarily limited because it only compares two different microsites. We cannot exclude that climate and plant communities within the control plots are not representative of the average conditions experienced in the landscape matrix surrounding the microrefugia, but instead are subject to another specific microclimate. For future studies, we recommend monitoring a range of control plots at each site with varying aspects and elevations, to better characterize the unique characteristics of microrefugia in terms of climatic and biological variables. However, field observations from a range of botanical experts and floristic inventories clearly indicate that in our study, the climatic and floristic originalities lie in the microrefugia and not in control plots where communities and associated EIVs are rather common for the Mediterranean region (Saatkamp et al., 2022).

5 | PERSPECTIVES

A long-term monitoring of these populations and their related microclimatic characteristics is needed to understand the functioning of putative microrefugia. Importantly the relative climatic stability of abyssal microrefugia needs to be tested during longer time periods. Perhaps, studying past and current heat waves would show whether microclimatic conditions remain stable during such events. This may give an indication about the temporal decoupling of microrefugia microclimates compared to regional fluctuations. Studying genetic variance between *O. acetosella* populations in these microrefugia and in its core circumboreal distribution would also show if their presence in cool spots at the trailing edge of the species range is related to microrefugia dynamics or to local adaptation (Lenoir et al., 2017). Finally, as advised by Greiser et al. (2020), in order to establish whether microrefugia are viable, long-term demographic studies should be considered: a metastable population would indicate that microrefugia are more likely to persist over time, whereas a decreasing or a shifting dynamic would suggest a gradual disappearance of such cool places. Nevertheless, this study clearly underlines that the microrefugia studied systematically benefit from colder microclimates, that temperature buffering is strong and can be detected from at least a 50 m distance, that the plant community composition mirrors this colder microclimate and that physiographic climate forcing factors that are generally used for downscaling climate in microclimatic top-down studies discriminate putative microrefugia from the surrounding landscape.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Dryad at https://doi.org/10.5061/dryad.j0zpc86j5.

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SUPPORTING INFORMATION

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