Rocky habitats as microclimatic refuges for biodiversity. A close-up thermal approach

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Abstract

In the present scenario of climatic change, climatic refugia will be of paramount importance for species persistence. Topography can generate a considerable climatic heterogeneity over short distances, which is often disregarded in macroclimatic predictive models. Here we investigate the role of rocky habitats as microclimatic refugia by combining two different analyses: exploring a thermal mechanism whereby rocky habitats might serve as refugia, and examining if the biogeographic pattern shows a high abundance of relict, endemic and peripheral species.

The thermal profile of two populations of relict and endemic plant species occurring in Pyrenean cliffs was investigated by infrared images and *in situ* temperature data-loggers. Despite occurring in crevices of a south oriented slope, *Androsace cylindrica* showed a narrower daily range of temperature than the surrounding matrix, thereby avoiding extreme high temperatures. *Borderea chouardii*, of tropical ancestors, also occurred in patches where temperatures were buffered during the growth season, experiencing lower mean temperatures than the surrounding matrix and nearby areas during the warmer part of the day, and similar temperatures during the colder. The rocky habitats of both species, therefore, reduced temperature ranges and exposition to extreme climatic events. Compared to other habitats, the rocky ones also harboured a high fraction of both endemics and peripheral plant populations according to the largest vegetation dataset available in the Pyrenees (18,800 plant inventories and 400,000 records). Our results suggest an association between the habitats of relicts, endemics and species at their distribution limit, driven by a stabilizing effect of rocky habitats on extreme temperatures. Given the important role of rocky habitats as hotspots of singular and unique plants, their characterization seems a sensible first step to identify potential refugia in the context of climate change.

Keywords

Plant inventories, endemics, peripheral populations, infrared images, Pyrenees, *Androsace cylindrica, Borderea chouardii*

Introduction

Predicting the effects of human-caused climate change on biodiversity and ecosystem functioning is one of the most important tasks facing ecologists today. Climate change is assumed to have caused major past changes in the abundance and distribution of many species (Sandel et al., 2011; Scheffers et al., 2016). Likewise, long-term monitoring and macroclimatic models alert about strong losses of biodiversity due to warming (see for example Engler et al., 2011, Gottfried et al., 2012). The real effects of climate change on biodiversity, however, are rather difficult to assess. On the one hand many organisms live in microclimates not identified by regional climatic models (Potter et al., 2013, Aalto et al., 2017). On the other hand, different species have different sensitivities to changes in climate (Stewart et al., 2010). In the end, persistence will depend on whether populations have the plastic or genetic capacity to endure or adapt to new local environmental conditions, and disperse to new locations with similar niche requirements (Graae et al., 2018). The survival of organisms with poor dispersal capacity such as many plants will be more dependent on endurance and successful short-distance migrations across climatically heterogeneous environments.

Topography can produce strong differences in temperatures over short distances (see for example Scherrer and Korner, 2011), which might have profound consequences for species persistence under the ongoing warming scenario. Microclimatic heterogeneity, for example, has been shown to buffer extreme temperatures by as much as 10ºC in the hot Australian landscape (Shoo et al., 2010). At the alpine environment, Scherrer and Korner (2010) also showed an unexpected wide range of temperatures at small scale, being of the same order of magnitude as along elevational gradients, so that many species could find suitable thermal habitats within 2 km^2 under projected scenarios of IPCC. Topographically heterogeneous areas are therefore good candidates to support locally favorable climates amidst unfavorable regional climates, so-called “microrefugia” (Dobrowski 2011).

As a consequence of their particular microclimate, microrefugia are thought to have allowed populations of species to persist and evolve outside of their main distribution areas, and consequently to host a higher frequency of endemic, relict lineages and disjunct range-edge populations than the surrounding landscape (Morelli et al., 2016, Harrison and Noos 2017, Molina et al., 2017, Abeli et al., 2018). Refugia are places of restricted or particular ecological conditions that have been safe havens for organisms, protecting them from perturbations and buffering against climatic fluctuations over geological times (Wetter 1918, Ohlemüller et al., 2008, Morelli et al., 2016, Harrison and Noos, 2017). Such places could be considered natural museums of biodiversity and are likely to play an important role under current global warming, making it urgent to incorporate them into biodiversity conservation planning. One way of identifying microrefugia is to explore the environmental conditions promoting the persistence or generation of endemics and disjunct populations of more common species (Ashcroft et al., 2012). A recent review demonstrated the link between climatic stability and endemism frequency at large spatial scale, mediated by rugged topography (Harrison and Noos 2017). Yet, in spite of much recent research focusing on microclimatic variation and the role of microrefugia, we still largely lack empirical evidence of the mechanisms underlying such sheltering.

In this paper we focus on rocky habitats as putative refugia (litho-refugia), because they are often considered to harbour a unique biodiversity and abundant endemics worldwide (see Baskin & Baskin 1988, Thompson et al., 2005, Speziale and Ezcurra 2014, Schut et al. 2014, Fitzsimons and Michael 2017, Tejero et al., 2017, Bátori et al. 2019). Following the conceptual model of habitat-based refugia proposed by Keppel et al. (2012), we test the role of rocky habitats as refugia by combining two different analyses: one potential mechanism and a biogeographic pattern. If rocky places are indeed refugia, we expect these island-like habitats (cliffs, outcrops, screes…) to contribute to high fine-scale climatic variability in the landscape, and to more stable (for past species to persist) and also cooler microclimates (for current species to survive climatic warming). As a consequence of this and the lack of important disturbances - both factors promoting long-term persistence -, we should find in rocky habitats a disproportionate abundance of endemic species and disjunct populations (Harrison and Noss 2017, Keppel et al. 2017).

This study was carried out in a topographically complex area: the Pyrenean range, a south European mountain that constitutes the limit between the Eurosiberian and the Mediterranean biogeographical regions. Around 3,400 native vascular plant species occur in this mountain range (about 5% endemic, Gómez et al., 2017), which has been recently nominated as one of the main marginal population hotspots of cold-adapted plants in Europe (Abeli et al., 2018). To test the buffering effect of rocky habitats, we investigated if crevices of cliffs lower the mean or amplitude of diurnal and seasonal variation in temperature compared to the surrounding areas. Thermal imaging and miniaturized temperature sensors were used to monitor two tertiary relict plant species of contrasting biogeographical affinities: the cold-adapted *Androsace cylindrica* and the warm-adapted *Borderea chouardii*. To test for a biogeographic pattern that would result from rocky habitats being refugia, we used 18,800 plant inventories across the Pyrenees. Inventories constitute the most extensive information in Europe and best way of describing typical communities of plants at different habitats, allowing us to examine if the proportion of endemic species and geographically peripheral populations in cliffs, screes and other predominantly rocky habitats, is significantly higher than in other habitats.

Methods

Temperature profiles in rocky habitats

To examine the thermal signature of microhabitats where relict plants occur, we selected a population of *Androsace cylindrica* and five patches of the only existing natural population of *Borderea chouardii*. These two plant species are very long-lived (García 2003, García et al. unpublished results) and show unusual morphological adaptations to avoid long-distance dispersal (elaiosome for ants, and autoshowing; García et al 2012), mechanisms suggesting that population survival through geological times is likely to have occurred at site rather than through dispersal to nearby sites differing in microclimate.

Androsace cylindrica is a cushion-form, endemic plant of the central Pyrenees restricted to crevices in calcareous cliffs, between 1,500-2,600 m a.s.l. It belongs to one of the most species-rich plant radiations in the Alpine system (Primulaceae). Recent studies concluded that the diversification of the group was not restricted to Pleistocene glacial cycles, but took place also at the end of Miocene age, and that this particular species diverged 4-5 Myr ago from its closest relative (Boucher et al., 2015, C. Roquet *pers. comm.*). The study population occupies a south facing cliff at 2,100 m a.s.l. (long.: -0.0459, lat.: 42.6342), where around one thousand individuals are estimated to occur. Given that the genus is cold-adapted (it has successfully colonized most temperate and arctic–alpine regions of the Northern Hemisphere) and that the species occurs in crevices, we expected this south facing cliff to somehow evade the effects of direct insolation in the warmest daily period, or to experience a lower mean temperature than the surrounding matrix.

Borderea chouardii (Dioscoreaceae) is a warm-adapted relict plant of tropical ancestors that belongs to the yam's family (there are paleontological evidences of extensive sub-tropical vegetation in the Pyrenees before quaternary glaciations; Barrón et al., 2010). Its global distribution consists of a single natural population, south of the Pyrenean range, between 600-800 m a.s.l. (long.: 0.7435, lat.: 42.3256), in a very rough terrain under Mediterranean climate with hot and dry summers. A few patches with around 10,000 plants are estimated to occur within an occupancy area of less than 2 km^2 (Goñi et al., 2015). The species shows an extraordinary longevity (over 300 years old) and stable population dynamics (García, 2003). This little yam grows in crevices along two NE facing cliffs and overhangs, and in this environment we expected the plant to be restricted to places with lower average and shorter daily amplitudes in temperature, than the surrounding areas.

Temperature profiles were examined in two ways: thermal images and *in situ* miniaturized temperature sensors. These two types of information are complementary and contribute to our understanding on the temporal dynamics of temperatures experienced in the populations. Thermal infrared cameras provide fine-scale surface temperature maps, and constitute a potentially powerful tool for ecological research (Faye et al., 2016). They yield microhabitat temperatures within landscapes, with high spatial resolution at a given point in time. Repetitions through time allowed us to examine spatio-temporal heterogeneity at daily (both species) and seasonal (*B. chouardii*) scale. *In situ* miniaturized temperature datalogger sensors (ibuttons, thermochron-type; Maxim integrated) are able to record temperature at different time intervals, and they are becoming very popular to describe microclimates and produce more precise topoclimatic models (Fawcett et al., 2019). These loggers offer temperature profiles over time at fine temporal scale, but restricted to a single point in the population occupancy area.

Infrared images of the two abovementioned species were taken with a thermo-camera (FLIR T-420): six images at 4 h intervals over a full day during a very hot period in August 2017 for the population of *A. cylindrica* (one of them failed), and two images per month on a single day over the full vegetation period (May-September 2015) for the five patches of *B. chouardii*, one during the warmest (2 pm) and another during the coolest (6 am) time of the day. To sample temperatures experienced by plants we drew several lines on the occupancy area with the FLIRtools software (see Fig. 1 A1 and B1; n=2 for *A. cylindrica* and n=2-5 for *B. chouardii*, depending on the size of the patch). In the case of *B. chouardii* images could be taken much closer than *A. cylindrica*, and then we could draw additional lines in the cliff just outside the area where plants occurred, that served as control (no plants; Fig. 1 B1 black lines). The frequency distribution of pixels at different temperatures was extracted from “occupancy lines” sampling within population (both species) and “control lines” (only for *B. chouardii*), as well as the whole picture (“thermal landscape”). Mean temperatures of occupancy and control lines were compared by GLMs for each patch and hour separately (Gaussian error distribution; month (May, June, July, August, Septemeber) and type of line were included as main effects, their interaction not being significant).

To illustrate other cases of thermal heterogeneity and buffering effect of rocky habitats in the Pyrenean range, some additional images were taken in summer in rocky places: in a hot day for two boreoalpine plants at their southern distribution limit (*Saxifraga cotyledon* and *Woodsia alpina*), and at night for a rocky outcrop sheltering many endemic and disjunct populations or alpine and boreoalpine plants.

iButtons were placed within populations to sample the microhabitat, and recorded at intervals of 4 hours. At the *A. cylindrica* site, one ibutton was placed in contact with plants growing in a crevice, and another one at 2 m in straight line from the cliff; both recorded temperatures from July 2015 to August 2018. At the largest patch of *B. chouardii* another ibutton was placed in contact with plants. It was recording from January 2012 to July 2016, and its microclimatic values were compared with the ones provided by the closest meteorological station, located at 16 km in straight line.

Rocky habitats as putative refugia

We downloaded and validated 18,795 Pyrenean plant inventories located between 400 and 3,300 m a.s.l. from SIVIM, a database of Ibero-macaronesian vegetation (http://www.sivim.info; Font et al., 2010; Fig. 2). Inventories contained more than 400,000 plant records, were carried out by professional botanists, and differed in terms of sampling area and total number of records (mostly depending on the type of habitat). We categorized inventoried areas as belonging to one of 12 typical habitats of temperate high mountains (two habitats with very high anthropogenic influence: ruderal communities and meadows, were excluded): alpine grasslands (Grass_alp), montane and subalpine grasslands (Grass_mont_subalp), montane and subalpine shrublands (Shrub_mont_subalp), aciculifolious forests (Forest_everg_Eur), caducifolious and mixed forests (including gallery forests; Forest_deciduous), forest mantle and margin communities & herbaceous and shrub mantle communities (Margin_mantle), eurosiberian nitrophilous herb communities (Eur_nitro_herb), mediterranean forests (Forest_med), mediterranean shurblands (Shrub_med), mediterranean nitrophilous or nitro-halophilous communities (Med_nitro_herb), cliffs, screes and other ridges (Rocks), and wetlands and very humid areas (including peat bogs, riverside vegetation, and hygrophylous grasslands; Wet_humid). Whereas some habitats are clearly associated to an specific altitudinal interval (the high alpine grasslands, and the low

Mediterranean forests for example), others extend over a wider altitudinal gradient (montane and subalpine shrublands) or are relatively independent of altitude because they are intimately associated to specific abiotic elements (rocks, wetlands).

After validating plant names at the species level according to the Atlas Flora Pyrenaea (https://www.opcc-ctp.org/es/florapyr), each taxon was classified as endemic or non-endemic to the Pyrenees, and as geographically peripheral or non-peripheral depending on whether or not populations were known to occur further north or south of the Pyrenees. Peripheral taxa were scored as N (Pyrenees constitute their northern distribution limit, i.e., taxa were mostly Mediterranean) or S (Pyrenees constitute their southern limit, i.e., taxa were mostly eurosiberian, alpine orophytes, or boreoalpine). Taxonomic genus for which species identification can be uncertain (i.e. the apomictic *Alchemilla* or *Hieracium*), were not scored.

To account for inventories containing different numbers of plant records (N=5-92), we did not calculate the proportion of endemics or peripherals within each inventory. Instead we calculated ratios of target *vs* non-target plants (i.e. endemics *vs* non-endemics, peripherals *vs* non-peripherals). A Generalized Linear Model was fitted (GLM), where the response variable was the ratio of target:non-target in each inventory, to search for significant differences among habitats (analysis of deviance with quasibinomial error due to overdispersion). Model results were back-transformed to obtain the estimated mean percentage of endemics and peripherals in each habitat.

Results

Temperature profiles of rocky habitats

The analyses of thermal images showed that the temperatures experienced by *A. cylindrica* at different hours during a hot day differed from that of the area surrounding the population (Fig. 3). In the occupancy area, the mean temperature had less extreme values than the mean of the matrix, and showed a narrower range (12ºC-29ºC *vs* 8º-40ºC; “all day” histogram). Despite the cliff got direct sunlight in the afternoon, it never had the highest temperatures of the thermal landscape, probably due to the rugged and slightly overhanded nature of the vertical cliff. Longer-term data from the paired temperature loggers recording over a year showed that the mean was slightly lower in the crevice than in an open place 2 m away, and that *A. cylindrica* plants are tamponed from extreme high temperatures in summer, confirming the infrared pattern of narrower temperatures range in the occupied area (Fig. 4). A closer up picture of crevices where plants occur show an important variability of temperatures across a short segment of the cliff (Fig. 1B and 1C; up to 9 ºC at midday), which is merged into a single pixel in the overall picture.

B. chouardii spreads over a few patches that seem not to be exposed to direct sunlight. Thermal images showed that during the warm season (May till September) the population always experienced lower mean temperatures than the surrounding matrix in the warm part of the day, (Fig. 1B and Fig. 5A). This pattern was similar when comparing mean temperatures of lines sampling the occupancy area *vs* control lines: target plants experienced a significantly lower mean temperature in 4 of 5 patches ($p < 0.0001$; "month" was always significant in the test, see also columns in Fig. 5A and 5B). Early in the morning, mean temperatures of the occupancy area also tended to be lower than the matrix (Fig. 5B). There were no significant differences in mean temperatures between the occupancy lines and control lines during the cold part of the day ($p > 0.05$ for all 5 patches). Similar to *A. cylindrica*, monthly mean temperatures recorded by the *in situ* temperature logger and the closest meteorological station were rather similar, but the buffering effect of extreme temperatures was rather symmetrical in this case (Fig. 4).

Snapshoots of other rocky places inhabited by peripheral boreoalpine plant populations also showed that plants were confined to cooler microhabitats offered by N sides or crevices at the hottest daily period (Fig. 6 A & B). This diurnal "cooling system" effect provided by crevices in summer (Fig. 6 C) contrasts with the nocturnal buffering effect found in a subalpine outcrop extremely rich in relict, endemic and peripheral plants (Fig. 6 D; 54% of species among the 29 inventoried in a 3*2 m area).

Rocky habitats as putative refugia

A total of 409,728 plant records belonging to 2,575 plant taxa were included in the dataset, covering 88% of the Pyrenean flora (N=2914 unambiguous taxa occurring above 400 m altitude). The number of Pyrenean endemic plants recorded was 81, corresponding to 84% of the total number occurring in the Pyrenees (N=97). Of species with peripheral occurrences in Pyrenees (N=677), at least 69% were included in the dataset. Therefore, inventories can be considered as representative of the Pyrenean flora.

Rocky places had the lowest number of species records per inventory (Table 1) but were the preferred habitat for endemics (Fig. 7). The average proportion of endemics (7.6%) was significantly higher than in all the other habitats (overall model testing the effect of habitats: $F = 474$, $df = 11$, $p < 0.0001$; explained deviance: 0.35; $p < 0.0001$ for all contrasts using Rocks as reference; Fig. 4). Rocky habitats also hosted the second highest proportion of peripheral species (32.4%) after alpine grasslands (46.6%) (overall model testing the effect of habitats: $F = 848$, $df = 11$, $p < 0.0001$; explained deviance: 0.33; $p < 0.0001$ for all contrasts using Rocks as reference). Alpine grasslands had a higher mean percentage of S (alpine, boreoalpine, and arctic-alpine species) than N peripherals (42% and 5%, respectively), while rocky habitats had a more balanced combination of S (22% of records on average) and N (12%) peripheral species. This difference between the two habitats is partly due to the altitudinal effect: alpine grasslands cover the highest part of the mountains and therefore shelter many S limit plants, whereas rocky inventories are distributed all over the altitudinal gradient. There was a significant interaction between habitat and altitude for both proportion of endemics and peripherals in the inventory (interaction effect $p < 0.0001$ in both cases; explained deviance: 0.45 and 0.60 respectively), meaning that their proportion across habitats depends on altitude. The proportion of endemics was much less dependent on altitude than in peripherals.

Discussion

By monitoring the thermic profiles of two relict plants, we showed that cliffs and crevices might buffer extreme temperatures of thermal complex landscapes. Our results also confirmed the “refugial effect” of rocky habitats across the Pyrenean range, based on the high proportion of endemics and peripheral plant populations compared to other habitats. We therefore propose that the buffering effect would have protected rocky plants from past climatic changes, promoting the accumulation of singular flora.

Topographically driven thermal profiles in complex surfaces

Both thermal imaging, and *in situ* loggers recording maximum and minimum temperatures over periods of time, showed that microhabitat conditions of rocky patches and crevices inhabited by two relict plants of different biogeographical affinities have thermal dynamics that markedly differ from the surrounding landscape where they occur. Despite being in a south-facing cliff, the population of the cold-adapted *A. cylindrica* enjoyed cooler mean temperature than the surrounding matrix most of the day in summer, and lowered extreme maximum temperatures over the year. The relict *Borderea chouardii* is restricted to small patches where the mean temperature was lowered during the warm period of the day than in areas a few meters away, and showed a narrower range of temperatures over the full vegetative season. Since *B. chouardii* occurs in a single natural population in the world, our results describe rather exactly the thermal niche of this species, and suggest that the persistence of other relict plants might have been promoted by stable climatic conditions. Snapshots in other plant populations also revealed the association of other relict, endemic or peripheral species to the cool crevices of rocky places during the hottest daily period compared with the surrounding, as well as a nocturnal “warming effect”.

The observed effects of topography could only be detected in our study with the use of devices recording temperatures at very fine spatial or temporal scale. The surface temperatures of the rocky microhabitat where the two relict plants investigated occur do not match the ones in the landscape, because mean temperatures are lowered and/or buffered from extreme ones. This situation fits two of the requirements proposed by Ashcroft et al. (2012) to identify microrefugia. The occurrence of climatically stable microhabitats, or highly variable climatic conditions within short geographic distances for species to migrate easily, is likely to be of paramount importance for the *in situ* persistence of plants under ongoing climatic change. Recent studies have proven that microtopography produces temperature mosaics with ranges at small spatial scales of the same order of magnitude as along elevational gradients (Scherrer and Körner, 2010). Such large variation of microclimate conditions in alpine landscapes will buffer the impact on biodiversity by offering refugia rather than forcing all species upslope to track climatic warming. Interestingly, our study did not highlight typical alpine sensitive systems; it showed the “thermal stabilizing” value of rocks in general, and expands elsewhere the possibility of refugia conditions they offer. This means that other non-alpine plants occurring in rocky habitats spread over mountainous landscapes might be more resistant to climatic warming than assumed.

Air temperature is not always a good proxy of temperatures experienced by plants (Körner and Hiltbrunner, 2018). The climatic niche or our two relict plants, for example, would have been impossible to model with standard climatic models because they do not account for microhabitat complexity and topography-driven patterns of temperatures and other important environmental attributes. Spatially fine resolution species distribution models yield more realistic scenarios (Randin et al., 2009), and a new generation of climatic models including topographic heterogeneity and other ecological variables are evidencing that fine-scale variation in temperatures is important in reducing species range retractions and extinction risks due to climatic change (Slavich et al., 2014, Maclean et al., 2015, Niskanen et al., 2017, Meineri and Hylander, 2017, Suggit et al., 2018). The survival of a very rare plant in the Alps, for example, could only be explained by the existence of topoclimatic microrefugia (Patsiou et al., 2014). Accounting for such microclimatic heterogeneity becomes necessary when predicting the effect of ongoing climatic change, in particular for plants restricted to rocky microhabitats.

Rocky habitats as refugia

Our analysis of thousands of plant inventories in one of the richest and southernmost European mountains, the Pyrenean range, demonstrated the importance of rocky habitats in harbouring a large fraction of endemics and peripheral populations at the geographical edge of species' ranges. The high frequency of endemics in rocky habitats had been qualitatively acknowledged from information included in regional floras (Tejero et al 2017), whereas the role of rocky habitats in hosting geographically marginal populations had passed rather unnoticed up to now.

The Pyrenees have been recently identified as one of the “marginal population hotspots” in Europe, based on the co-ocurrence of cold-adapted plant species (circumpolar, circumboreal and arctic-alpine species; Abeli et al., 2018). These species are often located high up in rocky areas, alpine grasslands and cold wetlands. In an exhaustive review of geomorphological landforms in alpine systems, Gentili et al. (2015) acknowledged the role of alpine landforms and deposits, particularly the rocky ones, in hosting numerous species by providing a multitude of microhabitats and ecological niches. Our study, based on the largest comprehensive dataset of the Pyrenean vegetation, identified other habitats as “refugial” for peripherals besides alpine grasslands, such as cliffs and screes occurring along the entire altitudinal gradient. While fast identification and mapping of potential refugia from new technologies like LiDAR are becoming of high importance in conservation planning (Schut et al., 2014), traditional fine scale inventories of biodiversity are needed to confirm the refugial value of those places.

Our study highlighted the value of rocky marginal habitats for the conservation of a very singular flora: narrowly distributed species, and peripheral populations of mainly north distributed or south distributed plants. The refugial value of rocks for maintaining biodiversity has also been proposed in other systems like Australia's rainforest fauna (Couper and Hoskin, 2008). These island-like patches constitute long-term “safe” places for natural or anthropogenic disturbances (including land use, herbivory and fire), despite that they might not always be large and contain a large number of individuals. Nevertheless, rocky plants show an extraordinary stable demographic dynamics and low extinction risks (Larson et al., 1999, Picó and Riba, 2002; García, 2003), allowing for long-lived organisms to persist in small patches under unfavourable climatic conditions in their own “slow world”. An interesting challenge will be to compare demographic responses to yearly climatic variation of relict and highly specialized species restricted to small and isolated rocky patches, with other plants.

Conclusion

The identification of microclimatic characteristics in hotspots of endemics and marginal populations might improve our understanding on the ecological attributes that characterize microclimatic refugia. Based on results of this study, we have suggested the existence of a “stabilizing thermal effect” at small scale in rocky habitats behind long-term persistence of old lineages over geological times. We cannot make inferences about how general such mechanistic buffering from variation in temperatures has been in the past. Besides, south-facing beaks, cliffs and screes where insolation heats the bedrock to higher temperatures than the surroundings, or where high exposition to wind reduces moisture, are also frequent in mountain landscapes. But the association between the buffering effect of extreme temperatures in rocky habitats and the high frequency of singular flora they shelter might spur further research.

Rocky habitats accumulate endemics and marginal populations, very singular elements of regional floras that are often listed as endangered species. They should therefore be important targets for conservation (Gentili et al., 2016; Keppel et al., 2015; Morelli et al., 2016). Not considering the microclimatic heterogeneity when modelling their future distribution under climatic change, or the “refugial effect” of rocky areas where they occur will overestimate extinctions rates. *In situ* conservation measures are always easier and cheaper to implement, and it seems sensible to start by identifying refugial locations, where little effort is needed to assure the persistence of occurring plants when the regional climate becomes unsuitable.

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Figure Legends

Figure 1- A: Population of *Androsace cylindrica* showing the occupancy lines (A1) and two close up images with overlapped thermal images in the insets under the sun (A2) and shadow (A3). B: One of the five patches of *Borderea chouardii*, showing control (black) and occupancy lines (red) (B1), and analysed images corresponding to the combination of month (May to September) and high or low temperature (HT: afternoon, LT: early in the morning, respectively) (B2).

Figure 2- Distribution of plant inventories carried out over the last century in the Pyrenean range. Inventories were geolocalized at two different scales: 1 km^2 (red squares) and 10x10 km (green squares; typical resolution for the oldest inventories).

Figure 3- Thermal profile at the *Androsace cylindrica* site over 5 different moments in a hot day of summer, and all together (“all day” histogram). Bars correspond to the frequency of pixels resulting from occupancy lines (green color) and the whole thermal landscape (grey bars). Dashed lines are mean temperatures.

Figure 4 – Logger temperatures of the two relict species studied. Above: *Androsace cylindrica* site; two ibuttons recorded simultaneously in a crevice where plants occur (Andr) and two meters away (Out). Below: *Borderea chouardii* site; data from an *in situ* ibutton (Bord) and the closest meteorological station (Station) located at 16 km in straight line and at similar altitude. The absolute maximum and minimum, and mean monthly temperatures (MAX_, MIN_, MEAN_ respectively) are shown.

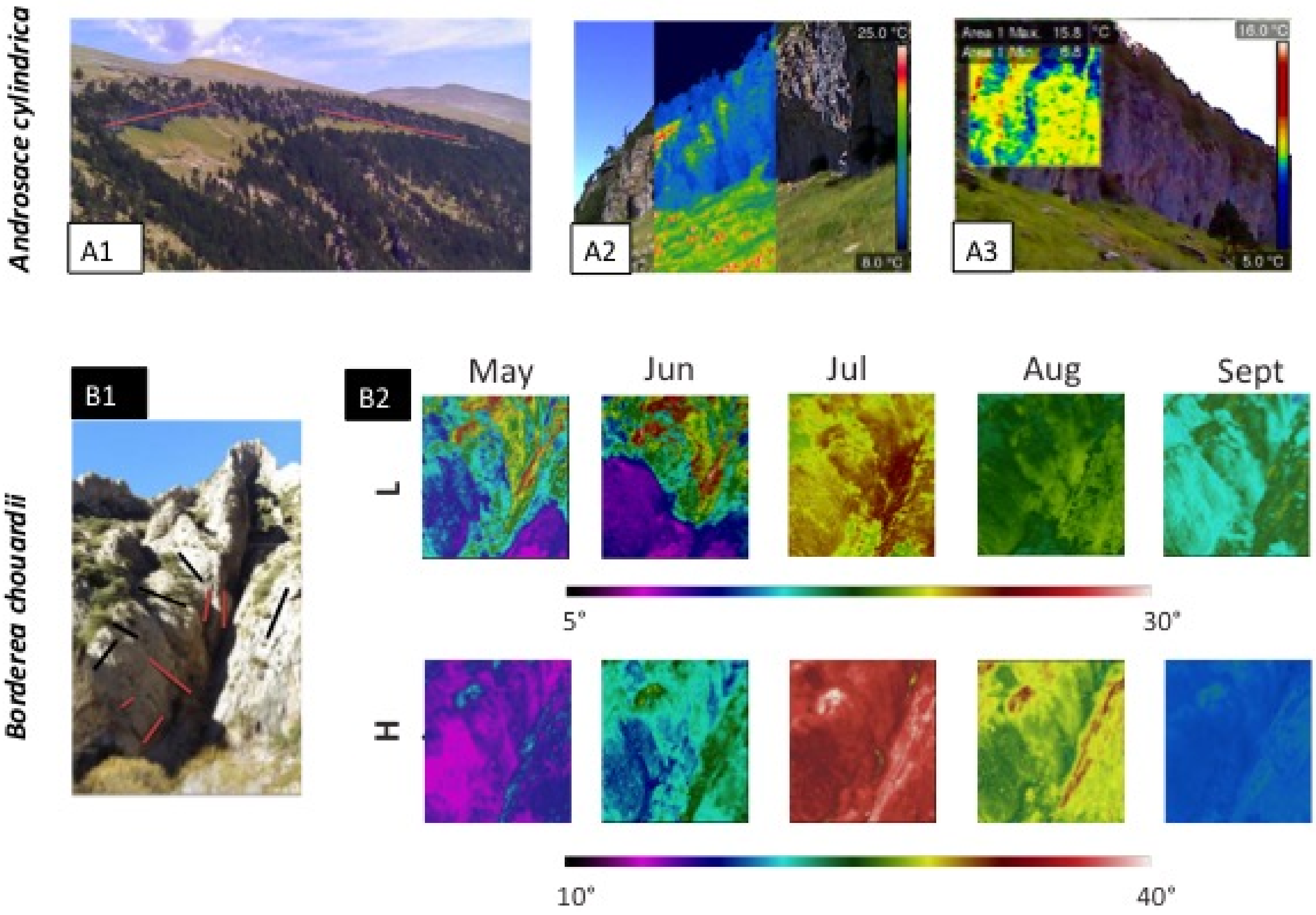
Figure 5- Thermal profile at the *Borderea chouardii* site. Each histogram represents the frequency distribution of temperatures at the warmest (A) or coolest (B) moment of the day, in five population patches during May-September 2015. Red colours: occupancy lines; Grey colours: thermal landscape; dashed lines: mean temperatures.

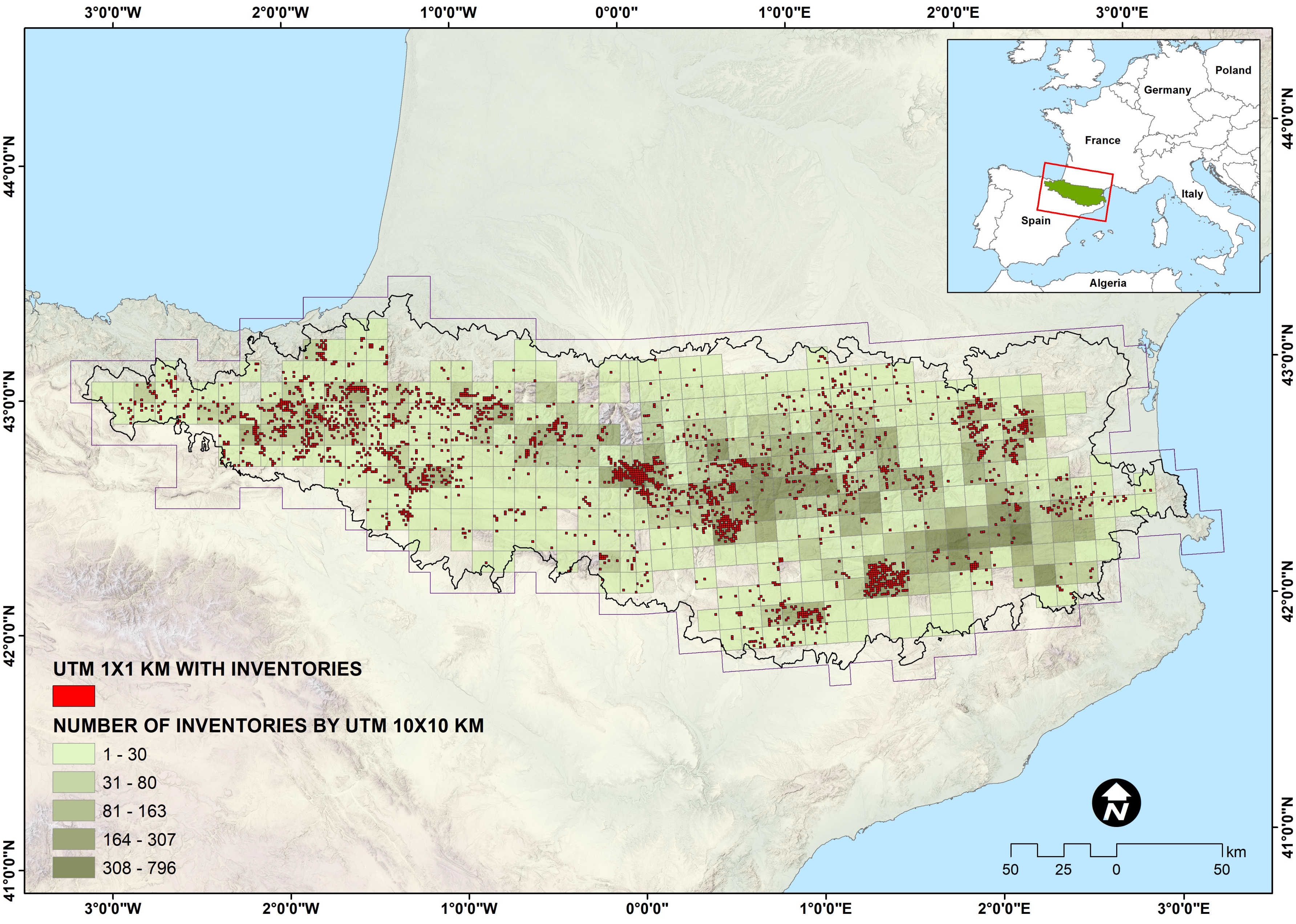
Figure 6.- Thermal and digital images of rocky places showing the effect of microtopography on temperature distribution: A) North facing boulders sheltering plants of the boreoalpine *Woodsia alpina* in one the its southernmost Pyrenean populations, (B) small cliff sheltering plants of the boreoalpine *Saxifraga colyledon* in one the its southernmost Pyrenean populations; (C) crevice just below a *S. cotyledon* plant, to show the cooler effect of the crevice, (D) digital image at midday of a subalpine north facing outcrop in the Ordesa and Monte Perdido National Park (left), and thermal image in the night (right) to see the warming effect of the rocks sheltering a community of plants where 54% were endemic and peripheral to the Pyrenees (note differences in the temperature range of both images).

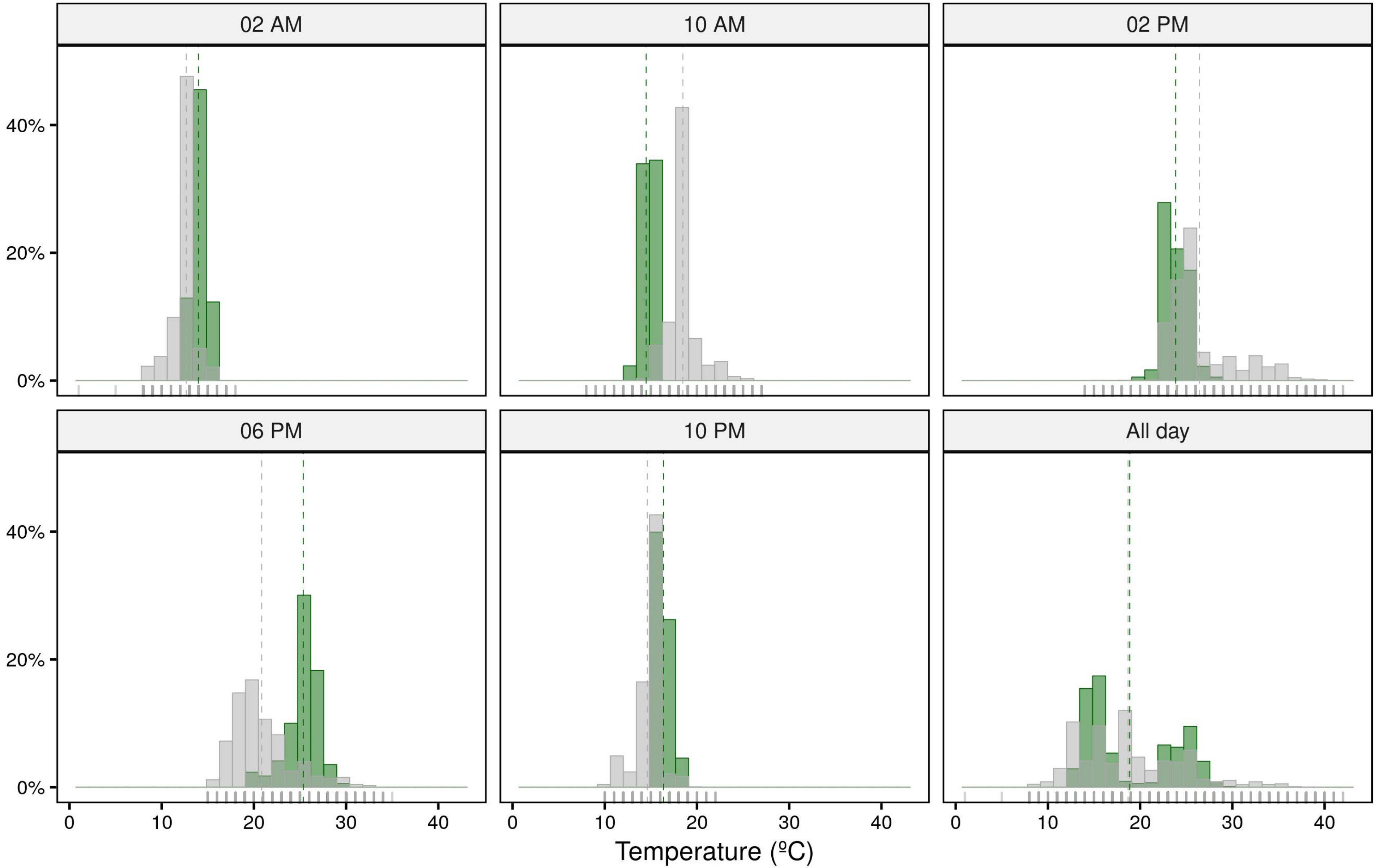
Figure 7- Estimated mean frequency of endemic and peripheral plant species across twelve Pyrenean habitats (see text for details on how values were estimated)

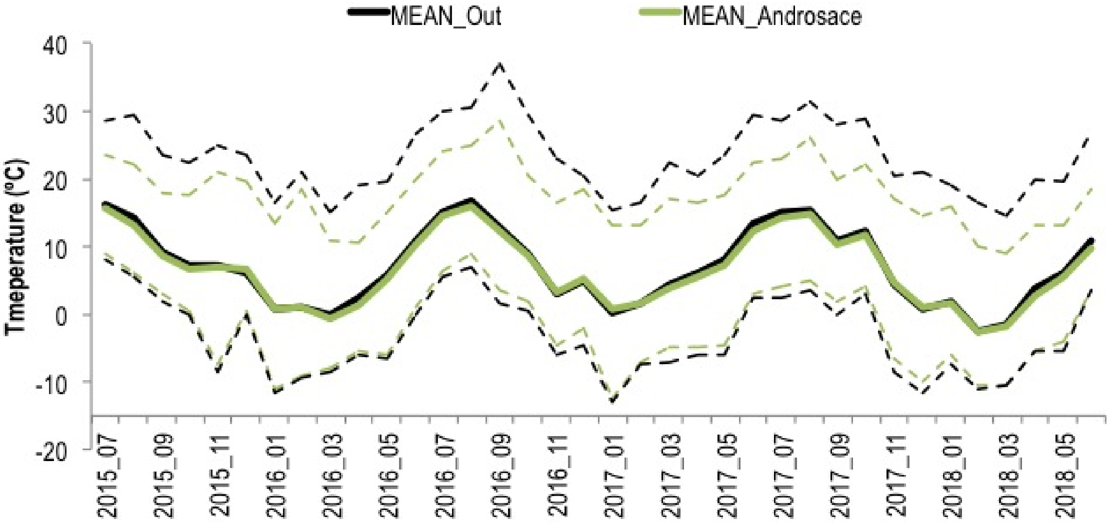
Table 1- Number of plant community inventories, records, and mean number of records per inventory in each Pyrenean habitat. Total number of taxa, endemics (END_taxa) and peripherals (LIM_taxa) in each habitat is also shown (notice that due to fact that the same taxa might occur in different habitats, italic numbers in the last line do not correspond to the sum through habitats but to total numbers).

	Inventories	Records	records/inventory	Total_taxa	END_taxa	LIM_taxa
Eur_nitro_herb	732	12465	17.0	975	7	81
Forest_deciduous	3594	100179	27.9	1286	15	183
Forest_everg_Eur	1155	25925	22.4	875	21	165
Forest_med	460	10230	22.2	658	7	66
Grass_alp	610	12979	21.3	409	24	143
Grass_mont_subalp	4718	124336	26.4	1592	47	312
Margin_mantle	1039	20973	20.2	1088	20	147
Med_nitro_herb	704	13561	19.3	986	4	63
Rocks	**2269**	**26759**	**11.8**	**1082**	**60**	**230**
Shrub_med	218	4518	20.7	597	5	79
Shrub_mont_subalp	1711	33868	19.8	1207	42	254
Wet_humid	1585	23935	15.1	822	8	128
Total	18795	409728	20.3	*2575*	*81*	*470*


Androsace cylindrica
A1
A2
25.0 °C
8.0 °C
A3
Area 1 Max. 15.8 °C
16.0 °C
5.0 °C
Borderea chouardii
B1
B2
May
Jun
Jul
Aug
Sept
L
5°
30°
H
10°
40°


3°0'0"W
2°0'0"W
1°0'0"W
0°0'0"
1°0'0"E
2°0'0"E
3°0'0"E
44°0'0"N
43°0'0"N
42°0'0"N
41°0'0"N
Poland
Germany
France
Italy
Spain
Algeria
UTM 1X1 KM WITH INVENTORIES
🟥
NUMBER OF INVENTORIES BY UTM 10X10 KM
1 - 30
31 - 80
81 - 163
164 - 307
308 - 796
N
km
50
25
0
50


02 AM
10 AM
02 PM
06 PM
10 PM
All day
0%
20%
40%
0
10
20
30
40
Temperature (ºC)


MEAN_Out
MEAN_Androsace
Tmeperature (ºC)
40
30
20
10
0
-10
-20
2015_07
2015_09
2015_11
2016_01
2016_03
2016_05
2016_07
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2018_01
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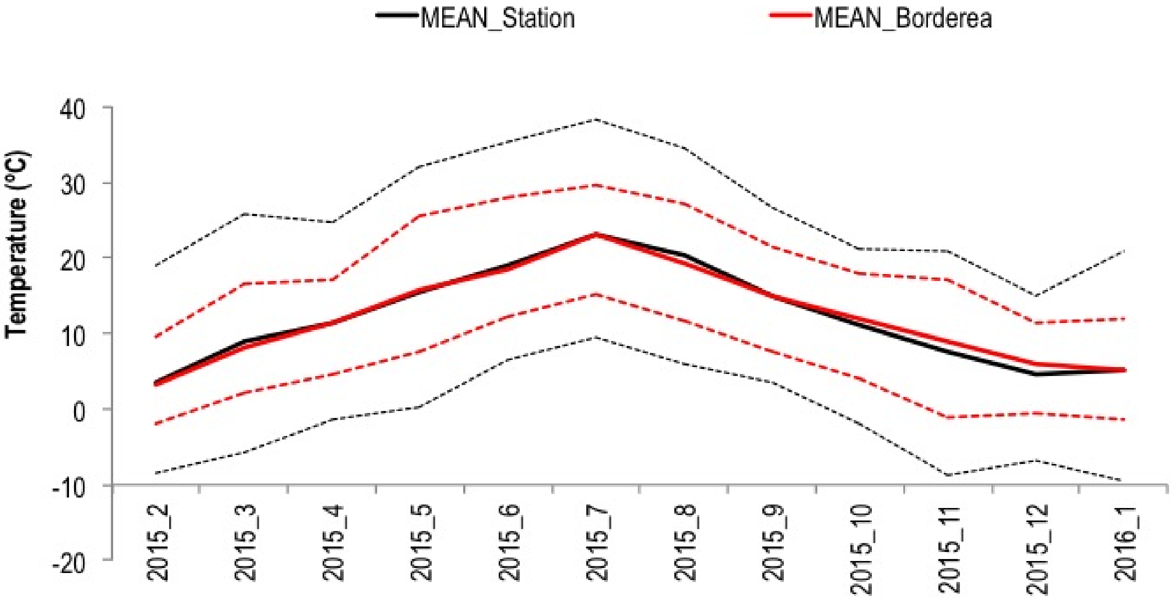
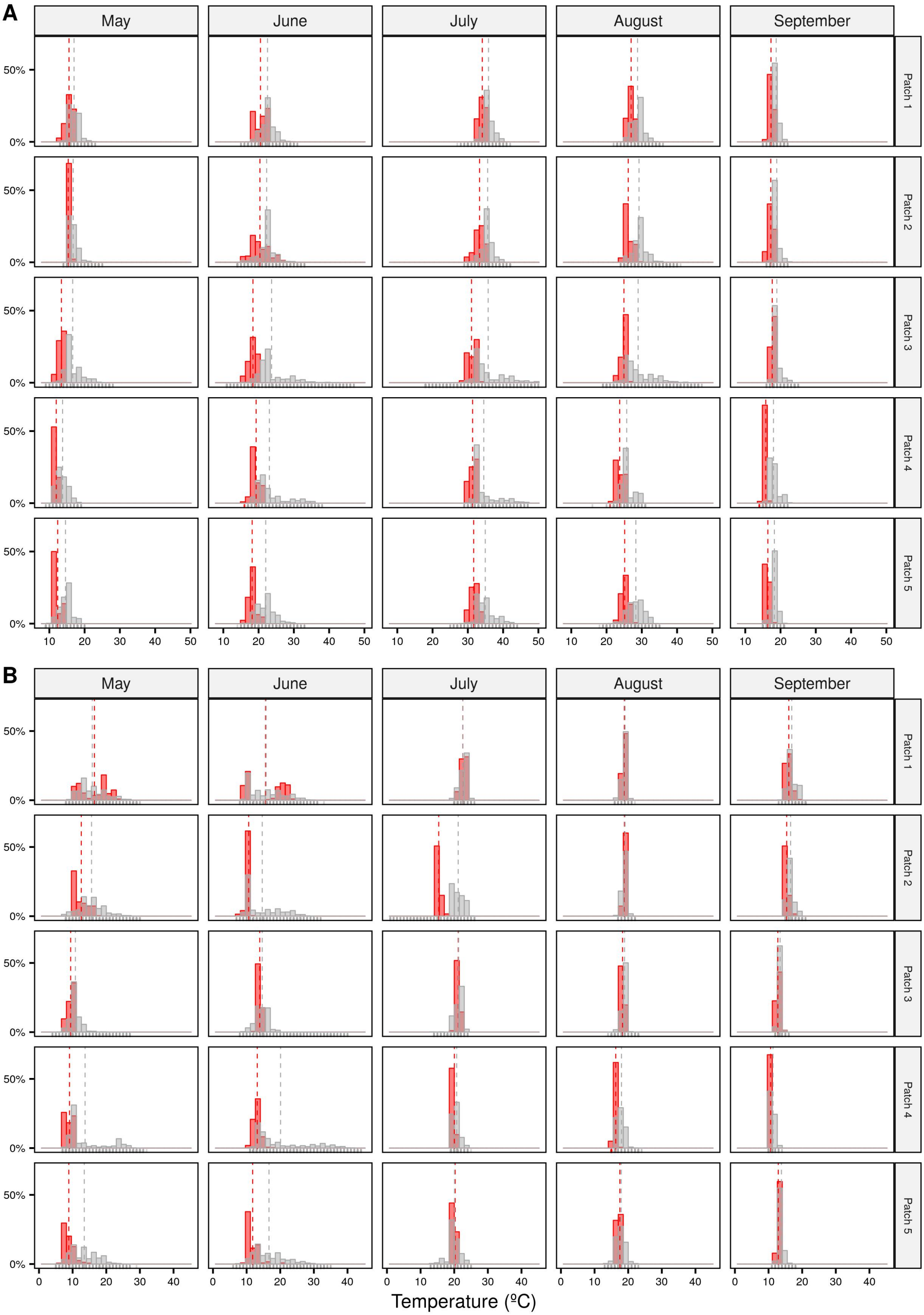
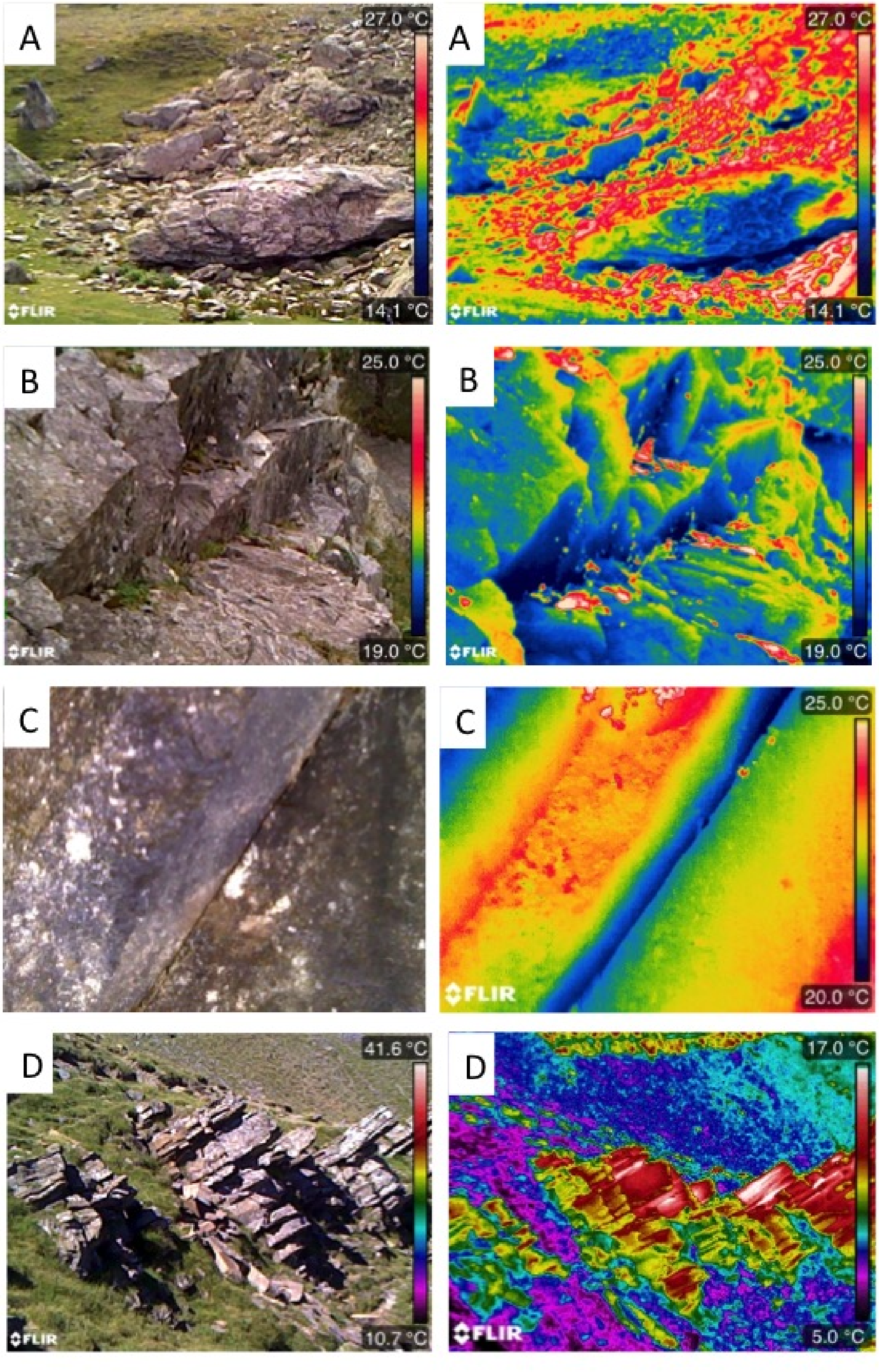
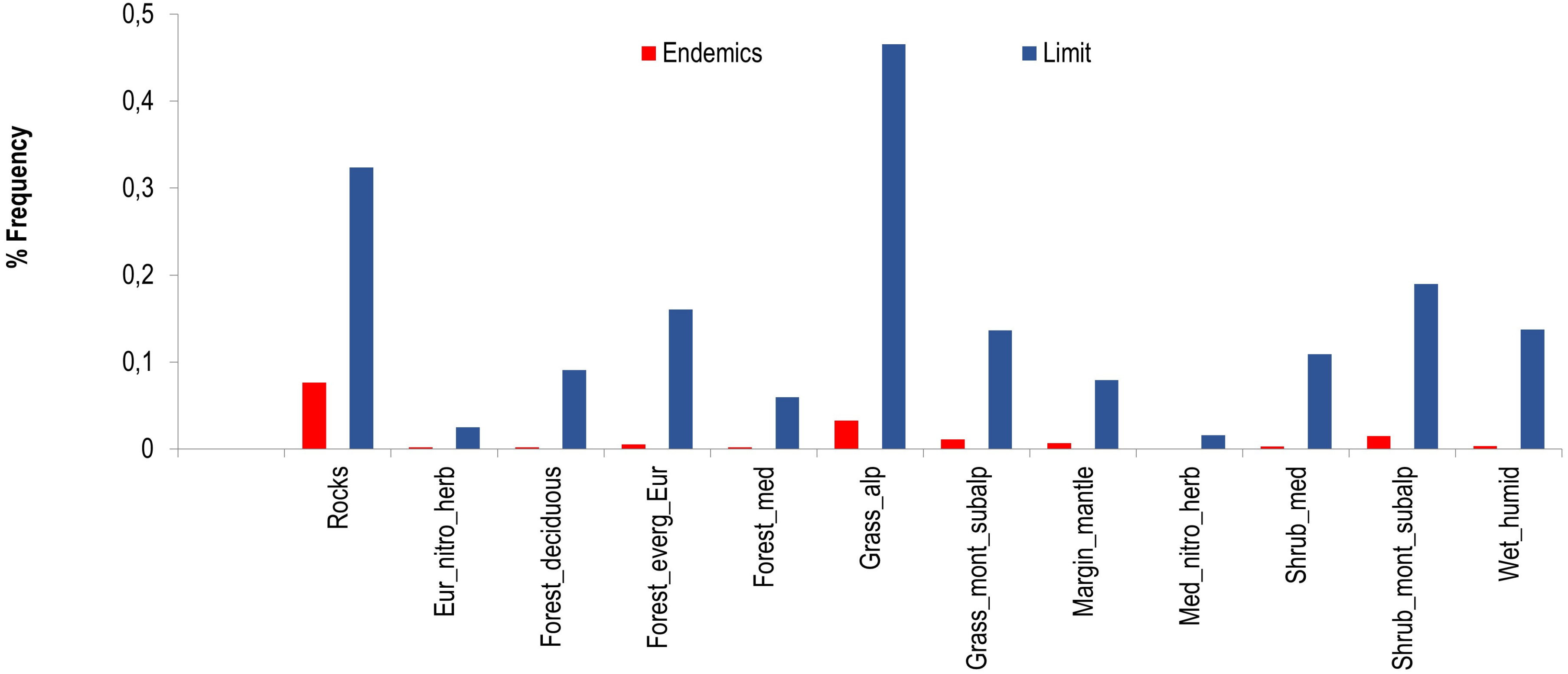
2018_05


MEAN_Station
MEAN_Borderea
Temperature (ºC)
40
30
20
10
0
-10
-20
2015_2
2015_3
2015_4
2015_5
2015_6
2015_7
2015_8
2015_9
2015_10
2015_11
2015_12
2016_1


A
May
June
July
August
September
Patch 1
Patch 2
Patch 3
Patch 4
Patch 5
50%
0%
10
20
30
40
50
B
May
June
July
August
September
Patch 1
Patch 2
Patch 3
Patch 4
Patch 5
50%
0%
0
10
20
30
40
Temperature (ºC)


A
27.0 °C
14.1 °C
FLIR
A
27.0 °C
14.1 °C
FLIR
B
25.0 °C
19.0 °C
FLIR
B
25.0 °C
19.0 °C
FLIR
C
C
25.0 °C
20.0 °C
FLIR
D
41.6 °C
10.7 °C
FLIR
D
17.0 °C
5.0 °C
FLIR


0,5
0,4
0,3
0,2
0,1
0
% Frequency
🟥 Endemics
🟦 Limit
Rocks
Eur_nitro_herb
Forest_deciduous
Forest_everg_Eur
Forest_med
Grass_alp
Grass_mont_subalp
Margin_mantle
Med_nitro_herb
Shrub_med
Shrub_mont_subalp
Wet_humid