Botanical Journal of the Linnean Society, 2024, **205**, 75–83
https://doi.org/10.1093/botlinnean/boad063
Advance access publication 23 March 2024
Original Article

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Functional traits of non-vascular epiphytes influence fine scale thermal heterogeneity under contrasting microclimates: insights from sub-Mediterranean forests

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ABSTRACT

Lichens and bryophytes contribute to regulating the forest microclimate and support ecosystem functions. Exploring the thermal heterogeneity at a trunk-level may help elucidate the effect of thermoregulation of epiphytes. We hypothesized that (i) the thermal patterns of epiphytic communities depend on the microclimatic conditions of the surrounding atmosphere and (ii) the thermal heterogeneity at a trunk-level may in turn depend on functional traits of epiphytic communities, such as thallus colour and growth form. We carried out two measurement sessions under contrasting microclimatic conditions (wet vs. dry). Using a thermal camera, we acquired infra-red (IR) images of 50 trees during the same time period under the contrasting wet and dry conditions. Results showed significant differences in thermal characteristics of the trees when contrasting wet with dry conditions and that colour and growth form were significantly associated with changes in thermal patterns at the trunk-level. The study highlights the importance of understanding the thermoregulatory processes of epiphytic communities.

INTRODUCTION

Temperature is a physical parameter that is crucial in determining the life cycle of organisms (Guisan and Zimmermann 2000). In particular, it is critical for sessile organisms that live in close contact with the substrate (Potter *et al.* 2013, Hannah *et al.* 2014). Surface temperature of the substrate, in turn, is a function of atmospheric temperature and certain physical–chemical characteristics, such as the heat capacity and the mass of the substrate material (Still *et al.* 2019). Moreover, an interaction between physical and biological factors produces effects on the temporal dynamics and spatial patterns of temperature, i.e. thermal heterogeneity (Caillon *et al.* 2014), that have a considerable ecological significance. An example on a landscape scale is the mitigating effect of the canopy trees. Chiefly, the canopy of a forest is crucial in buffering air temperature and relative humidity (De Frenne *et al.* 2021) reflecting and absorbing part of the solar radiation during the day (Geiger *et al.* 2009). Even at scales of greater detail, such as under the tree canopy, there may be biological processes determining changes in temperature that regulate ecosystem functions. For example, in sub-Mediterranean forests, different lichens and bryophytes find locally suitable conditions for colonizing their epiphytic environment (i.e. tree trunks and branches).

Despite their small size, non-vascular epiphytes support key ecosystem functions (Ellis 2012, 2019, Porada *et al.* 2013, Soudzilovskaia *et al.* 2013). Being non-vascular poikilohydric organisms whose water content tends to reach an equilibrium with the surrounding environment (Proctor and Tuba 2002), lichens and bryophytes contribute to regulating the forest microclimate. Notably, this role is related to functional traits that drive their responses to, or determine their effect on, environmental factors (Violle *et al.* 2007, Koch *et al.* 2019, Ellis and Eaton 2021). At the scale of the epiphytic environment, functional traits of lichens and bryophytes, such as the growth form and the thallus colour (Kershaw and Field 1975, Gauslaa 1984), act as effects traits (Violle *et al.* 2007, Ellis *et al.* 2021a) determining the surrounding temperature through the exchange of water and heat at the substrate–atmosphere interface (Rice *et al.* 2018). At large scale, studies have shown how the colour of the thallus changes the albedo by intercepting solar radiation (Aartsma *et al.* 2020).

Received 31 May 2023; revised 5 October 2023; accepted 8 October 2023

Other investigations consider the density of lichen and bryophyte mats and observed that the soil microclimate was affected by their thickness due to the different exchange of water and heat with contrasting peaks between bryophytes and lichens (Soudzilovskaia *et al.* 2013, Rice *et al.* 2018, van Zuijlen *et al.* 2020).

Although it is expected that similar thermoregulatory processes might also be observed at the trunk scale, this effect has still been little explored in the literature or quantified. Moreover, the thermal heterogeneity emerging from lichen and bryophyte traits could have consequences for other biotic components of the ecosystem, e.g. by enhancing the availability of areas with microclimatic conditions suitable for epiphytic microinvertebrates or other organisms associated with the bark environment (Senior *et al.* 2019).

Exploring thermal heterogeneity at trunk-level may help determine the thermoregulatory effect of epiphytes and, in perspective, this would lead to a quantification of the ecosystem functions supported by these organisms (Porada *et al.* 2013, Gauslaa 2014, Porada and Giordani 2021). Although thermal-imaging studies applied to ecology have developed a great deal in recent years (Senior *et al.* 2019), there are a few works dealing with the thermal characteristics of non-vascular plants or fungal communities (Gersony *et al.* 2016, Moore *et al.* 2019, Niittynen *et al.* 2020, Cordero *et al.* 2023).

In this work, we investigated epiphytic communities at the tree scale by thermal imaging, aiming to explore their thermal heterogeneity under contrasting microclimatic conditions. Since epiphytic communities tend to be in equilibrium with their environment, and water is crucial for regulating metabolic activity, we hypothesized that (i) the thermal patterns of the epiphytic communities depend on the microclimatic conditions of the surrounding atmosphere, such as T, RH, and rainfall. However, considering that at the tree scale the contribution of the biological activities of non-vascular epiphytes is quantitatively non-negligible and that these organisms may have a direct effect on temperature, we also hypothesized that (ii) the thermal heterogeneity on tree trunks may depend on functional traits of epiphytic communities that are involved in thermal dynamics, such as thallus colour and growth form.

MATERIALS AND METHODS

Study area

The study was carried out in a Sub-Mediterranean Forest site of the Ligurian Apennines (northern Italy), in the locality of Rovegno (44° 34′ 33.14″ N 9° 16′ 43.82″ E) at ~700 m a.s.l. The area is characterized by mixed forests with sycamore, oaks, and chestnuts.

Sampling

We selected sycamore trees (*Acer pseudoplatanus* L.) because the regular shape of their trunk and the smoothness of their bark made it easier to develop an experimental protocol. Within the forest, we geolocated all sycamore trees that had a circumference between 50 and 100 cm at 130 cm from the soil level, reaching a total of 50 sampled trees. The trees were distributed over an area of ~2 ha.

Microclimatic conditions during the measurements

We carried out two measurement sessions under contrasting microclimatic conditions: on a wet day (11 November 2021) that had been preceded by 10 rainy days with a total cumulative rainfall of 160 mm (hereafter the ‘wet condition’) and on a dry day (19 November 2021) that had been preceded by 4 days of no precipitation and dry north wind > 15 km/h with gusts of >30 km/h (hereafter the ‘dry condition’). Before and during the measurement from 12 a.m. to 3 p.m., microclimatic data were collected using a data logger (Onset HOBO MX2304 Weatherproof Bluetooth Temperature Data Logger with External Sensor) that recorded data every minute. Details of trends in temperature and humidity during the sessions are reported in Figure 1. While remaining within the area’s seasonal range, the atmospheric temperature during measurements in dry conditions was ~4°C higher than in wet conditions and the relative humidity was 20% lower than in wet conditions.

Infra-red and RGB images

At each session, we acquired infra-red (IR) images for each tree during the same period, from 12 a.m. to 3 p.m., after ascertaining from microclimatic measurements before the experiment that the temperature and humidity remained sufficiently stable during that period to ensure sufficiently different wet and dry conditions (Fig. 1). We placed a 20 × 50 cm sampling frame at the northern exposure of each tree, 1 m above the ground. Then, we took IR thermal images for a standardized distance of 60 cm between the camera and the trunk with the use of a tripod. To limit bias in thermal image acquisition, the sampling grid was positioned on the trunk, taking care not to touch the sampling area. The surface temperature measurements at high spatial resolution were collected in the field using a FLIR C5 thermal camera (FLIR Systems, Inc.). The camera has a display resolution of 640 × 480 pixels and captured images at IR resolution of 160 × 120 pixels, the spatial resolution (IFOV) is 6.3 mrad/pixel with a thermal sensitivity of < 70 mK. Alongside the FLIR C5 thermal camera, true colour (RGB) images were captured with a resolution of 5 megapixels. To accurately quantify surface temperature, the thermal camera FLIR was calibrated against atmospheric temperature and atmospheric relative humidity, which were collected by the datalogger.

Species diversity and morphological functional traits

After having acquired the IR images, we used the same sampling grid to sample the percentage coverage of epiphytic lichen and bryophyte species. Although this sampling grid is slightly bigger than the one usually used in lichen diversity surveys (Giordani and Brunialti 2015), a larger size of the sampled area allowed us to better capture the possible thermal differences of the epiphytic communities. Identifications as far as possible took place in the field so as not to alter the community. When necessary, lichens and bryophytes were sampled and observed in a laboratory with dissecting and standard light microscopes. Subsequently, we characterized every species according to a set of selected functional traits. In particular, we used the growth form and the colour of the thallus (Fig. 2). The growth form is associated with microhabitat conditions of water uptake and temperature, whereas the colour of the thallus

Figure 1. Details of microclimatic data of the air temperature (above) and air humidity (below) collected by means of HOBO data logger during the measurement sessions. In the graph, dashed lines refer to the wet condition while solid lines to the dry condition.

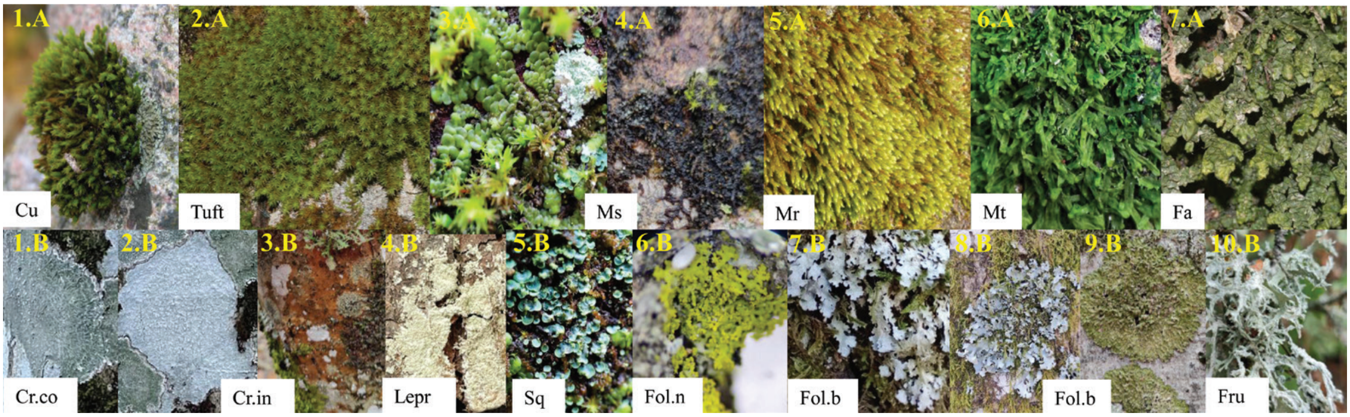

Figure 2. Group A, Bryophytes' growth forms are 1.A, cushion (Cu): dome-shaped colonies formed by variously oriented shoots with a central origin; 2.A, tuft: tufts, forming loose cushions not necessarily of central origin; 3.A, mat, smooth (Ms): shoots that creep over substratum, having leafy branches that generally lie flat; 4.A, mat, rough (Mr): shoots creeping substratum, having numerous erect lateral branches; 5.A, mat, thalloid (Mt): shoots that creep over substratum, composed of a layer of thalli; and 6.A, fan (Fa): shoots arising from vertical bark or rock, branching repeatedly in a horizontal plane. Group B, Lichens' growth forms are 1.B, crustose conspicuous (Cr.co); 2.B, 3.B, crustose inconspicuous (Cr.in); 4.B, leprose (Lepr); 5.B, squamulose (Sq); 6.B, foliose narrow-lobed (Fol.n); 7.B, 8.B, 9B, foliose broad-lobed (Fol.b); and 9.B, fruticose (Fru). The colour traits are green (2.A; 3.A; 4.A; 5.A; 1.B; 5.B); olive-green (1.A; 6.A; 9.B); brown (4.A); white (2.B; 4.B); pink-orange (3.B); yellow (6.B); grey (7.B); grey-bluish (8.B); and green-yellowish (10.B).

is linked to the occurrence of lichen acids that act as a protection against exposure to sunlight (Gauslaa and Solhaug 2001, Glime 2007, Nascimbene and Marini 2015, Rice *et al.* 2018). For lichens, we categorized traits by referring to the information reported in ITALIC v.7.0, the information system on Italian lichens (Nimis and Martellos 2023) with some modifications for the categorization of growth forms proposed by Di Nuzzo *et al.* (2022). Regarding bryophytes, we characterized each species by simplified growth forms according to Hill *et al.* (2007) that are important features in regulating water retention and reducing air resistance. We have identified 13 categories, seven for lichens: fruticose (Frut), foliose broad-lobed (Fol.b), foliose narrow-lobed (Fol.n), squamulose (Sq), leprose (Lepr), crustose conspicuous (Cr.co), crustose inconspicuous (Cr. in), and six for bryophytes: tuft (Tuft), mat thalloid (Mt), mat smooth (Ms), mat rough (Mr), fan (Fa), and cushion (Cu). Regarding thallus colour, we considered the following nine categories that are usually used in species descriptions for both lichens and bryophytes: yellow, white, pink-orange, olive-green, grey-bluish, grey, green-yellowish, green, and brown (Fig. 2).

Image processing and calculation of metrics of thermal heterogeneity

Images were extracted using the package ThermStats (Senior *et al.* 2019), which contains the necessary functions to quantify surface thermal heterogeneity. The get_stat function identifies spatial hot and cold spots, which are based on the G* variant of the Getis-Ord local statistic (Getis and Ord 1996), and calculates the statistics of each individual pixel that is compared to the local weighted average and the global average of the image. High positive values are classified as hot spots and low negative values as cold spots (Senior *et al.* 2019). This information is used to compute summary statistics such as the average temperature, which could be used as a measure of the macroclimate for small, surface-dwelling organisms, or thermal diversity indices that may be relevant to the thermoregulation of individuals. Also, we calculated thermal connectivity, which is the maximum temperature difference that can be achieved by traversing a gradient from hot to cold pixels. Furthermore, it is possible to calculate patch-level statistics. Specifically, patch-level statistics are (i) the absolute area, which is the total number of pixels and defines whether microclimates are larger or more numerous, increasing the opportunities for thermoregulation; (ii) abundance, which shows distinct hot and cold spots; and (iii) density, which represents the number of hot and cold spots per unit area. These two last indices show us that more numerous microclimates increase the community-wide opportunities for thermoregulation, i.e. potentially representing suitable requirements across a number of contrasting species. Finally, the shape index, the aggregation index, and the patch cohesion index describe the shape, aggregation, and cohesion of cold and hot spots with biological relevance to small animals that might locate dispersed microclimates more or less easily.

Statistical analyses

Principal component analysis was used to study the relationships between thermal heterogeneity [i.e. (i) average temperature, (ii) thermal diversity, (iii) thermal connectivity, (iv) thermal abundance, (v) patch cohesion index, and (vi) shape index] descriptors on the 50 trees sampled in both dry and wet conditions. The analysis was performed using the R package FactoMineR (Husson *et al.* 2016).

Next, a paired data *t*-test was used to compare the differences between the coordinates of the 50 trees on the two principal components (PC1 and PC2) in dry vs. wet conditions.

To assess the relationship between species functional traits and thermal heterogeneity, we performed a fourth-corner analysis. This procedure allows for testing the relationship between environmental variables and species functional traits by combining three matrices: (i) a sample units × species abundance matrix, (ii) a sample units × environmental variables matrix, and (iii) a species × traits matrix. In our case, we used deltaPC1 and deltaPC2 as environmental variables, considered for each sampled tree as the difference between its coordinates on the two principal components of the PCA in dry conditions minus those in wet conditions. We used the model-based approach proposed by Brown *et al.* (2014), fitting a model with all species at the same time as a function of environmental variables, species traits and their interaction. This method allows to test the significance of the association between environmental variables and traits and the intensity of such association. We fitted a generalized linear model with binomial error distribution through the traitglm function in mvabund Rpackage (Wang *et al.* 2014). The model was fitted with a least absolute shrinkage and selection operator penalty that simplified the model switching off all the terms that do not explain any variation to zero (Brown *et al.* 2014).

RESULTS

In the 50 trees surveyed, we found a total of 72 species, 64 lichen, and 8 bryophytes species. The range of species per tree varied from 9 to 22, with a mean of 17. The highest number of species belonged to the Cr.in growth form (21 species), followed by Fol.n (13 species) and Fol.b and Cr.co (both 12 species). The least represented growth forms in terms of the number of species were Tuft, Mt, Mr, Lepr, Fa, and Cu (all 1 species) followed by Frut (2 species) and Ms and Sq (3 species). The most represented colour was grey (21 species), followed by olive-green (14 species), green (11 species), and green-yellowish (7 species). By contrast, the least represented colours were grey-bluish (two species) followed by yellow and brown (3 species). In general, most of the epiphytic diversity identified was composed of pioneer communities, in particular, light-coloured crustose lichens (e.g. *Phlyctis* sp., *Lepra* sp.) and dark-coloured hepatics [e.g. *Frullania dilatata* (L.) Dumort.]. However, among the 50 trees, we also found the presence of foliose lichens (i.e. Physciaceae, Parmeliaceae) and dome-shaped colonies of bryophytes (e.g. *Hypnum cupressiforme* Hedw. *Orthotrycum* sp.).

The first two components of the PCA accounted for 56.8% of the variance associated with the thermal characteristics of the selected trees (Fig. 3A). The first component (PC1 = 31.5%) was associated with a gradient of increasing T max recorded within the sampling grid and, to a lesser extent, with an inverse gradient of the abundance of hot and cold spots. The second component (PC2 = 25.3%) was positively associated with an increase in hot spot shape irregularity (hot shape index); furthermore, PC2 also described a gradient from trees with large cold areas and high levels of cold cohesion (for negative PC2 values) to other trees with large hot areas and high hot cohesion values (for positive PC2 values) (Fig. 3). Figure 3B shows the raincloud plot, illustrating the paired comparison between the coordinates of the 50 trees on PC1 and PC2 in wet conditions and the coordinates of the same trees on PC1 and PC2 in dry conditions. Overall, the selected trees showed significant differences in thermal characteristics when contrasted from wet to dry conditions, both *t*-tests for paired data being highly statistically significant. To be clearer, Figure 4 shows a close-up of the different thermal patterns occurring in dry and wet conditions. Furthermore, as an example, the characteristics of the trees that showed the greatest differences in the contrast from wet to dry conditions are reported in Figure 3C: the shifts of five trees when comparing wet (thinner part of the line) and dry conditions (thicker part) are highlighted as coloured link lines in the PCA. The boxes show the condition of the trees in the VIS and the thermal images in wet and dry conditions. Tree 3 and tree 37 shifted predominantly along PC1, consistent with an increase in T max and a decrease in hot and cold-spot abundance. By contrast, trees 8, 13, and 14 changed their thermal

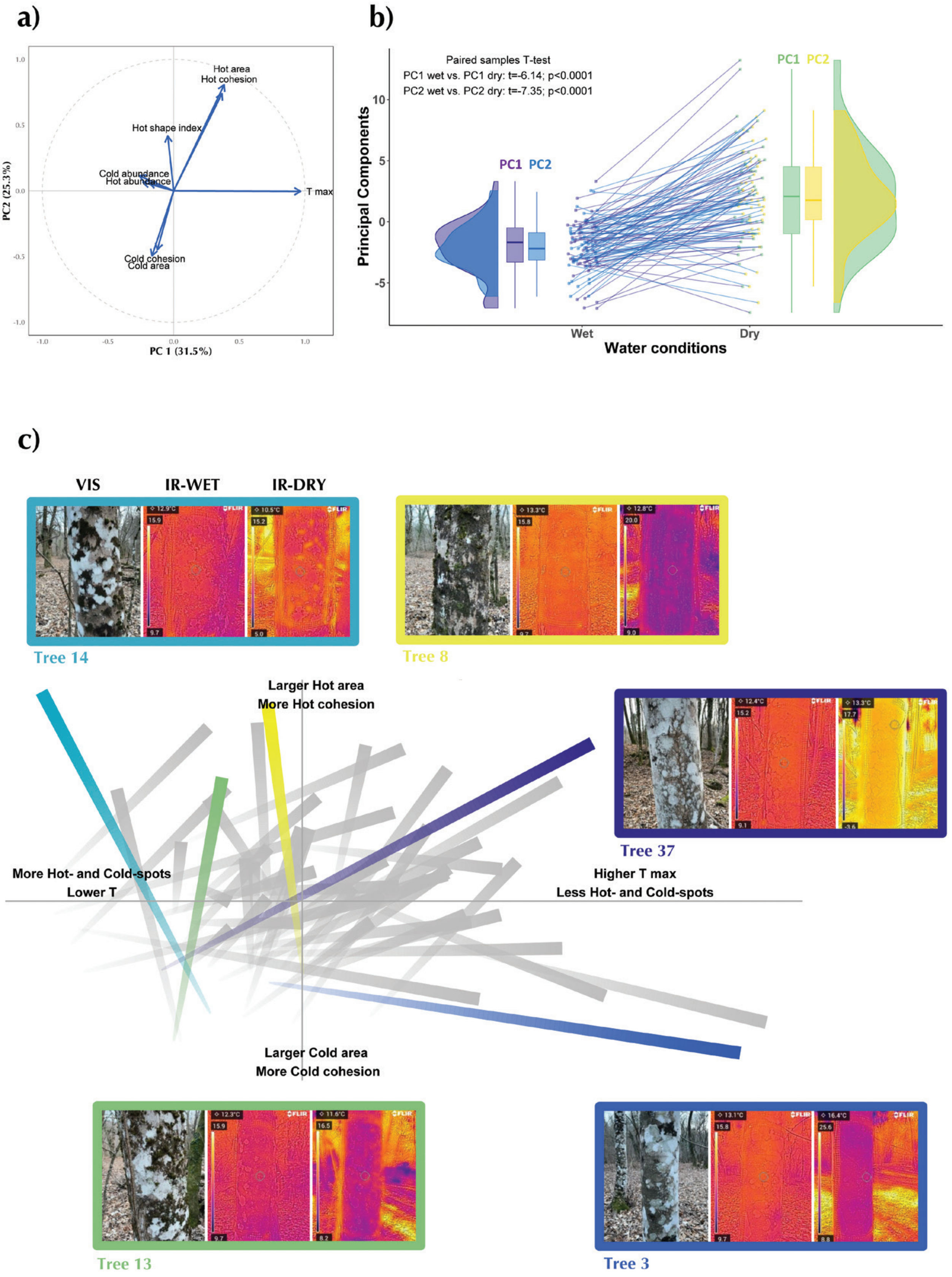

Figure 3. A, Representation of the first two factors of a principal components analysis of variables of thermal heterogeneity calculated for 50 trees in both wet and dry conditions. B, Paired sample *t*-test on the differences between tree coordinates on PCA principal components in dry vs. wet conditions. C, Variation in thermal heterogeneity of trees from dry to wet conditions. The lines represent the changes in the coordinates of individual trees in the space bounded by the two principal components of the PCA. For each line, the thinner end represents the position of the tree in wet conditions and the thicker end the position in dry conditions. By way of example, five trees are highlighted (coloured lines) for which the VIS image the IR image in wet conditions and the IR image in dry conditions are shown in the boxes.

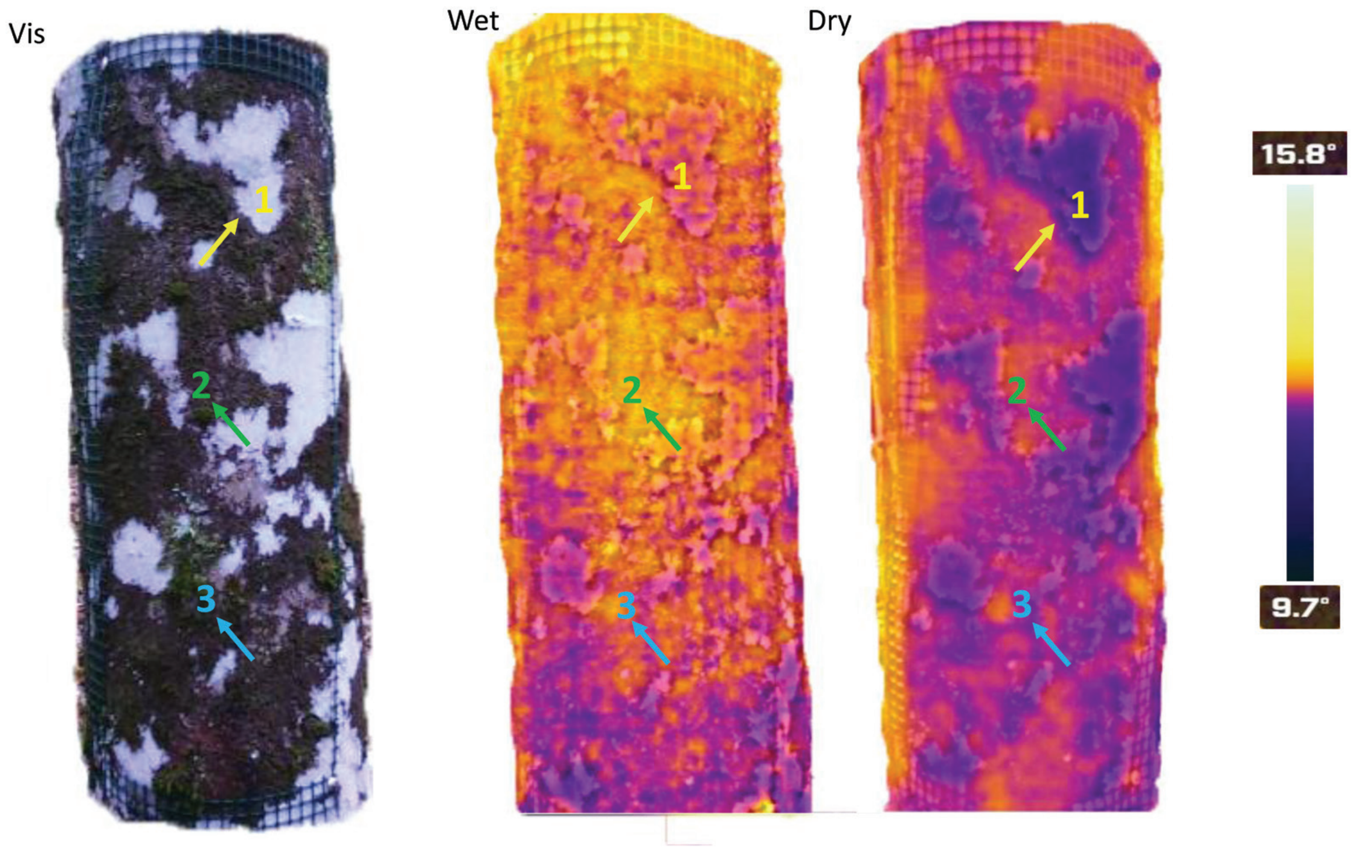

Figure 4. Epiphytic community traits driving different thermal spatial patterns between wet and dry conditions. The yellow arrow points to the white crustose lichen *Phlyctis argena* (Spreng.) Flot., the green arrow to the brown epiphyte *Frullania dilatata* and the blue arrow to the olive-green moss *Orthotrychum lyellii* Hook. & Taylor. The lighter colours (yellow arrow) have a lower temperature pattern than the darker ones (green and blue arrows) in both conditions. Conversely, the dome-shaped cushion (Cu) of *O. lyellii* (blue arrow) gives a warmer pattern in dry conditions than *F. dilatata* (green arrow), which has a mat, smooth growth form.

characteristics mainly along PC2, moving from large and cohesive cold spots to large and cohesive hot spots. In general, most trees radically changed their thermal characteristics, and the relative position of one tree to the others in the PCA space is not maintained in the difference between wet and dry conditions.

The fourth-corner analysis (Fig. 5) provides a detailed picture of the relationships between the abundance of functional traits in epiphytic communities and metrics of thermal heterogeneity when considering the difference between wet and dry conditions (i.e. Delta PC1 and Delta PC2). All categories of growth form (except Fol.n) and thallus colour (except brown) were significantly related to the changes in the thermal pattern of the trunk surveyed. High positive Delta PC1 values corresponded to overall higher surface T in dry conditions than in wet conditions. These values were significantly associated with different colour and growth form categories, but in particular were positively related to certain dark colours, such as olive-green (0.11) and green (0.06). In contrast, DeltaPC1 had negative correlations with Tuft (−0.07) and Fol.b (−0.05) growth forms.

High positive Delta PC2 values corresponded to a greater and more cohesive area of hot spots in dry conditions than in wet conditions. Delta PC2 was positively related to a high coverage of thalli with Fol.b growth form (0.11) and with grey-bluish (0.09) and green-yellowish thalli (0.06), whereas a negative association was observed with light-coloured thalli, such as pink-orange thalli (−0.06), and, above all, with the Mt growth form (−0.14).

DISCUSSION

In this work, thermal heterogeneity was studied for the first time on non-vascular epiphyte communities in their natural environment. Results confirmed our first hypothesis that the variation of the thermal pattern on tree trunks depends on the microclimate of the surrounding atmosphere. Overall, significantly higher surface temperatures on the trunk were observed during the dry and warmer measurement session than during the wet and cooler one. This finding might be apparently intuitive considering that poikylohydric organisms tend to reach thermal and water equilibrium with the atmosphere (Proctor and Tuba 2002). However, the dynamics of this equilibrium are potentially subtle, and even very large differences between the air and thalli temperatures occur depending on their state of hydration and the level of solar radiation to which they are subjected. The temperature of lichens can be related to a differential irradiance reflection between a hydrated and a desiccated thallus (Gauslaa 1984, Palmqvist and Sundberg 2000, Gauslaa and Solhaug 2001, McEvoy *et al.* 2007). However, it is unlikely to be possible to generalize that a dry thallus is always warmer than a wet one or vice versa, as the surface temperature is determined by an interaction

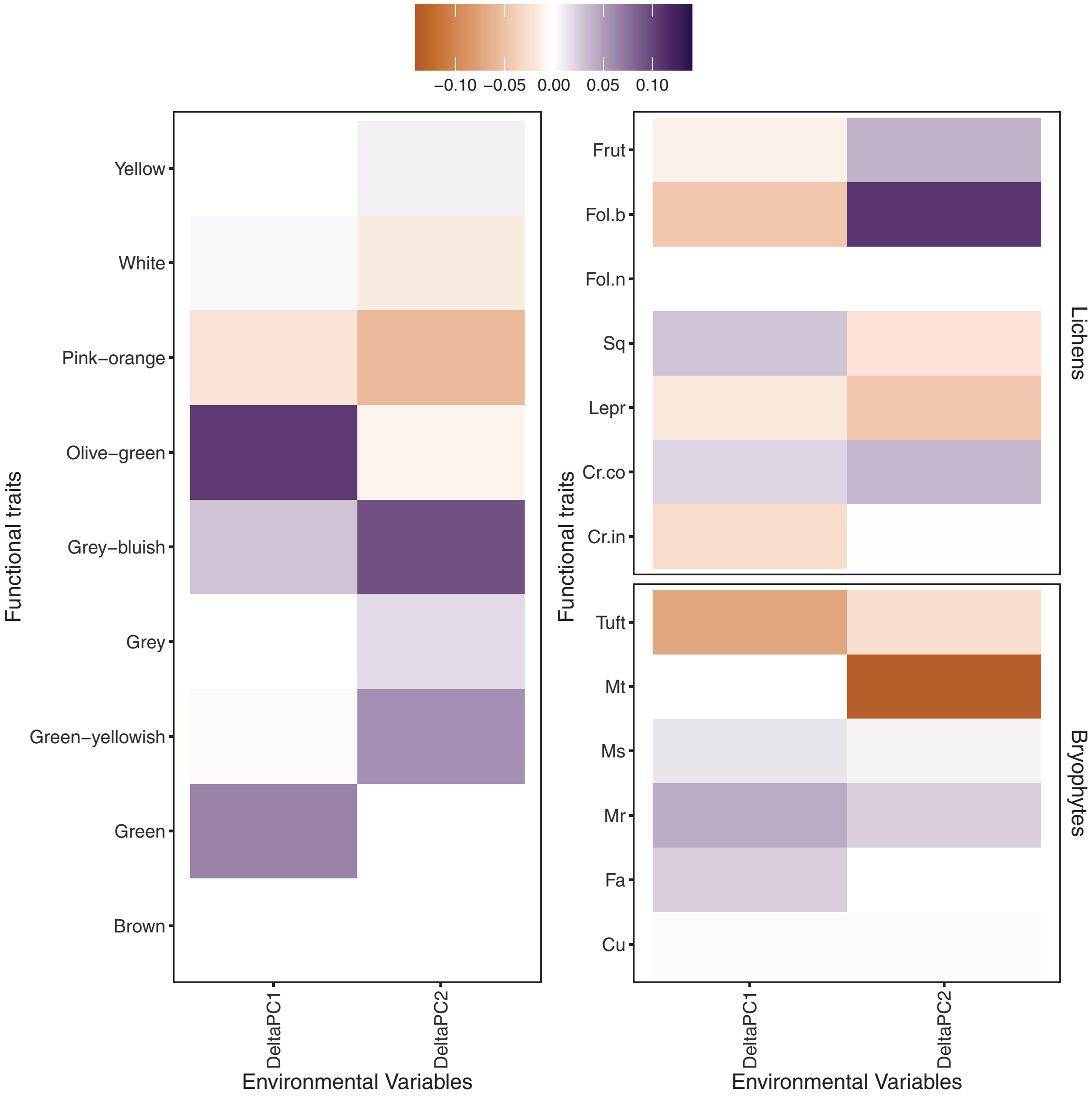

Figure 5. Results of the fourth-corner analysis between functional traits, colour (left) and growth form (right), deltaPC1 (gradient of increasing temperature), and deltaPC2 (thermal pattern of the trunk). Boxes are coloured according to traits fourth-corner coefficients: purple and brown indicate positive and negative significant trait-variable association, respectively. Colour brightness indicates the strength of the association: a brighter colour shows a stronger association.

between several macro- and microclimatic variables, such as solar radiation and water content.

Interestingly, the thermal heterogeneity in our experiment did not only refer to the maximum temperature, but also concerned the abundance, shape, and distribution of hot and cold spots on the trunk, i.e. areas of the trunk that are significantly warmer or colder than adjacent ones. According to our second hypothesis, this seems related to the effect of the functional traits of non-vascular epiphytes, particularly thallus growth form and colour. In fact, the fourth-corner analysis revealed significant relationships between thermal heterogeneity at the trunk-level and both growth form and thallus colour. The physical and physiological mechanisms underlying this phenomenon are not easily deduced. However, these results seem to provide support for the 'bundle effect' of functional traits (Ellis *et al.* 2021a), stating that some phenotypic traits are interrelated through their evolutionary history and interact at ecological scales producing a combined response to environmental factors.

Actually, our data provide a complex picture, but some trends clearly emerge. For example, there is no clear distinction between the response of lichens and bryophytes: for both groups, some growth forms are associated with greater warming in dry conditions, while others have the opposite effect, suggesting that the similarities between the morphologies of lichen and bryophyte thalli may have a greater effect than their physiological differences. Moreover, similarly to Gauslaa (1984), we observed that the cooling effect achieved by the lighter colours is generally lower than the warming effect achieved by darker thalli.

Despite the novelty of this work, it has some limitations that can, however, be taken as a starting point for future investigations. The experiment was conducted over 2 days, during which the image acquisitions took place within a delimited time, standardizing two extreme conditions (dry vs. wet). Lichens and bryophytes are subject to cycles of hydration and dehydration throughout the day. An advance for future works will be to monitor variation of thermal patterns for longer periods and during the whole day, to include time intervals during which variations in the water content of the thalli occur most abruptly (e.g. early morning and late afternoon). Furthermore, we limited the variability of the system by considering only the northern exposure of the tree trunk. More exhaustive information on thermal traits could be incorporated by considering the four contrasting exposures. An additional limitation is that we considered only one tree species. We know tree species identity is a crucial factor driving the colonization of non-vascular epiphytes (Price and Hochachka 2001, Kimmerer 2005). For example, pH, thickness, and texture of the bark influence their biodiversity (Barkman 1958, Jüriado *et al.* 2009). Instead, considering the thermal heterogeneity, the bark fissures of some trees (e.g. old chestnuts) may play an important role in the variation in both thermal and pattern gradients.

CONCLUSIONS AND PERSPECTIVES

The crucial importance of the microclimate is being increasingly emphasized in recent ecological research (De Frenne *et al.* 2019, Zellweger *et al.* 2019, 2020). Accordingly, our work underlines the need to investigate responses to climatic factors at the specific spatial and temporal scales of the organism group considered (De Frenne *et al.* 2021). In particular, our results confirm that at the centimetre-scale of the surface of a single trunk, the functional traits of non-vascular epiphytes are indeed effect traits, capable of determining considerable variations in temperature as both absolute values and patterns. Although not a specific objective of this work, these observations open the way to the possibility of obtaining more robust models for the ecosystem function of epiphytes at the landscape scale (Porada *et al.* 2013, 2023, Porada *et al.* 2016, Porada *et al.* 2018) and suggest that variations in the composition of epiphytic communities (e.g. as an effect of climate change) may result in non-negligible alterations of thermoregulation or biogeochemical cycles in forest ecosystems.

ACKNOWLEDGEMENTS

R.B. acknowledges the support of National Biodiversity Future Center (NBFC) to University of Florence, funded by the Italian Ministry of University and Research, PNRR, Missione 4 Componente 2, 'Dalla ricerca all'impresa', Investimento 1.4, Project number CN00000033.

AUTHOR CONTRIBUTIONS

G.C., L.D.N., and P.G. conceived the ideas and designed methodology; G.C., L.D.N., and P.G. collected the data; L.D.N. and P.G. analysed the data; G.C., L.D.N., P.G., R.B., and J.N. led the writing of the manuscript; R.B. and J.N. revised manuscript critically for important intellectual content. All authors contributed to the drafts and gave final approval for publication.

DATA AVAILABILITY

The data underlying this article are available in Figshare at https://doi.org/10.6084/m9.figshare.23999748.

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