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Very high-resolution digital elevation models: are multi-scale derived variables ecologically relevant?

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Summary

1. Digital elevation models (DEMs) are often used in landscape ecology to retrieve elevation or first derivative terrain attributes such as slope or aspect in the context of species distribution modelling. However, DEM-derived variables are scale-dependent and, given the increasing availability of very high-resolution (VHR) DEMs, their ecological relevance must be assessed for different spatial resolutions.

2. In a study area located in the Swiss Western Alps, we computed VHR DEMs-derived variables related to morphometry, hydrology and solar radiation. Based on an original spatial resolution of 0·5 m, we generated DEM-derived variables at 1, 2 and 4 m spatial resolutions, applying a Gaussian Pyramid. Their associations with local climatic factors, measured by sensors (direct and ambient air temperature, air humidity and soil moisture) as well as ecological indicators derived from species composition, were assessed with multivariate generalized linear models (GLM) and mixed models (GLMM).

3. Specific VHR DEM-derived variables showed significant associations with climatic factors. In addition to slope, aspect and curvature, the underused wetness and ruggedness indices modelled measured ambient humidity and soil moisture, respectively. Remarkably, spatial resolution of VHR DEM-derived variables had a significant influence on models' strength, with coefficients of determination decreasing with coarser resolutions or showing a local optimum with a 2 m resolution, depending on the variable considered.

4. These results support the relevance of using multi-scale DEM variables to provide surrogates for important climatic variables such as humidity, moisture and temperature, offering suitable alternatives to direct measurements for evolutionary ecology studies at a local scale.

Key-words: digital elevation models, generalized linear models, Landolt's ecological indicators, local scale, multi-scale analysis, temperature and humidity loggers, very high spatial resolution

Introduction

Digital elevation models (DEMs) are widely used in landscape and evolutionary ecology to understand the distribution of species and their genetic variation (Kozak, Graham & Wiens 2008). Their most common use in ecology consists in retrieving elevation, or in computing primary terrain attributes (i.e. slope, aspect and curvature), which underlie biophysical processes at local or regional scales, especially in mountainous areas (Elith & Leathwick 2009; Manel *et al*. 2010a). In many studies, primary attributes have been used as proxies for factors such as solar radiation (Fu & Rich 2002), evapotranspiration (Guisan & Zimmermann 2000), overland and subsurface flow (Broxton, Troch & Lyon 2009), soil water content (Moore, Grayson & Ladson 1991), wind, erosion/deposition rate, soil characteristics (Wilson & Gallant 2000), climatic variables as well as snow accumulation and thaw (Lyon *et al*. 2008; Dobrowski 2011). Their accuracy and increasing availability turned them into accessible indicators of topographic variability, though not necessarily those with the highest predictive potential (Guisan & Zimmermann 2000; Pradervand *et al*. 2014).

A large variety of DEM-derived variables can be computed. Conventionally, primary terrain attributes are calculated on the basis of 3 × 3 moving window (Wilson & Gallant 2000; Böhner *et al*. 2002), but more complex variables have been developed over the last two decades to model hydrological processes, solar radiation or local morphometry (Wilson & Gallant 2000; Kalbermatten *et al*. 2012). Named secondary topographic attributes, they are often a combination of primary attributes calculated using a moving window of varying size. Solar radiation, for example, combines slope, aspect, sunshine duration and adjacent relief (Wilson & Gallant 2000). The higher explanatory power of secondary topographic attributes such as wetness indices (Beven & Kirkby 1979), stream power (Moore, Grayson & Ladson 1991), terrain ruggedness (Riley, Degloria & Elliot 1999) or temperature (Wilson &

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Gallant 2000) may be of particular interest for assessing ecological patterns related to specific processes at a landscape scale. For example, Böhner & Selige (2006) used two secondary topographic attributes – a wetness index and a solifluction index – to model soil pH and snow cover. Secondary topographic attributes were also developed for specific purposes, such as differentiating habitats across different mountain ranges using the vector ruggedness measure (vrm) developed by Sappington, Longshore & Thompson (2007). Despite convincing examples of their usefulness, DEM-derived variables' diversity is rarely potentiated in species distribution models or landscape genetics.

Commonly used DEMs show a moderate to coarse resolution (≈30 m for ASTER GDEM, ≈90 m for SRTM) and a poor accuracy (Tachikawa *et al.* 2011). In addition, most studies would only consider DEMs at their original resolution or use GPS measurement to compute slope and aspect (Patsiou *et al.* 2014; Greenwood *et al.* 2015). However, the gradual emergence of very high-resolution (VHR, ≤1 m) elevation data offered unprecedented level of details for exploring the morphological characteristics of landscape and promoted new applications (see Lassueur, Joost & Randin 2006; Kalbermatten *et al.* 2012 and references therein).

Indeed, high resolution provides several advantages. It improves the modelling of species distribution in response to global changes, in particular the ability to identify microrefugia (Dobrowski 2011). Climate experienced by an organism is indeed a combination of regional climate pattern and local terrain influence, which defines the habitat pattern an organism is presented with. For example, cold air drainage, elevation, topographic position, slope and aspect are the main terrain factors influencing the coupling between micro- and regional climatic conditions (Barry 1992). On the other hand, VHR DEM-derived variables are not able to provide proxies to some important environmental variables (e.g. precipitation) and are more difficult to acquire and require a more demanding processing. In particular, the use of VHR elevation data invites reconsidering a number of scale issues raised 20 years ago by Levin (1992). Among them, it is crucial to remember that a high spatial resolution (a small grain) does not necessarily imply better models. Accordingly, it is a key to understand the scale dependency of topographic features and thus to evaluate the usefulness of VHR DEM-derived environmental variables for studies at local scales (≈1 km²) in the light of multi-scale analysis. With multi-scale, we designate the use of different grain sizes for a fixed extent. It is indeed necessary to use spatial resolutions matching the geographic distribution of phenomena under study and the accuracy of sampling's georeferencing. Accordingly, evaluating the influence of scale on the computation of environmental variables is essential. In particular, to what extent VHR elevation data likely evidence micro-relief and related microclimate physical phenomena that may not be grasped at coarser resolutions remains poorly known (Levin 1992; Marceau & Hay 1999; Cavazzi *et al.* 2013). Furthermore, no consensus has emerged yet on the benefits and drawbacks of very high resolution, and this is well illustrated by the multi-resolution approaches of Pradervand *et al.* (2014) that did hardly improve species distribution models of alpine plants at a regional scale, although the distribution of some plants known to live in microhabitats was significantly better predicted. Even though the relationship between species' occurrences and a given environmental variable does not necessarily hold across scales, most studies in ecology use variables at a single resolution with no consideration of scale representativeness.

The present work integrates the methodological constraints mentioned above to illustrate how VHR DEM-derived variables can be used to characterize mosaic habitats along a 2 km long alpine ridge encompassing the subalpine–alpine ecotone (Parisod & Christin 2008). Given the steep alpine configuration of this landscape, topography was assumed to be a major driver of air temperature and humidity, as well as soil moisture, thus ruling the distribution of plants (Körner 2003). Accordingly, our aims were to (i) assess the ecological relevance of VHR DEM-derived variables by modelling the relationship between primary as well as secondary VHR DEM-derived environmental variables (e.g. direct solar radiation, wetness index, vector ruggedness measure) and climatic variables measured in the field, and (ii) to identify relevant scales by computing VHR DEM-derived variables at spatial resolutions of 0·5, 1, 2 and 4 m and assessing the goodness-of-fit and significance of corresponding models. Climatic variables were obtained from different sources; 105 loggers were distributed along the ridge to measure temperature and humidity at high temporal resolution during several months. In addition, we obtained one-time measurements of soil moisture at high spatial density. Finally, we modelled the relationship between the same VHR DEM-derived variables and a series of ecological indicators derived from plant species composition (Landolt *et al.* 2010).

Materials and methods

STUDY AREA AND SAMPLING DESIGN

The focal study area is a narrow ridge (Fig. 1a) located in the Swiss Western Alps, at 'Les Rochers-de-Naye' (46°26′00′' N, 6°58′50′' E), covering an elevation range included between 1864 and 2043 m. Locally, adapted ecotypes of the plant *Biscutella laevigata* were shown to grow within a distance of <10 m from the cliff in contrasted microsites (Parisod & Bonvin 2008; Parisod & Joost 2010), and this area was thus selected as a suitable model landscape to highlight mosaic habitats across the local subalpine–alpine ecotone.

In order to assess the ecological relevance of VHR DEM-derived environmental variables, the design and the georeferencing of sampling locations are key elements since the precision of their location has to exactly match the highest resolution of the DEM described in the next section. Therefore, sampling locations were selected following a random cluster sampling guided by the population density of the focal species and guaranteeing that all data points are located within pixels representing 0·5 × 0·5 m in the field, resulting in sixty 4 × 4 m areas with at least five individuals of *B. laevigata* (see resulting distribution in Fig. 1a). Briefly, direct air temperature (DT) was measured with 60 uncovered temperature loggers placed at the centre of each

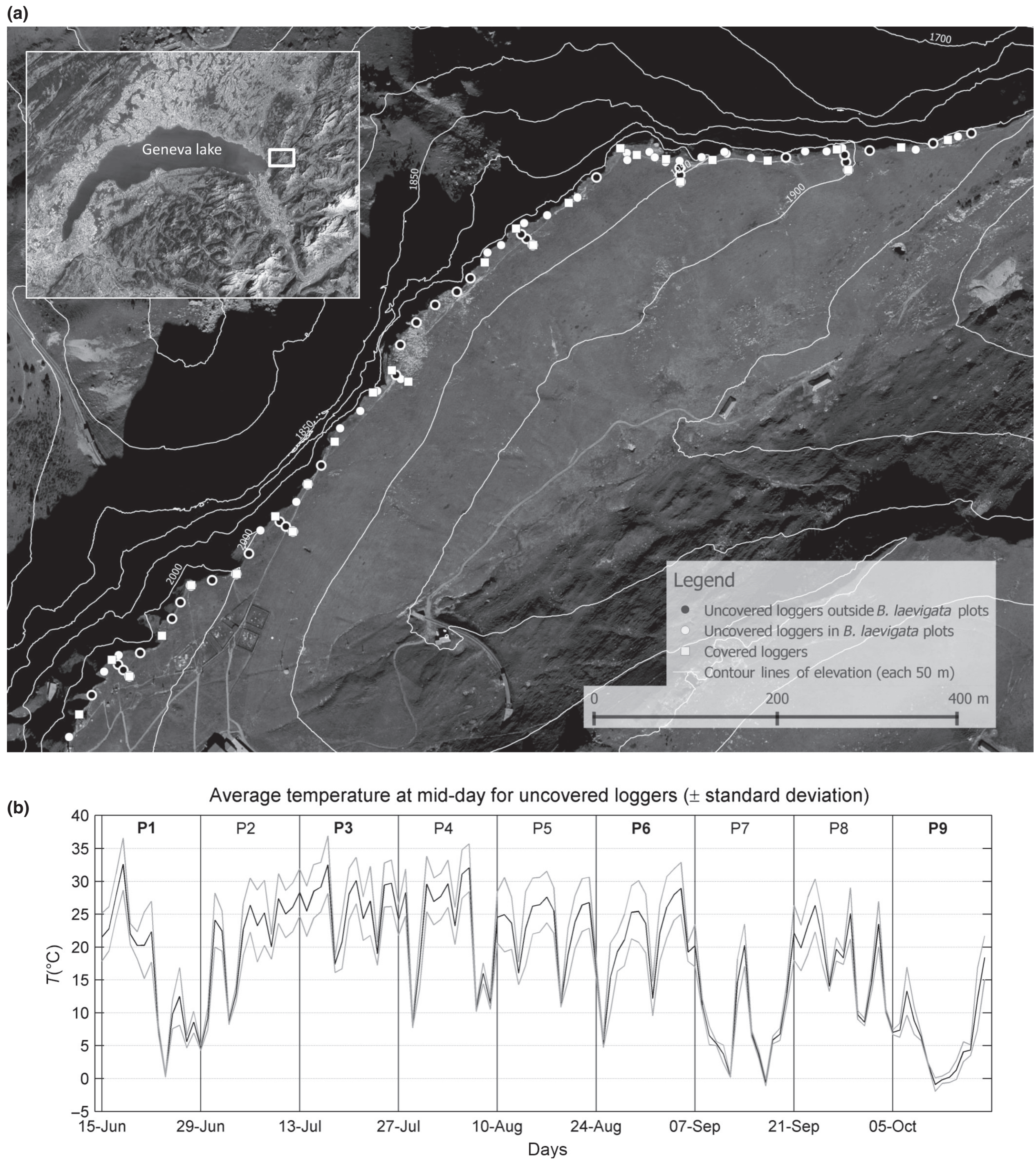

Fig. 1. (a) Study zone and sampling locations for loggers on the ridge of Les Rochers-de-Naye in the Swiss Western Alps. Uncovered and covered loggers were used to measure direct air temperature (DT) and ambient temperature, respectively [Background image with 50 m isoelevation lines: Swissimage © 2013 swisstopo (JD100064)]. (b) Mean daily DT and standard deviation (in grey) from the 15 June to the 18 October 2013, measured with uncovered loggers set 15 cm above soil level. Vertical lines delimit the defined periods. Retained periods for following analyses are in bold.

area as well as 20 additional ones installed at random locations along the ridge (Fig. 1a). Ambient temperature (AT) was measured with 25 temperature and humidity covered loggers, placed next to one uncovered logger over three. Soil moisture was measured at 201 sampling locations representative of the focal species (Fig. 2b). Furthermore, species composition was assessed in 452 plots of 0·2 × 0·2 m at the corners of 1 × 1 m squares located within the 60 areas as well as 53 additional ones randomly located along the ridge (Appendix S1, Supporting information).

Details on these measurements can be found in the next subsection.

All sampling points and loggers were georeferenced with a differential GPS unit (TOPCON-HIPer Pro, http://www.topcon.com.sg/survey/hiperpro.html) offering a horizontal accuracy of *c.* 2–3 cm and a vertical accuracy of *c.* 3–4 cm.

TEMPERATURE, HUMIDITY AND SOIL MOISTURE DATA

Air temperature and humidity

Direct air temperature was measured with uncovered IButton loggers (1922L) from Maxim Integrated (http://www.maximintegrated.com/) placed 15 cm above the ground. Furthermore, covered temperature and humidity loggers (IButton 1923) measured AT and humidity (HU) at 15 cm above the ground (Fig. 1a). These loggers were covered with a white shield pierced with several holes to avoid stagnant air. Loggers were set to record information with a frequency of 30 min during 126 days, from 15 June 2013 to 18 October 2013, with an accuracy level of 0·5 °C and 5% for humidity. These 126 days were grouped in 9 periods of 14 days (P1: June 15–28; P2: June 29–July 12; P3: July 13–26; P4: July 27–August 9; P5: August 10–23; P6: August 24–September 6; P7: September 7–20; P8: September 21–October 4; P9: October 5–18).

The following descriptive statistics were computed for DT, AT and HU during each period: minimum (MIN), maximum (MAX), mean (MEA), standard deviation (SD), median (MED), mean value at 1 am (M1A), mean value at 1 pm (M1P) and mean daily range (MDR).

Soil moisture

The soil volumetric water content was evaluated once with a FieldScout TDR 300 Soil Moisture Meter (Spectrum Technologies, Inc., Aurora, IL, USA, http://www.specmeters.com/). Following Le Roux *et al.* (2012), soil moisture values are highly correlated among distinct sampling events and a single measurement taken more than 24 h after rainfall was assumed to yield reliable measured soil moisture values (MSM).

ECOLOGICAL INDICATORS

Species composition was assessed in 452 plots (Appendix S1), with species cover estimated as the proportions (%) of the plot covered by the species. Landolt's ecological indicator values (Landolt *et al.* 2010) were used to provide an expert-based ecological characterization of sampling plots from their composition in plant species. Landolt's indicators specify tolerance of species of the Swiss flora to climatic or soil conditions, including competitive interactions between species. They are better adapted to the alpine flora than the more commonly used Ellenberg's ecological indicators (Ellenberg *et al.* 1991). The mean value of indicators, weighted by the square-rooted cover of species, was calculated at the plot level, providing a set of five soil indicators, *LDT-colloidal_dispersion* (soil aeration), *LDT-moisture*, *LDT-humus* (humus proportion), *LDT-nutritive_substances* (soil fertility, mainly nitrogen), *LDT-pH_reaction* (soil pH); and three climate indicators, *LDT-continentality*, *LDT-light* and *LDT-temperature*.

DIGITAL ELEVATION MODELS ACQUISITION AND PROCESSING

We acquired a VHR DEM based on airborne LIDAR (Light Detection And Range) technology. A Riegl VQ-480 laser scanner (http://www.riegl.com/) was installed on a helicopter in October 2011 by the HELIMAP Company (http://www.helimap.ch/) to get an average density of 25 soil points m^{-2}. The raw point cloud was then processed with the TERRASCAN software (TERRASOLID Ltd, Helsinki, Finland; http://www.terrasolid.fi/) to filter buildings, vegetation and all other surface elements in order to obtain a terrain model (Liu 2008). The final density of the ground class was 10 points m^{-2} on average, and the spatial resolution of the DEM was set to 50 cm. A few void locations (no data) were filled with the help of a 1 m resolution model obtained from the State of Vaud (ASIT-VD; http://www.asitvd.ch/) and using a Multilevel B-Spline Interpolation in SAGA GIS (Seungyong, Wolberg & Sung-Yong 1997).

A multi-scale analysis framework was used to understand how important micro-habitat conditions are and what level of detail is necessary to optimally correlate climatic variables with topographic-related variables. Our approach is based on the work of Kalbermatten (2010) and Kalbermatten *et al.* (2012), who showed that a wavelet transform pipeline is a suitable way to generalize topography and demonstrated the usefulness of B-splines, a generalization of Bezier curve, to model arbitrary functions, such as DEMs. Therefore, we took advantage of the Gaussian Pyramid algorithm implemented in MATLAB (MATLAB Version 12b; The MathWorks Inc., Natick, MA, USA) to approximate topography at multiple resolutions. The original VHR DEM (50 cm) was thus generalized to 1, 2 and 4 m to constitute the multi-scale DEM data sets.

We used SAGA GIS (Böhner, McCloy & Strobl 2006) and the R package RSAGA (Brenning 2008) to compute and automate the production of DEM-derived variables. We initially computed 16 DEM variables related to morphometry, hydrology and solar radiation, for which details are provided in Appendix S2. Solar radiation variables were computed during 1 month of the growing season (June).

SELECTION OF INDEPENDENT DEM-DERIVED VARIABLES

Correlation between each pair of variable was assessed (Appendix S3), and specific variables were omitted from subsequent analyses according to the following rules: (i) the maximum correlation threshold was set to 0·6, (ii) secondary attributes that were highly correlated (>0·6) with primary attributes (i.e. slope and eastness/northness) were deleted, and (iii) the remaining choice between eastness and northness was decided at random due to the high correlation between these two variables. In the end, eight independent variables were retained (Table 1): altitude (alt), terrain wetness index (twi), sine of aspect or eastness (eas), downslope distance gradient (ddg), slope (slo), horizontal curvature (hcu), vertical curvature (vcu) and vector ruggedness measure (vrm).

Given the limited number of covered loggers measuring ambient temperature and humidity (n = 25), correlations between retained DEM variables where higher than for uncovered loggers locations and we had to limit the study to five independent DEM-derived variables (Appendix S4): altitude (alt), eastness (eas), slope (slo), horizontal curvature (hcu) and terrain wetness index (twi).

REGRESSION ANALYSIS

Multivariate regression models were performed to explain the variability of climatic variables and ecological factors measured in the field, for each spatial resolution. We used a step generalized linear models (SGLM; Nelder & Wedderburn 1972) with a Gaussian family and controlled the addition or removal of a term based on the Akaike Information Criterion (AIC). After model completion, co-linearity between variables was controlled using variance inflation factors (VIF; Montgomery & Peck 1982), based on the threshold >3 (Zuur *et al.* 2009). Models with variables having VIF >3 were processed again, excluding the inflating variables. Landolt factors were log-transformed to fit at normal distribution, and all variables were standardized. Adjusted R^2 $((N - 1)/(N - k - 1)$ where N = number of observations and k = number of predictors) were calculated for each model.

Table 1. Description and parameters of selected digital elevation models (DEM) variables computed at each resolution (i.e. 0·5, 1, 2, 4 m). The full table can be found in Appendix S2

	Variable	Abbreviation	Description	Units	Parameters/Reference
Primary attributes	Altitude	alt	DEM altitude	m	
	Slope	slo	Proxies for water flow, snow movements, erosion, solar radiation	radians	Method = Zevenbergen and Thorne (1987)
	Sinus of aspect (eastness)	eas		radians	
	Profile curvature	vcu		radians m^{-1}	
	Plan curvature	hcu		radians m^{-1}	
	Downslope distance gradient	ddg	Quantify downslope controls on local drainage	radians	Vertical distance = 2 m (Hjerdt *et al.*, 2004)
Secondary attributes	Vector ruggedness measure	vrm	Quantifies ruggosity with less correlation to slope	no unit	Radius = 1 pixel (Sappington, Longshore & Thompson 2007)
	Terrain wetness index	twi	Quantifies topographic control on hydrological processes	Where *a* is the specific catchment area and *S* is the ddg	$W = \frac{a}{\ln(S)}$

Instead of generalized linear models (GLMs), generalized linear mixed models (GLMMs) (Breslow & Clayton 1993; Bolker *et al.* 2009) were performed on the data set of soil moisture and Landolt's indicators to take into account the possible effect of spurious spatial autocorrelation. These variables were indeed collected in plots, and the merging by plot was thus considered as a random effect. GLMMs were performed with the LME4 R package (Bates & Maechler 2009). As the package does not support step procedure, we used the resulting DEM-derived variables from SGLMs procedures as fixed effects in the GLMMs.

CONVENTIONS FOR VARIABLES ABBREVIATIONS

To facilitate understanding of the following chapters, the conventions used for abbreviations are here-below summarized.

Environmental variables from loggers are written in upper case and with two letters (DT, AT, HU). Landolt indicators are written in upper case with three letters in italic (ex: *LDT-moisture*) and MSM with three letters.

For DT, AT and HU models, measured variables are written in upper case with three letters (MEA, MED, MIN, MAX, MDR, M1A, M1P).

Finally, all DEM-derived variables are written in lower case (alt, slo, twi, vrm, eas, hcu, vcu, ddg).

Results

The distribution of average DT over the whole sampling period provides a global view on climatic conditions during summer 2013 (mean 12·1 °C; Fig. 1b). We focused here on four among the nine periods of 14 days representative of contrasted weather conditions at such altitude: P1 and P9 are representative of the beginning and the end of the growing season and present a cold and a snowy episode, respectively, whereas P3 and P6 are representative of early and late summer conditions, respectively, and are characterized by warm averages with high standard deviations.

Together with altitude (alt), terrain wetness index (twi), vector ruggedness measure (vrm), eastness (eas) and slope (slo) are the DEM-derived variables that best explain the variance of measured environmental variables. Hereunder, we present the VHR DEM-derived variables showing the best model fit to explain the variability of measured environmental variables and ecological factors, depending on different spatial resolutions and periods of time.

DIRECT AIR TEMPERATURE

Among all DT models, twi is the most frequently significant DEM-derived variable (47% of the models). It is positively correlated with measured variables related to high temperatures (M1P, MAX, MDR) and negatively correlated with those related to cold temperatures (M1A, MIN, MEA) (see Table 2 and Appendix S5). Similarly, alt is also frequently significant (55% of the models), but mainly with measured variables related to cold temperatures (M1A, MED, MEA, MIN). Other DEM-derived variables such as slope, eastness and ddg are less frequently significant.

Significance of DEM-derived variables varies considerably with spatial resolution, whereas it remains relatively constant at all resolutions for elevation. Although the significance for twi is lower when computed at 0·5 or 1 m than at coarser resolutions (Appendix S5), adjusted R^2 (aR^2) are usually highest in models at 0·5 or 2 m resolution and almost systematically lower at 4 m. Noticeably, aR^2 are higher for all measured variables (except for mean range) during periods P1 and P9, which correspond to the two coldest periods among the four analysed.

AMBIENT TEMPERATURE

Significant contributions of DEM-derived variables in AT models are much less frequent (49% of the models that converged) than for previously presented DT models (91%; Appendix S6). However, relevant variables are the same as for DT models, except that horizontal curvature (hcu) is significant at a 2 m resolution (Table 3). Like DT models, twi is positively correlated with measured variables related to high temperatures and negatively correlated with cold temperatures. Altitude also remains a good explanatory variable and is involved in the models with the highest R^2, particularly during the snow episode (P9).

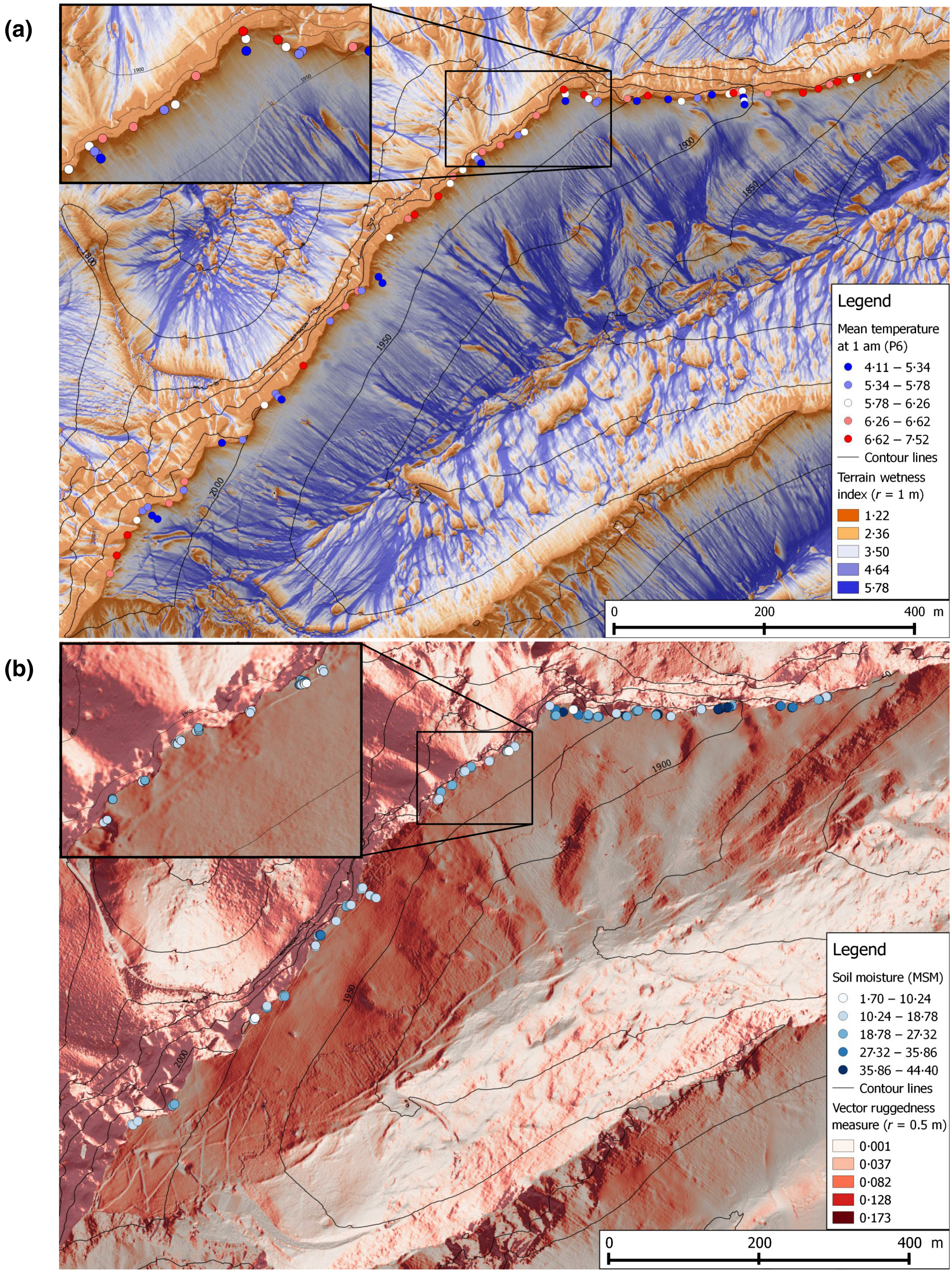

Fig. 2. (a) Map of the mean direct air temperature (DT) at 1 am (M1A) during period P6 (August 24–September 6). Terrain Wetness Index at 1 m resolution computed from the Digital elevation models (DEM) is in the background with 50 m iso-elevation lines. Additional zoom on the ridge to distinguish the loggers and visualize the correlation between the measured variable and the twi. (b) Map of one-time measurements of soil moisture (in %) with vector ruggedness measure at a 0·5 m resolution computed from the DEM is in the background with 50 m iso-elevation lines. Additional zoom on the ridge to distinguish the loggers and visualize the correlation between soil moisture and the vrm. For more details on these results, refer to Tables 2 and 5.

Table 2. Summary of multivariate generalized linear models sorted by adjusted R^2 (aR^2) in decreasing order for DIRECT AIR TEMPERATURE (DT), measured with uncovered loggers at 15 cm above soil level. First column is the abbreviation of the model showed, with different measured variables and time periods. The second column tells at which resolution (Res) the highest aR^2 was found

Model	Res	aR^2	alt	twi	vrm	eas	slo	hcu	vcu	ddg
DT-M1A-P9	0·5	0·69	−0·71***	0·17*	−0·21*					
DT-MIN-P9	2	0·50					0·28**			
DT-M1A-P6	1	0·46	−0·49***	−0·81***		0·25**		−0·20*		
DT-MED-P3	2	0·37	−0·40***	−0·57***						
DT-MEA-P6	2	0·32	−0·35**	−0·80***			0·41**			−0·45*
DT-MDR-P3	0·5	0·22	0·25*	0·47***		−0·41***				
DT-MDR-P1	2	0·19	−0·25*		−0·38***					
DT-MIN-P1	0·5	0·13	−0·37**							

Measured variables: MIN, minimum; MAX, maximum; MEA, mean; MED, median; M1A, mean temperature at 1 am; M1P, mean temperature at 1 pm; MDR, mean daily range. Time periods: P1 = 15–28 June, P3 = 13–26 July, P6 = 24 August to 06 September, P9 = 05–18 October. Digital elevation models-derived variables: alt, altitude; twi, terrain wetness index; vrm, vector ruggedness measure; eas, eastness; slo, slope; hcu, horizontal curvature; vcu, vertical curvature; ddg, downslope distance gradient.
Coefficients of each variable are showed when significant and significance is expressed with '*' where P-values <0·001 correspond to ***, <0·01: **, <0·05: *. All models at all resolutions can be found in Appendix S5.

Table 3. Summary of multivariate generalized linear models sorted by adjusted R^2 (aR^2) in decreasing order for AMBIENT TEMPERATURE (AT), measured with uncovered loggers at 15 cm above soil level. First column is the abbreviation of the model showed, with different measured variables and time periods. The second column tells at which resolution (Res) the highest aR^2 was found

Model	Res	aR^2	alt	twi	eas	slo	hcu
AT-MED-P9	0·5	0·89	−0·94***	−0·35**			
AT-MED-P6	4	0·80	−0·74***	−0·44**			
AT-MDR-P3	2	0·49	0·43*		0·52**		−0·69***
AT-MAX-P6	2	0·43				0·48*	−0·44*
AT-M1A-P3	2	0·40	−0·74***				0·48*
AT-MIN-P1	2	0·38	−0·81***	0·87**	−0·75**		0·55*
AT-MDR-P6	1	0·31				0·58*	
AT-MDR-P9	0·5	0·31				0·58*	

Coefficients of each variable are showed when significant and significance is expressed with '*' where P-values <0·001 correspond to ***, <0·01:
**, <0·05: *. All models at all resolutions can be found in Appendix S6. Abbreviations as in Table 2.

AMBIENT HUMIDITY

Among the 112 HU models computed, only 35 (40%) showed at least one significant variable (Appendix S7), contrasting with prior models for DT (90%) and AT (70%). This is likely related to the rare significance of altitude and of DEM-derived variables such as eastness, slo and hcu in HU models (5% of them). On the other hand, twi is the DEM-derived variable with most frequently and highly significant models (37%). It is significant for all categories of measured variables and all periods analysed, except during the snowy episode (P9). Like DT models, resolution influences twi significance and models have an aR^2 optimum at 1 or 2 m (Table 4).

To assess the importance of the time period for the three categories of environmental variables (DT, AT, HU), we computed models between DEM-derived variables and measured variables over the entire fieldwork season (i.e. 15 June–18 October) (Appendix S8). Although the same DEM variables are significant for almost the same measured climatic variables, our results show that periods of cold, cloud cover (P1) or snow cover (P9) contrasted with those of sunshine (P3, P6). Indeed, a stronger significance of eas, slo, twi and a weaker significance of altitude are observed during those sunshine periods. In addition, the use of several measured variables is justified in order to distinguish different ecological conditions, as recommended by Ashcroft, French & Chisholm (2011) and Vercauteren *et al.* (2012).

SOIL MOISTURE

In soil moisture models, vector ruggedness measure (vrm) was the only DEM-derived variable that had a significant contribution across resolutions (Table 5). However, its contribution was dependent on resolution, as models were less and less significant with coarser resolutions. Given that alt showed a stable contribution though scales, the highest aR^2 was obtained at 0·5 m resolution.

ECOLOGICAL INDICATORS

Determination coefficients of models including Landolt's ecological indicators were low at all resolutions. Only *LDT-moisture* and *LDT-nutritive_substances* showed aR^2 above 0·15. Two DEM-derived variables, twi and slope, showed a significant contribution to *LDT-moisture* across scales (Appendix S9). Unlike other models, GLMM's aR^2 values for *LDT-moisture* were stable through resolutions.

Discussion

Variables derived from DEMs are crucial for species distribution models or landscape genetics, but their ecological relevance remains subject to caution (Lassueur, Joost & Randin 2006; Dubuis *et al.* 2013). In particular, the relationship between DEM-derived variables and ecological features does not necessarily hold across spatial scales and appears highly

Table 4. Summary of multivariate generalized linear models sorted by adjusted R^2 (aR^2) in decreasing order for AMBIENT HUMIDITY (HU), measured with uncovered loggers at 15 cm above soil level. First column is the abbreviation of the model showed, with different measured variables and time periods. The second column tells at which resolution (Res) the highest aR^2 was found

Model	Res	aR^2	alt	twi	eas	slo	hcu
HU-M1A-P6	1	0·76		0·82***		0·48**	0·54**
HU-MDR-P1	2	0·48		−0·75***	0·42*		
HU-MED-P3	2	0·47		0·70**			
HU-M1P-P6	0·5	0·38		0·55*		−0·53*	
HU-M1P-P1	2	0·28		0·59**			
HU-MDR-P6	0·5	0·27		−0·63*		0·51*	
HU-M1P-P9	1	0·23		−0·47*			
HU-MDR-P3	1	0·19		−0·76*			

Coefficients of each variable are showed when significant and significance is expressed with '*' where *P*-values <0·001 correspond to ***, <0·01: **, <0·05: *. All models at all resolutions can be found in Appendix S7. Abbreviations as in Table 2.

Table 5. Summary of multivariate generalized linear mixed models on one-time measurements of SOIL MOISTURE sorted by adjusted R^2 (aR^2)

Res	aR^2	alt	twi	vrm	eas	slo	hcu	vcu	ddg
0·5	0·46	−0·26**		−0·43***					
1	0·43	−0·45***		−0·19**					
2	0·41	−0·46***		−0·20*					
4	0·35	−0·44***				−0·23**			

Coefficients of each variable are showed when significant and significance is expressed with '*' where *P*-values <0·001 correspond to ***, <0·01: **, <0·05: *. Abbreviations as in Table 2.

dependent on the spatial resolution. In order to foster application of DEMs in ecology and evolution, their relevance to approximate environmental features must be evaluated and suitable approaches should be further developed. Our results validate two essential concerns regarding DEMs at a local scale: (i) multi-scale approaches are valuable when facing topographic heterogeneity, and (ii) it is crucial to investigate a large diversity of DEM-derived variables in order to evaluate all topographic aspects that might influence climatic variability. Using a specific area with challenging features at the interface between subalpine and alpine conditions, we were able to show that DEM-derived variables can be used as relevant surrogates for environmental variables and to better understand relationships with local topography. Indeed, physiological activity and adaptation of plants are affected by temperature, humidity and soil characteristics (Körner 2003; Böhner & Selige 2006; Manel *et al.* 2012).

Our models consistently report decreased adjusted R^2 at 4 m spatial resolution, supporting the hypothesis that VHR elevation data provide a higher explanatory power in heterogeneous areas such as mountains. However, our models did not generally converge towards a clear optimal resolution and reveal that the most suitable resolution depends on the type of DEM-derived variable considered. This is particularly well illustrated by vrm, showing highest significance at 0·5 m and highlighting that soil characteristics are best grasped when initially computed with as much details as possible, whereas hydrology variables, such as twi, reach optima at different resolutions (Böhner & Selige 2006; Buchanan *et al.* 2013). Variation in the model fit across scales highlights the necessity of implementing multi-scale methods in ecological studies involving DEM-derived variables. The computation of such variables at multiple scales improves the modelling of microclimatic variables such as temperature, humidity and soil moisture in a mountainous area. Furthermore, using DEMs at their original grid resolution, without consideration of scale representativeness, likely leads to an underestimated role of topographic features in ecological models. In fact, a too fine resolution may hold an excess of details and generate too much noise, while too coarse resolution would only show generalized properties of the landscape and lose explanatory power (Cavazzi *et al.* 2013). Although most studies using DEMs at their original resolution often ended up with a minor contribution of topography in their models (Zimmermann & Kienast 1999; Manel *et al.* 2010b; Vercauteren *et al.* 2012; Patsiou *et al.* 2014), we show here that coupling VHR DEMs with a multi-scale approach generates variables with a high explanatory power. Accordingly, acquiring high-resolution or VHR DEMs and performing multi-scale analysis further on represent a suitable approach for local scale studies in ecology and evolution. At the moment, LIDAR represents the best DEM acquisition technology, providing great precision and high resolution across hardly accessible terrains, but still expensive (Liu 2008). Although they do not show the same level of precision like LIDAR, stereo-photogrammetry from unmanned aerial vehicles (UAV) constitutes a less powerful but suitable and cheaper alternative subject to intense research (Leempoel & Joost 2012).

Our results further bring advantages of using a large panel of DEM-derived variables. On the one hand, terrain wetness index (twi) showed the highest explanatory power among the DEM-derived variable here tested, highlighting a relevant proxy for dryness across the studied landscape (Fig. 2a). In addition, models including more variables such as eastness and slope best predicted temperature, probably because these primary attributes have a high influence on radiation and wind exposure (Wilson & Gallant 2000; McVicar *et al.* 2007; Appendix S5). For instance, in our specific study area, twi partially accounted for the distance to the ridge as well as for the protection from wind, which could further contribute to temperature and humidity variability. In fact, distance to ridge and twi were moderately correlated at high resolution (i.e. 0·6 at 0·5 m and 0·7 at 1 m) and dropped to 0·3 at coarser resolutions. Although such correlations are inevitable and likely blur interpretations, our models showed that most of the significant contribution of twi was obtained at 0·5 and 2 m, when the correlation between twi and distance to ridge was not the strongest. This, again, highlights the relevance of a multi-scale analysis.

Among other overlooked DEM-derived variables in the literature, vector ruggedness measure (vrm) appeared as the best surrogate for soil moisture (MSM), suggesting that vrm at such high resolution is a suitable proxy for the distribution of stony soils along the ridge and thus for soils with different porosities. Accordingly, the negative coefficients observed here support this hypothesis that high roughness highlights stony soils implying low soil moisture, whereas low roughness reflects developed soils retaining higher moisture. This vrm variable, measuring vector dispersion across the central pixel rather than being a derivative of slope, represents a much better proxy than related proxies such as Terrain Ruggedness Index (Appendices S3 and S4), as previously stressed by Sappington, Longshore & Thompson (2007). Nevertheless, the present models demonstrate a variety of DEM-derived variables as suitable or complementary surrogates to *in situ* measurements for characterization of plant habitats and we recommend to go beyond their traditional use of elevation, slope and aspect (Dobrowski 2011).

In addition, DEM-derived variables are easy-to-compute proxies of environmental features, involving limited fieldwork but good knowledge of Geographic Information Systems, DEM-derived variables should thus be widely used as proxies of environmental features in ecology and evolution (Kozak, Graham & Wiens 2008). Furthermore, open source GIS alternatives (e.g. SAGA GIS, Quantum GIS and GRASS) provide algorithms to process a variety of secondary terrain attributes.

The distribution of the focal species along an apparently homogeneous ridge showing a constant slope and slight changes in orientation, in fact turned out to be highly heterogeneous at a high resolution. Prior work on ecotypes of *B. laevigata* (Parisod & Christin 2008) suggested a mosaic distribution of subalpine and alpine habitats, and the use of VHR DEM-derived variables here permitted to highlight the topographic control on micro-climatic patterns. Our results indeed show a significant contribution of micro-topography to model micro-habitat, even though unmeasured factors may play a major role. For instance, high elevation and exposed sites are more likely to be coupled with free air environment as compared with low elevation sites that are protected (Pepin & Seidel 2005). However, we observed 5 °C difference in ranges for AT and up to 8 °C for DT. Such important temperature variability over short distances cannot only be due to large-scale effects and support our evidence for a micro-topographic control (Fridley 2009). In addition, VHR DEM-derived variables in our models highlighted the lower relevance of elevation as compared with studies at regional or continental scale. Despite a correlation of $-0{\cdot}99$ reported between temperature and elevation across Switzerland (Zimmermann & Kienast 1999), we here showed that the 0·5 °C decrease per 100 m elevation increase did not hold at a local scale. Therefore, the important variability of temperature observed here is likely valid in various mountainous areas, even when microhabitats variability is only partially distinguished from large-scale factors. Our results thus confirm that proxies other than elevation can – and in fact probably better – account for temperature variability in as mountainous areas.

On top of micro-climatic factors, meso-climatic ones might affect climatic variables in the study area. For instance, varying wind patterns and cloud cover across the studied ridge could impact on the variability of local climates. The results obtained here for micro-topography are, however, not disqualified by meso-climatic patterns. In contrast to common cloudiness on the highest part of the study area early and late during the growth season, the contribution of DEM-derived variables appeared consistently significant at different time periods, demonstrating a substantial effect of micro-topography. In addition, several DEM variables such as protection index, sky view factor or ruggedness might constitute surrogates for protection from wind at a micro-climatic level. Noticeably, temperatures measured during the snow episode provide an indirect measure of snow cover, as loggers situated under the snow during that period did not show a daily cycle of temperature at sampling locations. Therefore, modelling of snow cover heterogeneity could be improved by combining topographic variables (Gottfried, Pauli & Grabherr 1998; Randin *et al.* 2009) with the daily cycles of loggers. Our results thus highlight the role of micro-topographic effects and the need to consider different measured variables and temporal variability at a scale pertinent for plants, as previously reported by Körner (2003) and Scherrer & Körner (2011).

Noticeably, variables derived from VHR DEM approximate Landolt indicators derived from species distribution with less accuracy than climatic variables. Insufficient variability in this biological data set compared to extension of Landolt's indicator values (attributed to species across the whole Alps (Landolt *et al.* 2010) certainly explains such limited relevance of micro-topography to a large extent. Our data are indeed restricted to a single site and may thus not show sufficient variation for indicators such as temperature (here, only alpine belt), continentality (only oceanic conditions), light (only open, alpine grasslands), soil pH (only calcareous soils), humus and aeration (mainly humic and silty soils). Furthermore, Landolt's indicators include biotic interactions such as competition that were not taken into consideration by DEM-derived variables, and the small area used for plant inventories ($0{\cdot}2 \times 0{\cdot}2$ m) restricts the list to a part of the plant community, what probably creates a random variation in the calculated mean values at the community scale. Although the exact reasons underlying the relatively low adjusted R^2 in models derived from biotic data remain elusive, this work shows that models using VHR DEM-derived variable were generally significant for ecological indicators showing a high variability at local scale in mountainous environment, that is soil moisture and fertility (Körner 2003). Variables retained in models (i.e. wetness index, ruggedness, slope and curvature) were indeed highly coherent with factors related to micro-topography and to slope, such as lower soil humidity on steep slopes leading to higher drainage and in superficial soils likely developing on mounds rather than in hollows (Gobat, Duckert & Gallandat 1989; Burga *et al.* 2010).

DEMs are underexploited compared with the large diversity of variables that can be derived from them. In this paper, we showed that VHR DEM-derived variables constitute robust surrogates for ecological conditions and that they are relevant to properly represent local topographic-related features, enabling the computation of multi-scale climatic variables. Despite the applicability of VHR DEMs across much larger extents is likely to be limited, our results suggest that a multi-scale approach is valuable to evaluate VHR relevance at different scales in mountainous areas.

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Data accessibility

Measurements of all climatic variables, values of DEM-derived variables at sampling locations and R scripts used to compute multivariate models are available on Dryad: doi:10.5061/dryad.43md3.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S9. Summary of multivariate generalized linear models and generalized linear mixed models for *LDT-moisture*.

Appendix S1. Map of *LDT-moisture* (background: Terrain Wetness Index at 0·5 m resolution).

Appendix S2. Description and parameters of DEM-derived variables computed at each resolution (i.e. 0·5, 1, 2, 4 m).

Appendix S3. Table of Spearman correlations coefficients calculated between DEM-derived variables showing a spatial resolution of 0·5 m at Landolt sampling locations.

Appendix S4. Table of Spearman correlations coefficients calculated between DEM-derived variables 15 showing a spatial resolution of 0·5 m at covered loggers locations.

Appendix S5. Summary of multivariate generalized linear models for DIRECT AIR TEMPERATURE (DT), measured with uncovered loggers at 15 cm above soil level.

Appendix S6. Summary of multivariate generalized linear models for AMBIENT TEMPERATURE (AT), measured with uncovered loggers at 15 cm above soil level.

Appendix S7. Summary of multivariate generalized linear models for AMBIENT HUMIDITY (HU), measured with uncovered loggers at 15 cm above soil level.

Appendix S8. Summary of multivariate generalized linear models for DT, AT and HU over the entire fieldwork season (15 June–18 October).

Appendix S9. Summary of multivariate generalized linear models and generalized linear mixed models for 42 LDT-moisture.