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- 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 meters, we generated DEM-derived variables at 1m, 2m and 4m 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).
- Specific VHR DEM-derived variables showed significant associations with climatic factors. In addition to slope, aspect and curvature, the underused wetness and ruggedness indices modeled 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 2m resolution, depending on the variable considered.
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Very high resolution digital elevation models: are multi-scale derived variables ecologically relevant?

Short running title: Ecological relevance of VHR DEM-derived variables

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Abstract

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determination decreasing with coarser resolutions or showing a local optimum with a 2m resolution, depending on the variable considered.

- 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.

Keywords: Digital Elevation Models, Multi-scale analysis, Very High Spatial Resolution, Temperature and Humidity Loggers, Landolt’s Ecological Indicators, Generalized Linear Models, Local Scale
Introduction

Digital elevation models (DEMs) are widely used in landscape and evolutionary ecology to understand the distribution of species and their genetic variation (Kozak et al. 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 et al. 2009), soil water content (Moore et al. 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 3x3 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 et al. 1991), terrain ruggedness (Riley et al. 1999) or temperature (Wilson & 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 et al. (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 (≈30m for ASTER GDEM, ≈90m 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, ≤1m) elevation data offered unprecedented level of details for exploring the morphological characteristics of landscape
and promoted new applications (see Lassueur et al. 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 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 micro-climate 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. (2013) 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 modeling 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 meters 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).

**Material and Methods**

### a. Study area and sampling design

The focal study area is a narrow ridge (Figure 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 less than 10 meters 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 0.5x0.5m in the field, resulting in 60 4x4m areas with at least five individuals of *B. laevigata* (see resulting distribution in Figure 1A). Briefly, direct air temperature was measured with 60 uncovered temperature loggers placed at the centre of each area as well as 20 additional ones installed at random locations along the ridge (Figure 1A). Ambient temperature 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 (Figure 2B). Furthermore, species composition was assessed in 452 plots of 0.2 m x 0.2 m at the corners of 1m x 1m squares located within the 60 areas as well as 53 additional ones randomly located along the ridge (Appendix S1).
Details on these measurements can be found in the next sub-section.

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

b. Temperature, humidity and soil moisture data

Air temperature and humidity

Direct air temperature (DT) was measured with uncovered IButton loggers (1922L) from Maxim Integrated (http://www.maximintegrated.com/) placed 15cm above the ground. Furthermore, covered temperature and humidity loggers (IButton 1923) measured ambient temperature (AT) and humidity (HU) at 15cm above the ground (Figure 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 minutes during 126 days, from June 15, 2013 to October 18, 2013, with an accuracy level of 0.5 degrees C° and 5% for humidity. These 126 days were grouped in 9 periods of 14 days (P1: June 15 to 28; P2: June 29 to July 12; P3: July 13 to 26; P4: July 27 to August 9; P5: August 10 to 23; P6: August 24 to September 6; P7: September 7 to 20; P8: September 21 to October 4; P9: October 5 to 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 1am (M1A), mean value at 1pm (M1P), mean daily range (MDR).

Soil moisture

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

c. 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-*pHReaction* (soil pH), and three climate indicators, LDT-*continentality*, LDT-*light*, and LDT-*temperature*.

d. DEM 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/m². The raw point cloud was then processed with the TERRASCAN software (TERRASOLID Ltd, Helsinki; http://www.terrasolid.fi/) to filter buildings, vegetation and all other surface elements in order to obtain a terrain model (Xiaoye Liu 2008). The final density of the ground class was 10 points/m² on average and the spatial resolution of the DEM was set to 50cm. A few void locations (no data) were filled with the help of a 1m 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 et al. 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. Natick, Massachusetts: The MathWorks Inc., 2010) to approximate topography at multiple resolutions. The original VHR DEM (50cm) was thus generalized to 1, 2 and 4 meters to constitute the multi-scale DEM datasets.

We used SAGA GIS (Böhner et al. 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 one month of the growing season (June).
e. 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 where 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 observations available for covered ambient temperature (AT) and air humidity (HU) variables (n=25), correlations between retained DEM variables where higher than for uncovered loggers locations and we had to limit the study to 5 independent DEM-derived variables (Appendix S4): altitude (alt), eastness (eas), slope (slo), horizontal curvature (hcu) and terrain wetness index (twi).

f. 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.

Instead of GLMs, Generalized linear mixed models (GLMMs) (Breslow & Clayton 1993; Bolker et al. 2009) were performed on the dataset 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.
g. 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 measured soil moisture with three letters (MSM).

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 direct air temperature (DT) over the whole sampling period provides a global view on climatic conditions during summer 2013 (mean 12.1°C; Figure 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.

a. Direct air temperature (DT)

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 1m than at coarser resolutions (Appendix S5), adjusted R² (aR²) are usually highest in models at 0.5 or 2m resolution and almost systematically lower at 4m. Noticeably, aR² 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.

b. Ambient temperature (AT)
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 R², particularly during the snow episode (P9).

c. Ambient humidity (HU)
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 aR² optimum at 1 or 2m (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 to 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 et al. 2011; Vercauteren et al. 2012).
d. 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 through scales, the highest aR² was obtained at 0.5m resolution.

e. Ecological indicators

Determination coefficients of models including Landolt’s ecological indicators were low at all resolutions. Only $LDT$-moisture and $LDT$-nutritive_substances showed aR² above 0.15. Two DEM-derived variables, twi and slope, showed a significant contribution to $LDT$-moisture across scales (Table 6). Unlike other models, GLMM’s aR² 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 et al. 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 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 R² at 4m spatial resolution, supporting the hypothesis that VHR elevation data provides 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 0.5m 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 micro-climatic 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. According to acquiring high or very high resolution DEMs and performing multiscale 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 (Xiaoye 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 (Figure 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 0.5m and 0.7 at 1m) 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 were obtained at 0.5 and 2m, when the correlation between twi and distance to ridge were 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 (Appendix S3&4), as previously stressed by Sappington et al. (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 et al. 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 *Biscutella 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 -0.99 reported between temperature and elevation across Switzerland (Zimmermann & Kienast 1999), we here showed that the 0.5°C decrease per 100m 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 et al. 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 dataset 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 (0.2 x 0.2 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, i.e. 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 et al. 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.

Acknowledgments

This work was funded by a grant from the Velux Stiftung (Project 705 to CP) and by the Swiss National Science Foundation (SNSF) grant no CR3213149741/1 (GENESCALE). We thank Philippa Griffin for her help producing and improving R scripts. We thank our fieldwork helpers: Amélie Bardil, Daniela Biosa, Benjamin Dauphin, Timothée Produit and Ivo Widmer. Finally, we thank the two anonymous reviewers for their useful comments and for the general improvement of the manuscript.

References


Tables and Figures

Figure 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 and ambient temperature respectively. (Background image with 50 m isoelevation lines: Swissimage © 2013 swisstopo (JD100064)). (B) Mean daily direct air temperature 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.

Figure 2 (A) Map of the mean Direct air Temperature (DT) at 1am (M1A) during period P6 (August 24 to September 6). Terrain Wetness Index at 1m 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 the measured variable and the twi. (B) Map of one-time measurements of soil moisture (in percent) with Vector Ruggedness Measure at a 0.5m 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 table 2 and 5.
Dear editor,

Thank you for your globally positive comments and interest towards our article. We modified our manuscript according to the remarks received on the 13 of April. Responses can be found under each remark.

I urge a little more humility in relation to the applicability of your methodological framework. Your resulting models are descriptive, with untested generality. Their applicability to novel environments is likely to be quite poor. This does not make them less important or less useful, but it also doesn't make them superior to all other models.

Modifications were brought to paragraph at Line 295-308, as well as at Line 317, 319 and at Line 410-413.

The term VHR appears to be used inconsistently as a modifier describing a type of data, and perhaps in place of very high resolution elevation data. E.g., "...of VHR DEM-derived environmental variables" versus "... to what extent VHR likely evidence ..." Can you please clean up these inconsistencies?

Modifications at Line 77 (VHR DEM-derived variables), Line 80 (VHR elevation data), Line 88 (VHR elevation data), Line 91 (very high resolution), Line 317 (DEM-derived variables).

Please indicate in the introduction what multi-scale variables and studies mean.

Additional sentence at Line 84-85.

Technically, the term "prediction" is used inappropriately throughout the MS.

Modifications at Line 26 (modelled), Line 56 (explanatory), Line 61 (to model), Line 277 (variables), Line 279 (explanatory variable), Line 282 (variable), Line 319 (a higher explanatory power), Line 343 (explanatory), Line 364 (best surrogate for), Line 416 (approximate).

L70 - I suggest acknowledging the costs of going to finer scale data (compute time, lack of data for some important variables, etc).

Additional sentence at Line 77-79.

L70 I suggest removing "general".

Removed
L70-71 Awkward phrasing
Paragraph was rephrased at Line 72-77

L72 the claim about more accurate estimations of species distribution in relation to climate change needs more nuancing. As it stands it is misleading.
Modified, Line 73

L73 shapes
Modified, Line 75

L73-74 define the habitat patterns an organism is presented with.
Modified, Line 75

L92-93. I don't doubt that the topic it is worthy of investigation, but this assertion is unsupported.
Sentence deleted

L112 (hemisphere indicators follow coordinates.
Coordinates modified

L305 R2
Adjusted R², Line 309

L312 - "multi-scale methods..."
Modified, Line 316

L407-411 - Phrasing is awkward.
Conclusion at Lines 410-413 was modified
Reviewer: 1 Comments to the Corresponding Author

I thank the authors for their comprehensive response to my original comments. I hope the authors agree with me that the extra effort has resulted in a more convincing manuscript. Increased clarity regarding the ecological context and true objectives makes for a much better read. I feel the issue of position/distance to ridge is now adequately addressed and this critical appraisal puts the authors in a better light.

I remain concerned that the lack of applicability of VHR DEMS across much larger scales (e.g. for SDMS) is not discussed. The authors show that they add value at the local scale, but there is a clear limitation which needs to be mentioned somewhere (to prevent the naive reader from predicting occurrence of B. laevigata by TWI alone.). This does not detract from the work, but is an important caveat..possibly touched on, but one clear sentence is required. (I recommend acceptance contingent on this trivial revision)

Additional sentence in the conclusion at Line 413 to 415. In addition, nuances were provided in paragraph at Line 295-308, as well as at Line 317, 319 and at Line 410-413 also evoke the limitations of this approach.

63: grammar "variables diversity"?
Modified (variables’ diversity)

70: grammar "it permits to get safer"
Modified, Line 72 (It allows a safer)

362: grammar "here brought clear evidence"
Modified, Line 366 (Our results indeed show)

409: grammar ", a VHR DEMS is mandatory to model properly"try "VHR DEMS are required to properly represent"
Conclusion modified, Line 410-413
Table 1: Description and parameters of selected DEM variables computed at each resolution (i.e. 0.5, 1, 2, 4m). The full table can be found in Appendix S2.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Abreviation</th>
<th>Description</th>
<th>Units</th>
<th>Parameters/Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Altitude</td>
<td>alt</td>
<td>DEM Altitude</td>
<td>m</td>
<td></td>
</tr>
<tr>
<td>Slope</td>
<td>slo</td>
<td>Proxies for water flow, snow movements, erosion, solar radiation</td>
<td>radians</td>
<td>Method= Zevenbergen and Thorne, 1987</td>
</tr>
<tr>
<td>Sinus of Aspect (eastness)</td>
<td>eas</td>
<td></td>
<td>radians</td>
<td></td>
</tr>
<tr>
<td>Profile curvature</td>
<td>vcu</td>
<td></td>
<td>radians/m</td>
<td></td>
</tr>
<tr>
<td>Plan curvature</td>
<td>hcu</td>
<td></td>
<td>radians/m</td>
<td></td>
</tr>
<tr>
<td>Downslope distance gradient</td>
<td>ddg</td>
<td>Quantify downslope controls on local drainage</td>
<td>radians</td>
<td>Vertical distance = 2m (Hjerdt et al., 2004)</td>
</tr>
<tr>
<td>Vector Ruggedness Measure</td>
<td>vrm</td>
<td>Quantifies ruggosity with less correlation to slope</td>
<td>no unit</td>
<td>Radius = 1 pixel (Sappington et al., 2007)</td>
</tr>
<tr>
<td>Terrain Wetness Index</td>
<td>twi</td>
<td>Quantifies topographic control on hydrological processes</td>
<td>W = ( \frac{a}{ln(S)} )</td>
<td></td>
</tr>
</tbody>
</table>
Table 2: Summary of multivariate generalized linear models sorted by adjusted R² (aR²) 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 aR² was found. 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. Abbreviations are the following. Measured variables: minimum (MIN), maximum (MAX), mean (MEA), median (MED), mean temperature at 1am (M1A), mean temperature at 1pm (M1P), mean daily range (MDR). Time periods: P1=15 to 28 June, P3=13 to 26 July, P6=24 August to 06 September, P9=05 to 18 October. DEM-derived variables: Altitude (alt), Terrain Wetness Index (twi), Vector Ruggedness Measure (vrm), Eastness (eas), Slope (slo), Horizontal Curvature (hcu), Vertical Curvature (vcu), Downslope Distance Gradient (ddg)

<table>
<thead>
<tr>
<th>Model</th>
<th>Res</th>
<th>aR²</th>
<th>alt</th>
<th>twi</th>
<th>vrm</th>
<th>eas</th>
<th>slo</th>
<th>hcu</th>
<th>vcu</th>
<th>ddg</th>
</tr>
</thead>
<tbody>
<tr>
<td>DT-M1A-P9</td>
<td>0.5</td>
<td>0.69</td>
<td>-0.71***</td>
<td>0.17*</td>
<td>-0.21*</td>
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<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>DT-MIN-P9</td>
<td>2</td>
<td>0.50</td>
<td></td>
<td></td>
<td></td>
<td>0.28**</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>DT-M1A-P6</td>
<td>1</td>
<td>0.46</td>
<td>-0.49***</td>
<td>-0.81***</td>
<td>0.25**</td>
<td>-0.20*</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>DT-MED-P3</td>
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<td>0.37</td>
<td>-0.40***</td>
<td>-0.57***</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>DT-MEA-P6</td>
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<td>0.32</td>
<td>-0.35**</td>
<td>-0.80***</td>
<td>0.41**</td>
<td>-0.45*</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>DT-MDR-P3</td>
<td>0.5</td>
<td>0.22</td>
<td>0.25*</td>
<td>0.47***</td>
<td></td>
<td>-0.41***</td>
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<td></td>
</tr>
<tr>
<td>DT-MDR-P1</td>
<td>2</td>
<td>0.19</td>
<td>-0.25*</td>
<td></td>
<td>-0.38***</td>
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<tr>
<td>DT-MIN-P1</td>
<td>0.5</td>
<td>0.13</td>
<td></td>
<td></td>
<td>-0.37**</td>
<td></td>
<td></td>
<td></td>
<td></td>
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</tr>
</tbody>
</table>
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. 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.

<table>
<thead>
<tr>
<th>Model</th>
<th>Res</th>
<th>aR(^2)</th>
<th>alt</th>
<th>twi</th>
<th>eas</th>
<th>slo</th>
<th>hcu</th>
</tr>
</thead>
<tbody>
<tr>
<td>AT-MED-P9</td>
<td>0.5</td>
<td>0.89</td>
<td>-0.94***</td>
<td>-0.35**</td>
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<tr>
<td>AT-MED-P6</td>
<td>4</td>
<td>0.80</td>
<td>-0.74***</td>
<td>-0.44**</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>AT-MDR-P3</td>
<td>2</td>
<td>0.49</td>
<td>0.43*</td>
<td>-0.35**</td>
<td>-0.69***</td>
<td></td>
<td></td>
</tr>
<tr>
<td>AT-MAX-P6</td>
<td>2</td>
<td>0.43</td>
<td>-0.74***</td>
<td>0.48*</td>
<td>-0.44**</td>
<td></td>
<td></td>
</tr>
<tr>
<td>AT-M1A-P3</td>
<td>2</td>
<td>0.40</td>
<td>-0.74***</td>
<td></td>
<td>0.48*</td>
<td></td>
<td></td>
</tr>
<tr>
<td>AT-MIN-P1</td>
<td>2</td>
<td>0.38</td>
<td>-0.81***</td>
<td>0.87**</td>
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<td>0.55*</td>
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<td>AT-MDR-P6</td>
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<td></td>
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<tr>
<td>AT-MDR-P9</td>
<td>0.5</td>
<td>0.31</td>
<td></td>
<td></td>
<td></td>
<td>0.58*</td>
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</table>
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. 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>
<thead>
<tr>
<th>Model</th>
<th>Res</th>
<th>(aR^2)</th>
<th>alt</th>
<th>twi</th>
<th>eas</th>
<th>slo</th>
<th>hcu</th>
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<tbody>
<tr>
<td>HU-M1A-P6</td>
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<td>0.76</td>
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<td>0.82***</td>
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<td>0.48**</td>
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<td>0.42*</td>
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<tr>
<td>HU-MED-P3</td>
<td>2</td>
<td>0.47</td>
<td></td>
<td>0.70**</td>
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<td>HU-M1P-P1</td>
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<td>HU-MDR-P6</td>
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<td>0.51*</td>
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<tr>
<td>HU-M1P-P9</td>
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<td>-0.47*</td>
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<tr>
<td>HU-MDR-P3</td>
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<td>-0.76*</td>
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Table 5: Summary of multivariate GLMMs on one-time measurements of SOIL MOISTURE sorted by adjusted R² (aR²). 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

<table>
<thead>
<tr>
<th>Res</th>
<th>aR²</th>
<th>alt</th>
<th>twi</th>
<th>vrm</th>
<th>eas</th>
<th>slo</th>
<th>hcu</th>
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<th>ddg</th>
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<td>−0.26**</td>
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<tr>
<td>1</td>
<td>0.43</td>
<td></td>
<td>−0.45***</td>
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<td></td>
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<tr>
<td>4</td>
<td>0.35</td>
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<td>−0.44***</td>
<td></td>
<td>−0.23**</td>
<td></td>
<td></td>
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<td></td>
</tr>
</tbody>
</table>
A

Legend
- Uncovered loggers outside B. laevigata plots
- Uncovered loggers in B. laevigata plots
- Covered loggers
- Contour Lines of Elevation (each 50m)

B

Average temperature at mid-day for uncovered loggers (± standard deviation)