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Gabriela Hofer

Helene H. Wagner

Felix Herzog

Peter J. Edwards

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**Effects of topographic variability on the scaling of plant species richness in
gradient dominated landscapes**

Gabriela Hofer¹, Helene H Wagner², Felix Herzog¹ Peter J Edwards³

¹ FAL Agroscope Reckenholz, Swiss Federal Research Station for Agroecology and Agriculture, Zürich, Switzerland, gabriela.hofer@art.admin.ch and felix.herzog@art.admin.ch

² WSL, Swiss Federal Research Station for Forest, Snow and Landscape, 8903 Birmensdorf, Switzerland, helene.wagner@wsl.ch

³ Institute of Integrative Biology (IBZ), Swiss Federal Institute of Technology, ETH, Universitätsstrasse 16, 8092 Zurich, Switzerland, edwards@env.ethz.ch

Abstract

The variation of abiotic and biotic site conditions is often associated with the variation of niches, which in turn is hypothesised to constrain species richness of an area. Based on theoretical considerations, abiotic variation is often used as an estimator of species richness at broad scales, while the variation of habitats is used at finer landscape scales. However, habitat estimators imply a discrete, patchy structure of the landscape with homogenous patches and sharp boundaries, which does not apply well in gradient dominated landscapes. The aim of this study was therefore to investigate effects of abiotic heterogeneity at a finer landscape scale on plant species richness and their (α) and beta (β) components at microsite, habitat and local landscape level. For 12 landscapes of 1 km² the effects of two simple and one complex measures of topographic variability on species richness components were analysed and compared by linear regression models. Species richness of landscapes was explained to a high extent by the standard deviation (SD) of altitude ($R^2 = 0.63$), but the complex measure, SD of solar radiation, explained it even better ($R^2 = 0.82$). The β diversity components increased as expected significantly with topographic variability of local landscapes. There was, however, an additional context effect of landscape heterogeneity on α diversity components at microsite level, indicating a shift of mean microsite conditions. Further analyses revealed that the effects of topographic variability on species richness originated mainly from grassland, although woody habitats also had an influence. The effects of abiotic variability on landscape species richness and their diversity components suggest that – even at a fine landscape scale – the underlying abiotic pattern cannot be neglected if we are to understand patterns of species richness and the processes that maintain them.

Keywords

Environmental heterogeneity, topographic variability, species richness, meso scale, local landscapes, additive partitioning, alpha and beta species richness components.

Introduction

Biodiversity of an area (gamma diversity) is composed of the diversity at sites (α component) and the heterogeneity between sites (β component) (Whittaker 1977, Allan 1975). As local diversity is spatially limited, gamma diversity is expected to be strongly dependent on the heterogeneity between sites (Plotkin & Müller-Landau 2002). In contrast to mean ecological conditions, ecological heterogeneity is associated with the variance of niches in an area and has therefore been hypothesized to be an important driver of species richness at broad and fine scales (Palmer & Dixon 1990, Plotkin & Müller-Landau 2002). While the heterogeneity of abiotic parameters is often included in modelling to account for variance in species richness at broad scales (Richerson & Lum 1980, Currie 1991, Riera et al. 1998, Gaston 2000, Coblenz & Riitters 2004), the heterogeneity of discrete patches e.g. habitats, land cover or land use are mainly included to predict variance in species richness at landscape scale (Moser et al. 2002, Benton et al. 2003) which corresponds to the meso scale in the spatio-temporal hierarchy of Delcourt & Delcourt (1988). This reflects theoretical considerations saying that climate and topography deliver the abiotic envelope for the occurrence of species at broad scales, while their realized occurrence is thought to be determined at meso and micro scales by biotic interactions, land-use pattern, disturbance and succession (Cornell & Lawton 1992, Klijn & DeHaes 1994). Based on the biodiversity concept of Whittaker (1977) and Allan (1975) habitat heterogeneity is expected to be an appropriate correlate of species richness in landscapes with a simple, two dimensional patch mosaic structure with low variation within habitats and discrete borders among habitats. However, in topographically heterogeneous landscapes those two basic criteria are only partly met. Steep abiotic gradients cause gradual shifts in species

compositions within and between habitats (McGarigal & Cushman 2005) which makes the delineation of homogenous patches conceptionally unsatisfying and hardly reproducible in practice. However, the topographic relief of a landscape has a strong impact on abiotic micro-site conditions (Swanson et al. 1988), which in turn affect vegetation patterns (Larcher 1973, Ellenberg 1986, Franklin 1995) as well as land use patterns (Dorner et al. 2002, Wrbka et al. 2004). Consequently, we hypothesized that variability of topography is not only an appropriate surrogate of niche diversity and estimator of species richness at broad scales as currently used, but also at landscape scale. It remains an open question how to quantify topographic variability so as to maximize correlation with plant species diversity.

Most studies which integrated topographic variability used the SD of altitude (e.g. Richerson & Lum 1980, Currie 1989, Moser et al. 2005, Pausas et al. 2003, Luoto et al. 2002), some authors used the SD of slope (Coblentz & Riitters 2004) or other measures like for example the SD of curvature (Wrbka et al. 2004), all derived from digital elevation models (DEM). While the aspect is well known to be relevant for the occurring vegetation type (e.g. Bale et al. 1998, Benayas et al. 1999, Ortega et al. 2004, Sebastia 2004), these measures of topographic variability ignore the variability of aspect. Variability measures which integrate aspect are therefore expected to explain species richness pattern better. Franklin et al. (2000) called variables which combine topographic and direct or resource variables (e.g. solar radiation or wetness) ‘complex topographic variables’ and showed that they explain vegetation pattern in general better than simple topographic variables. In the present study, we therefore compared two established, simple measures of topographic variability (SD of altitude and SD of slope) with a complex topographic variable (SD of the potential yearly solar radiation), expecting that the complex variable integrating aspect is a better measure of abiotic variability.

The surface area of a landscape increases as a function of topographic variability. This collinearity caused confusion in numerous studies investigating heterogeneity effects because it could not be separated from a simple surface area effect (Forman 1995). After the suggestion of Whittaker et al. (1998) this problem is avoided by the assessment of an equal number of samples of a comparable total area within study units of different topographic variability. Biotic heterogeneity between sites can then be assessed by the partitioning of species richness data in α and β species richness components (Whittaker 1977, Allan 1975, Lande 1996, Wagner et al. 2000, Crist et al. 2003), expecting an increase of the β (heterogeneity) components with topographic heterogeneity. Lande et al. (1996) extended the additive diversity approach of Allan (1975) and demonstrated how several scale levels of diversity can be linked in an ecological system with commensurate α and β diversity components. This is an advantage compared to the multiplicative approach of Whittaker (1977) where α and β components have different units and are therefore not comparable. Additive partitioning allows to investigate and compare diversity at several scale levels coevally – one of the important claims of the hierarchy theory (O'Neill 1986) to assess the context and explaining details for the phenomenon of interest. As in mountainous areas topographic variability often increases with altitude, a problematic collinearity is also expected between altitude and its variability, and climatic heterogeneity might be a potentially confounding parameter for variance in species richness. One way to investigate microsite variability independently of climatic variability or broad scale shifts in species pools along altitudinal gradients is to define an environmentally homogenous study area where a common species pool is assumed.

The ecological interpretation of total species richness (gamma diversity) of a landscape requires not only the integration of hierarchical levels and the calculation of α and β components but also the distinction of species richness in different habitats (Zobel 1997). While e.g.

grassland species richness increases with decreasing nutrient values in the soil, the richness of woody species is expected to be higher at nutrient rich sites (Cornwell & Grubb 2003), and this example demonstrates that even constant species richness might cover contrary dynamics. Especially in improved agricultural landscapes, edges are known to be refuges for species sensitive to intensification (Smart 2002) and this is why in addition to the present habitats, species richness in edges might be important to understand the distribution of species richness in a landscape.

This meso scale study investigates the effect of topographic variability on plant species richness in local landscapes in the Swiss pre-Alps. To exclude potential confounding effects caused by shifts in species pool, we choose a climatically and biogeographically homogenous study area. To avoid confounded variables of species richness and area we assessed a standardized sample of 40 plant species relevées within 12 study units of 1 km² each. The research questions are parted in one main and three sub questions:

Is topographic variability an effective estimator of species richness at landscape scale?

a) How to quantify topographic variability so as to maximize correlation with plant species diversity?

b) Which species diversity components increase with topographic variability?

c) Does the influence of topography vary between habitat types?

Methods

Study area

The study area was a mountainous region in Canton Lucerne, Switzerland, covering 250 km² within the “montane” altitudinal belt (600 to 1000 meters above sea level). Land cover is pre-

dominantly shared by agriculture, mostly grassland (53%) and forest (37%). The mean annual precipitation is between 1500 and 1800 mm/m² and the mean annual temperature 11.3°C.

Sampling of local landscapes

All topographic variables used in this study were derived from a digital elevation model (DEM) (Swisstopo 2001) with a resolution of 25 m. Starting with a 1-km grid, three components of Topographic Variability (TV) were calculated for each of the 250 cells: SD of altitude (TV_{SDALT}), SD of slope (TV_{SDSLOP}), and SD of potential annual solar radiation (TV_{SDRAD}), a measure including the variability of orientation). The potential sum of shortwave solar radiation per year (short: radiation) was calculated with “DiGem” (Conrad 2002) based on the DEM. We assumed an atmospheric transmittance of 60 percent (standard of DiGem), and the variable was estimated based on calculations every 15 days with time steps of two hours. The three components of topographic variability were standardized by constraining the observed range between zero and one (Sneath and Sokal 1973).

The sum of the three components (TV_{SUM}) was used to derive a stratified sample of the 250 cells. To do this we ranked the cells and grouped them into septiles; three 1-km² cells were then sampled randomly from the first, third, fifth and seventh septile, yielding a sample of 12 local landscapes. With this stratification, we were sure to cover the whole range of topographic variability in the study area. Because of our focus was on agricultural landscapes, cells with less than 40 percent of open landscape were excluded.

Sampling within the local landscapes

Sampling was based on stratification by habitat class and topography, with the aim of maximizing variability of vegetation types and species composition among sampling units. Habitat classes were digitized from true-colour ortho-photographs with a resolution of 0.5 m, and the data were analysed using ARCGIS, version 8.3. All elements of at least two meters width and

100 m² area were digitized as polygons. A simple habitat classification with ten classes was applied (Table 1). The class “Urban, buildings, settlement” was excluded, and forest was only included in the edge class. The nine remaining habitat classes were aggregated into three habitat types: grassland/arable land, woody and edges (Table 1).

To quantify topographic site conditions, a total of seven topographic variables were extracted from the DEM - four local site variables (altitude, slope, radiation and curvature) and three variables to characterize the context (SD of altitude, slope and radiation within a window of five by five cells of 25 m). On the basis of k-means, these topographic variables were clustered for each local landscape into four groups per habitat type.

The four classes of topographic site conditions were crossed with the nine habitat classes, and one point was sampled for each combination (Tab. 1). Because grassland was the dominating habitat class, the sampling effort for grassland was increased and two relevés were made for each combination of grassland with the topographical clusters. Because there was only one arable field in the whole investigation area, the habitat type “grassland/arable” consisted exclusively of grasslands or orchards except for this one sample. We therefore call this group furthermore “grassland habitat”. If a specific combination of habitat class and topographic cluster did not occur within a local landscape, an alternative point was drawn randomly within the same habitat class, ignoring the topographical cluster class. If this failed, a point was drawn randomly within the same habitat type.

Forty plant species relevés of 25 m² were recorded within each of the 12 local landscapes to assess species richness components. The shape of the relevés was adapted to the habitat type: “grassland/arable” was sampled using 5 m by 5 m squares, while the linear habitats “edge” and “woody” were sampled using 1 m by 25 m rectangles.

Numerical analyses

Effect of topographic variability on landscape species richness

The effect of topographic parameters on total observed species richness within the 12 local landscapes was analyzed with multiple linear regression. To select the model with the highest likelihood, we compared the explanatory power of the mean (T_M) and the SD of the topographic parameters. The model selection criterion of Akaike for small sample sizes AICc was used, giving advantage to models with few parameters (Burnham & Anderson 1998). Variables with a Pearson correlation coefficient $r \geq 0.6$ were avoided within the same model. Another aim of this selection process was to choose the most appropriate model for investigating the effect of topographic variability on species richness components.

Additive components of species richness

We estimated α and β components of species richness using the approach of additive partitioning first suggested by Allan (1975) and further developed by Lande (1996). As suggested by Lande (1996), Wagner et al. (2000) and Crist et al. (2003), three scale levels - microsite, habitat and landscape - were linked within each of the 12 local landscapes. For level i , an α component is calculated by the average species number within the pooled samples at level i . The β component of level i results from the difference between α_i and α_{i+1} :

Landscape (12)	α_3 (= gamma diversity)
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Habitat type (3 x 12)	α_2 + β_2
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Plot (40 x 12)	α_1 + β_1
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Effect of topographic variability on species richness components

The effect of topographic variability on each species richness component was assessed with a linear regression on TV_{SDRAD} , based on the best fitting model from the previous analysis. Normality of the residuals was tested with Shapiro Wilk's test for normal distribution; in addition, we checked the random distribution of the residuals with a scatter plot of predicted versus residual values.

Results

We recorded a total of 413 plant species in 480 samples (25 m^2) distributed within 12 local landscapes. The number of species recorded in individual local landscapes ranged from 161 to 208.

Quantification of topographic variability

The correlation matrix (Tab. 2) shows the Pearson correlation coefficients of the six variables which were thought to be included in the model selection procedure. However, as slope was correlated with all the variability variables it was omitted, because it would not have been possible to separate heterogeneity effects from effects of mean conditions. Combinations and subsets of the four remaining topographic variables were included in the model selection procedure if they did not reach an $r \geq 0.6$.

In the model selection procedure, the highest likelihood (which is lowest AICc) was reached by a regression model with one single variable, TV_{SDRAD} . After the rule of thumb of Burnham and Anderson (1998), further candidate models are those with an AICc value differing from the best model by less than two; in our case only one model, with TV_{SDRAD} and T_{MRAD} , met this criterion. In addition to the two candidate models that were identified, Table 3 summarizes for purposes of comparison the regression models including only one of the four topo-

graphic variables. For TV_{SDRAD} , the R^2 (0.82) was substantially higher than for the next best single variables T_{MSLOP} (0.64) and TV_{SDRAD} (0.60). TV_{SDRAD} was therefore used as a surrogate for topographic variability in subsequent analyses. The best model without the variable TV_{SDRAD} had an R^2 of 0.72 and AICc rank five.

Effect of topographic variability on plant diversity components

The linear regressions for the different species richness components are shown in Figure 1 for the whole landscape and in Figure 2 for the three habitat types separately. For the whole landscape, partitioning into variability (α) and heterogeneity (β) components at three levels showed that all components increased with topographic variability. At the microsite level, topographic variability explained comparable amounts of α and β components (R^2 of 0.78 and 0.80 respectively), while at the level of habitat type, topographic variability explained more of the α component than of the β component (R^2 of 0.82 and 0.47 respectively).

The separate calculation of species richness components for each habitat type revealed consistent strong effects of topographic variability on all diversity components of the “grassland” habitat type, with R^2 between 0.79 and 0.88. The species richness in the habitat type “edges” was consistently higher than in the other habitat types, but the components of species richness were unaffected by topographic variability. In contrast, the species richness components of the “woody” habitat type were significantly affected by topographic variability on the β_1 ($R^2 = 0.29$) and α_2 ($R^2 = 0.36$) level, but with comparably low R^2 . There was no effect of topographic variability on the α_1 level.

Discussion

Topographic variability is an effective landscape-scale estimator of species richness

The high amount of variance in plant species richness explained by topographic variability supported the hypotheses that those measures are not only efficient estimators at macro and broad meso scales (*sensu* Delcourt & Delcourt 1988) but also at a finer meso scale such as the local landscapes of 1 km² in this study. It is important to recognize that the effects of topographic variability differed from the effects of the mean conditions for altitude and radiation because those parameters varied independently. Two studies at the border of meso to macro scale (*sensu* Delcourt & Delcourt) derived contradicting results concerning the importance of topographic heterogeneity. While Pausas et al. (2003, extent: 31900 km², grain size: 10 by 10 km²) estimated topographic heterogeneity as significant for species richness but not distinguishable from the confounded increase of area, Moser et al. (2005, extent: 50500 km², grain size: 6 by 6 km²) found that topographic heterogeneity was not important at the scale of their study. Several reasons might be responsible for these conflicting results, because besides of the probably real differences, the quality of the species richness data might be different, different measures of topographic heterogeneity were used and the model selection procedure was not the same. It might therefore be easier to derive the reasons for the consistently detected effects at finer meso scale: The present study and Luoto (2002) cover both a climatically homogenous area and are therefore able to exclude important climate induced shifts in the presence of species and habitats which are expected to be confounded with heterogeneity. Although there are certainly additional parameters influencing species richness in local landscapes the strong effects of topographic variability indicates the significant impact of the abiotic envelope on local processes (microsite conditions, land use) and challenges the common notion of the environmental envelope being relevant only at broader scales.

Complex topographic parameters are better predictors of species richness

Studies in grasslands and in forests have shown the importance of aspect for biodiversity, vegetation types and species composition (e.g. Miller & Franklin 2002, Bale et al. 2004, Sebastia et al. 2004). We therefore explain the best fit of the linear regression model based on TV_{SDRAD} ($R^2 = 0.82$) as due to the additional information about the variability of aspect; this information that is not represented in the parameters slope or altitude. Our results confirm the findings of Franklin et al. (2000) that in explaining the distribution of plant species complex topographic parameters that are linked to resource or direct environmental variables (sensu Austin and Smith 1989) have more predictive power than simple topographic variables. The best model without TV_{SDRAD} included both T_{MALT} and TV_{SDALT} ($R^2 = 0.72$), suggesting that by including the variability of the orientation to the sun, there was at least a 10 % gain in variance explained. Nevertheless, also the simple regression model including TV_{SDALT} ($R^2 = 0.63$) as predictor was able to explain species richness to a considerable degree.

Alpha and beta diversity components contribute both to the landscape species richness

The additive partitioning of landscape species richness in α and β components at the microsite and habitat level revealed two important points. First, the expected and confirmed significant increase of β diversity (heterogeneity) between microsites with increasing topographic variability was a strong support for the heterogeneity hypotheses and excluded a simple species – area effect like described by Forman (1995). Secondly, α components increased significantly with increasing topographic variability, too, and therefore the heterogeneity components were not exclusively responsible for an increase of landscape species richness with topographic variability. The phenomenon of the context or matrix landscape affecting local α diversity has been found before in patch mosaic landscapes (e.g. Dauber et al. 2003, Aviron et al. 2005, Gabriel et al. 2005), showing that the share of certain habitats in the surrounding affects diversity at sites. The hypothesis of these studies are based on the meta population theory, ex-

298 pecting a higher rate of immigration with a higher share of habitat in the context, leading to
 299 more saturated local communities (species pool effect, Hanski & Gaggiotti 2004). Kumar et
 300 al. (2006) found effects of context patch heterogeneity on local α diversity (species richness)
 301 while in the present study, we found effects of context topographic heterogeneity on local
 302 species richness for a gradient dominated landscape, where biotic heterogeneity should not be
 303 estimated by patch heterogeneity (Cushman & Mc Garigal 2005). In addition to meta popula-
 304 tion effects, other processes are expected to contribute the significant increase of microsite
 305 species richness with topographic landscape variability. In the present study, the topographic
 306 variability of the context is expected to affect accessibility for land use and might cause less
 307 intensive, biodiversity promoting land use practices with increasing topographic variability.
 308 Abiotic site conditions were not only more variable in landscapes of higher topographic vari-
 309 ability like indicated by the β species richness components, but the increase in α diversity
 310 components suggests in addition an ecological shift of the mean microsite conditions. The
 311 increase of α diversity components with topographic variability in the investigated local land-
 312 scapes could be an effect of either an increasing local species pool or decreasing management
 313 intensity. Although we did not investigate these causes in the present study, the strength of the
 314 effect suggests that the underlying topographic pattern in our study area governs the most
 315 important patterns determining species richness.

317 **The effect of topographic variability depends on the habitat type**

318 The separate analysis of the diversity components within the three habitat types grassland,
 319 edges and woody is an important step to better understand the effect of topographic variabil-
 320 ity. Topographic variability did not affect all habitat types equally (Figure 2a-c): Total species
 321 richness within habitat types (α_2) increased strongest in grassland but also in woody habitats,
 322 while edges made no contribution to this effect. As we know from earlier studies, topography

affects species composition of various grassland types (e.g. Sebastia et al. 2004, Benayas et al. 1999) and woody habitats (Bale et al. 1998, Ortega et al. 2004). The fact that the β components at the microsite level increased in both the grassland and woody habitat types is therefore not surprising and suggests that differences in species composition among microsites tended to be greater in landscapes with high topographic variability; this is presumably due to higher microsite variability in such landscapes. However, grassland and woody habitats differed in the behaviour of the α_1 components at the microsite level. Grassland species richness tends to be higher at nutrient poor sites, both wet and dry, than at nutrient rich sites (Cornwell & Grubb 2003). These favorable site conditions for biodiversity are more likely to occur on steeper slopes which are naturally less fertile, though they may also persist in flat areas that are not intensified because of poor accessibility. The α_1 microsite components of woody habitat types did not increase with topographic variability which might indicate that for woody habitats, heterogeneity components were almost exclusively contributing to the increase of total species richness with topographic variability.

Several reasons may explain higher species richness in edges compared to grassland and woody habitat types: 1) edges may contain species from two contiguous habitats (Zonneveld 1995), 2) they are known to provide residual habitats for plant species that have otherwise been lost from intensively managed agricultural landscapes (Smart 2002), and 3) a high variability in site conditions can be expected in edges because of the contrasting influences of adjacent habitats (e.g. wet, dry, shady). The effects 2) and 3) would both cause a higher relative contribution of edges to observed total species richness (α_3) in topographically homogeneous and more intensively managed landscapes than in landscapes with higher environmental variability and would lead to the observed results.

Conclusions

Abiotic heterogeneity explained high amounts of landscape species richness. This contradicts the common notion that abiotic parameters are estimators of broad meso and macro species richness patterns while patch heterogeneity is needed to explain species richness at finer scales. While an increase of β diversity components was expected with abiotic variability reflecting the increase of niche variability, the additional effects of landscape level heterogeneity at microsite level indicate that the abiotic heterogeneity of the context affected local microsite conditions. The results show, that even at finer meso scale, the underlying pattern of topography cannot be neglected if we are to understand patterns of species richness and the processes that maintain them.

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Table 1: Stratification matrix for the sampling within each of the 12 local landscapes of 1 km²: Nine habitat classes were combined with four classes of topography. In total, 40 points were sampled randomly within each local landscape (36 points plus 4 grassland points extra). The numbers of samples is indicated in the four columns of the matrix.

Habitat types	Habitat classes	Topographic Clusters			
		1	2	3	4
Grassland and arable habitats	1 Grassland	2	2	2	2
	2 Orchards	1	1	1	1
	3 Arable land	1	1	1	1
Edge habitats	4 Roads/tracks/paths	1	1	1	1
	5 Waters	1	1	1	1
	6 Forest edge	1	1	1	1
Woody habitats	7 Hedgerow	1	1	1	1
	8 Riparian Woods	1	1	1	1
	9 Other Groups of Bushes/Trees	1	1	1	1
Rest	10 Buildings, Settlements				

Table 2: Pearson's correlation coefficients (r) of the investigated explaining topographic variables. Bold printed are significantly correlating r coefficients with $p < 0.05$. The topographic parameters were abbreviated as following: Prefix T stands for topographic parameter and prefix TV for topographic variability. Inferior abbreviations: mean = M, standard deviation = SD, altitude = ALT; slope = SLOP; radiation = RAD.

	T _{MALT}	T _{MSLO}	T _{MRAD}	TV _{SDALT}	TV _{SDSLOP}	TV _{SDRAD}
T _{MALT}	1.00					
T _{MSLO}	0.47	1.00				
T _{MRAD}	-0.10	-0.27	1.00			
TV _{SDALT}	0.07	0.81	-0.36	1.00		
TV _{SDSLOP}	-0.16	0.67	-0.48	0.78	1.00	
TV _{SDRAD}	0.49	0.95	-0.32	0.78	0.65	1.00

Table 3: Selected regression models explaining observed total species richness of the 12 local landscapes of 1-km² are shown ranked by Akaike's criterion for small sample sizes (AICc rank). For abbreviations of included variables see Table 2.

AICc rank	Variables included	Multiple R	Multiple Rsquares	Adjusted Rsquares	F(1,10) / F(2,9)	p	Std. Error
1	TV _{SDRAD}	0.91	0.83	0.82	49.56	0.0000	7.34
2	TV _{SDRAD} /T _{MRAD}	0.92	0.84	0.80	23.48	0.0003	7.57
7	TV _{SDALT}	0.80	0.63	0.60	17.24	0.0020	10.85
9	T _{MALT}	0.42	0.18	0.09	2.14	0.1741	16.25
10	T _{MRAD}	0.37	0.14	0.05	1.63	0.2303	16.60

Figure legends:

Figure 1: Effects of topographic variability - measured as standard deviation of solar radiation - on species richness components at microsite level (α_1 , β_1), habitat type level (α_2 , β_2) and landscape level (α_3). Simple linear regressions were performed based on all 40 plant species relevées within a local landscape of 1km². (* = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$)

Figure 2: Effect of topographic variability - measured as standard deviation of solar radiation - on species richness components within habitat types on microsite level (α_1 , β_1) and habitat type level (α_2). Simple linear regressions were performed within the three habitat types “grassland”, “edge” and “woody” separately. (* = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$)

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516 Hofer, Wagner, Herzog & Edwards

517 Figure 1

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523 Figure 2