MULTI-SCALE EFFECTS OF TOPOGRAPHY ON
PLANT DIVERSITY IN
MOUNTAINOUS AGRICULTURAL LANDSCAPES

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Summary

The high plant diversity of mountainous farmland is recently threatened by land use change, especially by abandonment of agricultural land use. Sensitive biodiversity indicators and efficient sampling designs are therefore needed to monitor these areas. Although topography is known to affect abiotic and biotic patterns in several ways, none of the standard approaches for assessing and monitoring plant diversity takes account of topography in the sampling design.

This thesis has two main aims. The first is to investigate and compare, in agricultural landscapes, the effect of topographic variables derived from a digital elevation model on the variability of species richness and composition at several scale levels. The second is to develop a standardized and generally applicable approach for assessing plant species diversity in topographically complex areas. The main study was conducted using plant species data collected for the purpose in 12 local landscapes of 1 km² in a dairy region of the Swiss pre-Alps. In Chapter 3, the conclusions from this study are tested using a larger data set for 187 local landscapes of 1 km² provided by the Swiss Biodiversity Monitoring project. In both parts of the study information on topographic variability was derived from a digital elevation model with a resolution of 25 m.

The three chapters cover the following questions:

1) Which aspects of topography best explain the species richness of local landscapes? How do these aspects affect alpha and beta components of plant species richness at different scale levels? Does the influence of topographic variability vary according to habitat type?

2) Does maximum variation sampling based on topographic variables increase sampling efficiencies at the landscape and microsite levels? Which measure of topographic variability best explains species composition at the landscape level and ecological variability between microsites? How much of the variance in species composition at the microsite level is explained by habitat type and how much in addition by topographic variables? Does the importance of topographic variables in explaining species variance increase as topographic variability increases?
3) Is the finding that plant species richness and composition in agricultural landscapes change with topographic variability confirmed in 13 climatically and biogeographically different sub-regions of Switzerland? Which is the most effective measure of topographic variability for this purpose? Should topographic variability be included in the sampling designs used for national monitoring schemes of biodiversity?

In Chapter 1, the hypothesis is investigated that topographic variability at a landscape scale has a significant influence on plant species richness. Of four measures of topographic variables tested (means and standard deviations of altitude and solar radiation), 'variability of solar radiation' was the one that best explained plant species richness at the landscape level. Alpha and beta diversity components of all levels were significantly related to this measure of topographic variability, with $R^2$'s between 0.47 and 0.82. More detailed analyses indicated that the effects of topographic variability on species richness originated mainly from grassland, although woody habitats also had an influence. These results suggest that topographic variability might be of general use in sampling topographically complex areas.

Chapter 2 presents a standardized, hierarchical sampling approach for assessing plant species diversity in mountainous agricultural areas. Topographic variables derived from a digital elevation model were used to maximize abiotic heterogeneity between samples at two spatial scales: 1) among twelve randomly sampled local landscapes of 1 km$^2$, and 2) among 40 randomly sampled microsites (plant species relevées) within each local landscape, stratified according to coarse habitat types (480 samples in total). At the landscape level, species composition changed along a gradient of topographic variability, which explained 18% of the species variance. At the microsite level, the variance in species composition explained by habitat types could be increased from 11% to 17% (adjusted $R^2$ values) by including local and neighbourhood topographic variables. The variability of solar radiation as a measure of topographic variability correlated best with shifts in species composition at the landscape level and with ecological variability (measured by ecological indicator values of the species relevées) at the microsite level. At the microsite level, the proportion of variance explained by habitat type decreased with increasing topographic variability, but there was no corresponding increase in the variance explained by topography. I conclude that the sampling strategy used within local landscapes eliminated some important practical constraints associated with conventional stratification approaches based on fixed topographic categories and improved sampling efficiency at both the landscape and microsite levels.
Chapter 3 investigates whether the relationships between topographic variability and species richness and composition demonstrated in chapters 1 and 2 at a landscape scale also apply across much larger areas within biogeographically and climatically different sub-regions. Plant species richness and composition from 187 local landscapes of 1 km$^2$ throughout Switzerland within 13 sub-regions of different climate and biogeography were investigated. The expected effects of topographic variability were confirmed in two thirds of sub-regions when using species composition data, but only in one third of sub-regions when using information on species richness. Variability of solar radiation was the measure of topographic variability that explained species composition best, but none of the measures investigated was clearly superior in explaining species richness. I conclude that the efficiency of a national, hierarchical sampling design can be improved by integrating the variability of solar radiation as a surrogate of microsite variability at the landscape level. As a wide range of climate and biogeography was covered by the 13 sub-regions, I propose that this measure of microsite variability can also be used in other agricultural areas.
Zusammenfassung


In den drei Kapiteln werden folgende Fragen behandelt:

1) Welche topographischen Parameter erklären die Artenzahl von Landschaftsausschnitten am besten? Welchen Einfluss haben diese Parameter auf die alpha und beta Diversitätskomponenten auf Habitats- und auf Mikrostandortebene? Ist der Einfluss der Topographie vom Habitattyp abhängig?

2) Kann eine topographiebasierte, varianzmaximierende Beprobungsstrategie die Beprobungseffizient auf Ebene Landschaft und Mikrostandort erhöhen? Welches Mass für topographische Variabilität erklärt die botanische Artzusammensetzung von Landschaften und die ökologische Variabilität von Mikrostandorten am besten? Wieviel Varianz der botanischen Artzusammensetzung an Mikrostandorten kann mit dem Habitattyp erklärt werden, wieviel
zusätzlich durch topographische Variablen? Nimmt die relative Bedeutung topographischer Variablen für die Artzusammensetzung an Mikrostandorten zu, wenn die topographische Variabilität der Landschaft zunimmt?

3) Können die Erkenntnisse, dass sich die Artenzahl und –zusammensetzung mit zunehmender topographischer Variabilität der Landschaft verändert, in 13 klimatisch und biogeographisch unterschiedlichen Gebieten der Schweiz bestätigt werden? Welches Mass für topographische Variabilität erklärt die untersuchten Zielgrössen am besten? Soll topographische Variabilität auf nationaler Ebene zur Beprobung von botanischer Artenvielfalt berücksichtigt werden?

In Kapitel 1 wird untersucht, ob die Artenzahl auf Landschaftsebene mit topographischer Variabilität zunimmt. Von vier getesteten topographischen Variablen (Mittelwerte und Standardabweichungen von Höhe und Sonneneinstrahlung) erklärte die Variabilität der Sonneneinstrahlung die erfasste Gesamtartenzahl auf Landschaftsebene am besten. Alpha und beta Diversitätskomponenten nahmen auf allen drei untersuchten Ebenen signifikant mit diesem Mass für topographische Variabilität zu ($R^2$ zwischen 0.47 und 0.82). Detailliertere Analysen zeigten, dass die Effekte der topographischen Variabilität auf die Artenzahlen hauptsächlich durch Graslandhabitate verursacht wurden, wobei auch die Artenzahlen in Gehölzen zunahmen. Die Resultate lassen vermuten, dass topographische Variabilität auf diesem Massstab allgemein ein wichtiger Parameter zur Beprobung topographisch komplexer Gebiete sein könnte.

In Kapitel 2 wird ein standardisiertes, hierarchisches Beprobungsverfahren zur Erfassung der botanischen Vielfalt im Berggebiet vorgestellt. Auf zwei Massstabsebenen wurden topographische Variablen aus einem Höhenmodell zur Maximierung der abiotischen Varianz zwischen Stichproben verwendet: 1) Zwischen 12 zufällig gezogenen, 1 km$^2$ grossen Landschaftsausschnitten und 2) zwischen 40 Zufallsstichprobenpunkten an Mikrostandorten (Vegetationsaufnahmen) innerhalb jedes Landschaftsausschnittes, welche nach groben Habitattypen stratifiziert wurden (insgesamt 480 Aufnahmen). Die topographische Variabilität konnte 18% der Unterschiede in der Artzusammensetzung zwischen den 12 Landschaftsausschnitten erklären. Auf Ebene der Mikrostandorte erklärte der Habitattyp einen Anteil von 11% der Artenzusammensetzung, welcher durch den Einbezug von topographischen Variablen auf 17% (korrigierte Werte) erhöht wurde. Die Variabilität der Sonneneinstrahlung als Mass für topographische Variabilität korrelierte am besten mit den Änderungen der Artzusammenset-
zung auf Landschaftsebene und mit der ökologischen Variabilität der Mikrostandorte (Variabilität der ökologischen Indikatorwerte der botanischen Aufnahmen). Mit zunehmender topographischer Variabilität der Landschaft nahm der Anteil erklärter Varianz an den Mikrostandorten durch Habitatve wie erwartet ab, hingegen nahm der durch Topographie erklärte Anteil wider Erwarten nicht zu. Gegenüber konventionellen Methoden, welche Stratifizierungen aufgrund fixer topographischer Kategorien vornehmen hat die vorgestellte, standardisierte Beprobungsstrategie eine bessere Allgemeingültigkeit, da sie nicht auf vordefinierte Kategorien angewiesen ist. In dieser Fallstudie erhöhte sie die Beprobungseffizient auf Landschafts- und Mikrostandortebene.

General introduction

Agriculture and biodiversity

Land use change in agriculture is one of the main causes for the dramatic loss of biodiversity in Europe in recent decades (e.g. Körnecke & Sukopp 1988, Gates & Donald 2000). Because of intensification, many agriculturally favorable areas have lost species by increased fertilisation, the application of pesticides, drainage or irrigation, the use of high yielding crop varieties and the removal of areas of semi-natural habitat (Matson et al. 1997). It has also been recognized, however, that in less favorable areas biodiversity suffers from abandonment of agriculture, which often leads to forest succession on formerly species rich grassland (MacDonald et al. 2000). To conserve and promote biodiversity, environmental monitoring programmes have been launched to assess trends in biodiversity and to investigate the effects of politically inspired agro-environmental measures (Bischoff & Dröschmeister 2000, Kleijn & Sutherland 2003). As the monitoring of biodiversity is complex and the financial sources are limited, the development of appropriate indicators is crucial for scientific as well as applied purposes.

Scale and hierarchical levels

A prerequisite for understanding the dynamics of populations and habitats is to assess the data at the appropriate scale (Wiens 1989, Turner et al. 2001) and to build up a sound framework of hierarchically structured levels (Allan & Starr 1992). An observed increase in species at patch level cannot simply be extrapolated to the landscape level, as opposite processes - like successful recolonisation by rare species or the spreading of generalists - could be a reason for different consequences at the landscape level. It was therefore recognized that to understand species dynamics, it is important to consider not only the levels of the patch and habitat type, but also the landscape level (Wiens 1976, Franklin 1993). An important principle of hierarchy theory is to include at least three scale levels in an ecological study: the level of immediate interest (e.g. agricultural landscape), one level above constraining the context (e.g. region of common species pool), and one level below (e.g. habitat level) providing details to explain the results at the focal scale (O’Neill et al. 1986). Recognizing the importance of the landscape scale in understanding species dynamics, many biodiversity monitoring projects have chosen local landscapes of around 1 km$^2$ as study units, which represent one of several scale levels in
a sampling design (e.g. Haines-Young et al. 2000, Dramstad et al. 2001, Hintermann et al. 2002, Cooper & McCann 2002).

**Quantification of biodiversity in agricultural landscapes**

Biodiversity of a landscape (gamma diversity) is composed of the diversity at sites (alpha component) and the heterogeneity between sites (beta component) (Whittaker 1960, Allan 1975). A decrease of biodiversity at landscape scale is therefore either caused by species loss at sites or/and a loss of heterogeneity between sites. Although the multiplicative approach of Whittaker (1960) to calculate these diversity components is now widely accepted, recent studies (Lande 1996, Wagner et al. 2000, Crist et al. 2003) have further developed the additive approach of Allan (1975). One of the big advantages of the additive approach is that measures of alpha and beta diversity at different levels (e.g. species richness or other diversity measures) can be summed, which allows the species components at different hierarchical scale levels in an ecological system to be quantified and linked (Lande 1996). However, for ecological surveys or monitoring projects, an exhaustive assessment of species diversity components in landscapes is not realistic. The search for estimates and surrogates of species diversity and the development of biodiversity indicators is therefore an important field in ecology.

As local diversity is limited even at species rich sites, the diversity of species in a landscape is strongly dependent on the heterogeneity or beta diversity of sites (Plotkin & Müller-Landau 2002). In numerous farmland studies, it has been shown that measures of landscape heterogeneity (e.g. of habitats, land cover or land use) can provide convenient and cost-efficient indicators of plant, insect and bird species diversity at the landscape scale (see Moser et al. 2002 and Benton et al. 2003 for review). These approaches are based on a perception of the landscape as a mosaic of patches (Forman 1995), each of which can be unambiguously assigned to a discrete habitat type. Aerial photographs or satellite images deliver convenient data for delineating patches and assigning habitat types, either by spectral interpretation alone or with ground-truthing at sampling points. Diversity metrics such as area and number of habitat types as well as measures of spatial configuration are then calculated (McGarigal & Marks 1995). It has been shown that stratified random field sampling based on such habitat maps is efficient for assessing species diversity (e.g. Hirzel & Guisan 2002). As mentioned above, to understand species dynamics it is important to have information at several levels of spatial scale. However, in most landscapes it is not only the aim to promote as high a species rich-
ness as possible, but to conserve and promote site specificity (Wagner & Edwards 2001), which leads to a high beta diversity.

**Patch-mosaic landscapes and gradient dominated landscapes**

Based on the biodiversity concept of Whittaker (1960) and Allan (1975), habitat heterogeneity is a good indicator of species diversity at a landscape scale - but only if variability among habitat types is high and variation within habitat types is low. These requirements usually apply in agricultural landscapes in the lowlands but not in mountainous areas. The main reason for this is that mountainous landscapes with their steep environmental gradients do not fit the patch-mosaic model well (McGarigal & Cushman 2005); in contrast to flat areas, clear boundaries between habitats are often missing while gradual transitions are common between and within patches. This means that only a coarse distinction of habitats - for example between forest and grassland - is possible; and measures of habitat heterogeneity based on such a coarse classification are not likely to deliver satisfying results. To better assess beta diversity, it is therefore necessary to assess heterogeneity of species composition between sites directly by species relevées rather than using the indicator 'habitat heterogeneity'.

In the British Countryside Survey (Haines-Young et al. 2000) – the pioneer of such ecological surveys in Europe – the special problems of sampling in mountainous areas were recognized, and these areas were sampled by a systematic random point sampling of species relevées. Compared to the stratified sampling of the clearly defined habitat types in patch-mosaic landscapes, however, a systematic random sampling is less efficient for assessing the full range of ecological diversity; this is because habitats of very limited extent are less likely to be sampled than more abundant habitats, but they may make a large contribution to the overall heterogeneity. Additional, ecologically relevant variables are needed if the heterogeneity within coarse habitat types is to be sampled efficiently.

The topographic relief of a landscape has a strong impact on abiotic microsite conditions (Swanson et al. 1988), and these in turn affect vegetation pattern (Larcher 1973, Ellenberg 1986, Franklin 1995) as well as land use pattern (Wrbka et al. 2004). For this reason, we might predict that biotic heterogeneity or beta diversity of a landscape would correlate positively with abiotic microsite heterogeneity and could therefore be used as an estimate of site heterogeneity. This hypothesis has indeed been supported by numerous studies from landscape to regional scales (e.g. Riera et al. 1998, Luoto et al. 2002, Pausas et al. 2003, Moser et
al. 2005, Dufour et al. 2006). If it also proved to apply in agricultural landscapes, then it would justify the use of some measure of topographic variability as the basis for a more efficient sampling strategy of landscape units in mountainous areas (Gillison & Brewer 1985). Although exposition is known to be significant for vegetation patterns (Bale et al. 1998, Ortega et al. 2004), the measure of topographic variability most commonly used is one that neglects this factor, namely the standard deviation of altitude. It remains therefore an open question whether measures that integrate exposition are better estimators of biotic heterogeneity at the landscape level.

In estimating the variability of species composition topographic variables are useful factors for distinguishing sites with different abiotic characteristics - and thus potentially different species composition - and they have therefore sometimes been used as a basis for stratified sampling (e.g. Goedickemeier et al. 1998, Luoto et al. 2003, Sebastia 2004). Against this background, and given the availability of high resolution digital elevation models, it would make practical and ecological sense to include topographic variables in surveys to assess species diversity at microsite level more efficiently. However, existing approaches (Goedickemeier et al. 1998, Luoto et al. 2003, Sebastia 2004) base stratification on fix, individually defined topographic categories that are defined by expert knowledge for a restricted investigation area. For general applicability, however, it is necessary to develop an approach that is independent of expert knowledge.

**Outline of the thesis**

This thesis has two main aims. The first is to investigate and compare, in agricultural landscapes, the effect of topographic variables derived from a digital elevation model on the variability of species richness and composition at several scale levels. The second is to develop a standardized and generally applicable approach for assessing plant species diversity in topographically complex areas. These objectives were investigated in the context of the development of agri-environmental indicators for Switzerland (Gaillard et al. 2003). Whilst indicator methods for the lowlands can be adopted from existing methodologies proposed by e.g. OECD (NIJOS/OECD 2003) or from the IRENA project (EEA 2006), these concepts can only partly be transferred to gradient dominated mountainous landscapes, which are expected to host an important share of agricultural biodiversity of Switzerland (MacDonald et al. 2000).
For our case study, we chose the UNESCO biosphere reserve 'Entlebuch' in the Pre-Alps of Switzerland, which is a diary farming area with complex relief. Landscape units of 1 km\(^2\) have been used in numerous other European studies (e.g. Haines-Young et al. 2000, Hintermann et al. 2002, Dramstad et al. 2001) including the Swiss Biodiversity Monitoring project, and we wanted to be able to integrate our data into the database of this project. We therefore adopted 1 km\(^2\) as the size of our basic landscape units, recognizing this decision to be a compromise between theoretic and applied arguments (Bunce et al. submitted). Plant species data from the case study delivered the data for Chapter 1 and Chapter 2, while in Chapter 3, plant species data from the Swiss Biodiversity Monitoring Project (Hintermann et al. 2002) were used.

In Chapter 1, we hypothesized that topographic variability has a significant influence on plant species richness. We wanted to know which aspects of topography best explain species richness of local landscapes, how these aspects affect alpha and beta components of plant species richness at different scales and if the influence of topographic variability varies according to the habitat type (grassland/arable, edge, woody habitats). Effects of four measures of topographic variability derived from a DEM on estimates of total plant species richness in 12 local landscapes of 1 km\(^2\) are compared.

In Chapter 2, a generally applicable, hierarchical sampling approach for assessing plant species diversity in mountainous agricultural areas is presented. Topographic variables derived from a digital elevation model are used to maximize abiotic heterogeneity at two spatial scales: 1) among twelve randomly sampled local landscapes of 1 km\(^2\), and 2) among 40 randomly sampled microsites (plant species relevées) within each of those 12 local landscapes, stratified according to coarse habitat types (480 relevées in total). The gain in efficiency by integrating topographic variables is estimated at both the landscape and microsite levels. Using these data, the hypothesis is tested that the gain of including topography at microsite level increases with topographic variability. By analysing the data using plant species indicator values (Landolt 1977), the chapter also delivers a basis for interpreting the ecological gradients within and among the 12 local landscapes.

The main aim of Chapter 3 is to investigate whether the relationships demonstrated between topographic variability and species richness and composition at a landscape scale (Chapters 1 and 2) also apply across much larger areas. Plant species richness and composition from 187 local landscapes of 1 km\(^2\) within 13 climatically and biogeographically different sub-regions
throughout Switzerland (Swiss Biodiversity Monitoring programme; Hintermann et al. 2002) were available to answer this question. This chapter also addresses the practical question of whether it is desirable to integrate topographic variability into the sampling design for national biodiversity monitoring projects in order to increase their efficiency.

References


Chapter 1

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

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**Abstract**

It is commonly assumed that variation in abiotic site conditions influences the number of niches in a landscape, which in turn constrains the potential species richness. Based on theoretical considerations, abiotic variation is often used as an estimator of species richness at broad scales, while at finer landscape scales variation of habitat types is used. However, habitat estimators assume the landscape to be composed of discrete, homogeneous patches with sharp boundaries, and such a concept is hard to apply in gradient-dominated landscapes. The aim of this study was therefore to investigate effects of abiotic heterogeneity on plant species richness, and their alpha (α) and beta (β) components at microsite, habitat and local landscape levels. Using floristic data from 12 'landscapes' of 1 km² we investigated the influence on species richness components of two simple and one complex measures of topographic variability. While the standard deviation (SD) of altitude explained a high proportion of the variation amongst the landscapes (linear regression model $R^2 = 0.63$), the
complex measure, SD of solar radiation explained it even better ($R^2 = 0.82$). As expected, the β diversity components increased significantly with topographic variability of local landscapes. There was, however, an additional context effect of landscape heterogeneity on α diversity components at the level of the sample plot. Further analyses revealed that the effects of topographic variability on species richness were strongest for grassland and to a lesser extent from woody habitats. The effects of abiotic variability on landscape species richness and their diversity components suggest that to understand patterns of species richness the underlying abiotic pattern cannot be neglected.

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

**Introduction**

The biodiversity of an area (gamma diversity) can be quantified in terms of the diversity at sites (α component) and the heterogeneity among sites (β component) (Allan 1975, Whittaker 1977). As local diversity is spatially limited, gamma diversity is expected to be strongly dependent on the heterogeneity among sites (Plotkin & Müller-Landau 2002). In contrast to mean ecological conditions, environmental heterogeneity influences the diversity of niches in an area and is therefore thought to be an important factor constraining species richness at broad and fine scales (Palmer & Dixon 1990, Plotkin & Müller-Landau 2002). In modelling studies aimed at predicting patterns of species richness, variation in abiotic parameters is often used to estimate species richness at broad scales (Richerson & Lum 1980, Currie 1991, Riera et al. 1998, Gaston 2000, Coblentz & Riitters 2004) while at a finer scale - corresponding to the meso-scale in the spatio-temporal hierarchy of Delcourt & Delcourt (1988) - some measure of the heterogeneity of landscape patches is used (e.g. habitats, land cover or land use; Moser et al. 2002, Benton et al. 2003). This contrast in approaches reflects the theoretical assumption that climate and topography provide the abiotic envelope for the occurrence of species at broad scales, while their realized occurrence is 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 habitat patches and discrete borders among habitat patches. However, in topographically heterogeneous landscapes these two basic criteria are met only partially. Steep abiotic gradients cause gradual shifts in species compositions within and between habitat types (McGarigal & Cushman 2005) which makes the delineation of homogeneous patches conceptually unsatisfying and difficult to reproduce in practice. However, the topographic relief of a landscape has a strong impact on abiotic microsite conditions (Swanson et al. 1988), which in turn affect vegetation patterns (Larcher 1973, Ellenberg 1986, Franklin 1995) as well as on land-use patterns (Dorner et al. 2002, Wrbka et al. 2004). Consequently, we hypothesized that variability of topography is not only appropriate as a surrogate of niche diversity at broad scales, as currently used, but also for estimating species richness at the landscape scale.

There is no general agreement about how topographic variability can best be quantified for ecological purposes. 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 in general they explain vegetation pattern better than simple topographic variables. In most studies, SD of altitude has been chosen as the measure of variability (e.g. Richerson & Lum 1980, Currie 1989, Luoto et al. 2002, Pausas et al. 2003, Moser et al. 2005), though other measures also derived from digital elevation models (DEM) have sometimes been used, e.g. SD of slope (Coblentz & Riitters 2004) or SD of curvature (Wrbka et al. 2004). None of these measures takes account of variability in aspect; however, since this parameter can have an important effect upon the distribution of species and habitats (e.g. Bale et al. 1998, Benayas et al. 1999, Ortega et al. 2004, Sebastia 2004), it is reasonable to suppose that variability measures that integrate aspect would better explain patterns of species richness.

In addition to finding a suitable metric for topographic variability, several other factors may complicate the study of the relationship between species richness and topographic variability. First, the surface area of a landscape increases as a function of topographic variability. This collinearity has caused confusion in numerous studies investigating heterogeneity effects because it could not be separated from a simple surface area effect (Forman 1995). Whittaker et al. (1998) show that this problem can be avoided by assessing an equal number of samples with a similar total area within study units of different topographic variability. Biotic heterogeneity between sites can then be assessed by the partitioning of species richness data.
into $\alpha$ and $\beta$ components (Allan 1975, Whittaker 1977, Lande 1996, Wagner et al. 2000, Crist et al. 2003); when this is done, one would expect the $\beta$ (heterogeneity) components to increase with topographic heterogeneity. Lande et al. (1996) extended the additive diversity approach of Allan (1975) and demonstrated how several levels of diversity can be linked in an ecological system with commensurate $\alpha$ and $\beta$ diversity components. This is an advantage over the multiplicative approach of Whittaker (1977) - in which $\alpha$ and $\beta$ components are not comparable because they have different units.

A second problem in attempting to predict species richness in mountainous areas is that topographic variability often increases with altitude. Thus there may be collinearity between altitude and its variability, which could lead to a confounding of topographic variability with climatic heterogeneity. 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 homogeneous study area where a common species pool is assumed.

Thirdly, to interpret the total species richness (gamma diversity) in a landscape it is necessary to take account of the variation in species richness in different habitats (Zobel 1997). For example, species richness commonly declines with increasing soil fertility in grasslands, while a reverse trend is often observed in woody plant communities (Cornwell & Grubb 2003); thus a relative constant species richness across a range of soil fertility conditions could be the result of contrasting dynamics at a finer spatial scale. In many agricultural landscapes, habitat margins are known to be refugia for species sensitive to intensification (Smart 2002); to understand species richness in such landscapes it may therefore be necessary to consider the edges of habitats as separate units.

The overall objective of this study was to determine whether topographic variability can be used as an estimator of species richness at a landscape scale. We chose our study area in the Swiss Alps because it was climatically and biogeographically uniform but offered a wide gradient of topographic variability. Within this study area we investigated plant species richness using a standardised sampling scheme in 12 study units of 1 km$^2$ that differed in their topographic variability. Following the suggestion of Franklin et al. (2000), we compared two 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 would prove to be a better measure of abiotic variability.
The specific research questions were:

a) How can topographic variability be quantified so as to maximize the correlation with plant species diversity?
b) Which species diversity components increase with topographic variability?
c) Does the influence of topography vary among habitat types?

Methods

Study area
The study area was a mountainous region in Canton Lucerne, Switzerland, covering 250 km$^2$ within the “montane” altitudinal belt (600 to 1000 meters above sea level). Land cover is predominantly shared by agriculture (grassland 53%) and forest (37%). The mean annual precipitation is between 1500 and 1800 mm/m$^2$ 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 aspect). The potential sum of shortwave solar radiation per year (short: radiation) was calculated with “DiGem” (Conrad 2002) using data from 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-km$^2$ 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 m$^2$ 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).

Table 1: Stratification matrix for the sampling within each of the 12 local landscapes of 1 km$^2$: Nine habitat classes were combined with four clusters of topography. In total, 40 points were sampled randomly within each local landscape (36 points plus 4 grassland points extra). The number of samples is indicated in the four columns of the matrix.

<table>
<thead>
<tr>
<th>Habitat types</th>
<th>Habitat classes</th>
<th>Topographic Clusters</th>
</tr>
</thead>
<tbody>
<tr>
<td>Grassland (and arable) habitats</td>
<td>1 Grassland</td>
<td>2 2 2 2</td>
</tr>
<tr>
<td></td>
<td>2 Orchards</td>
<td>1 1 1 1</td>
</tr>
<tr>
<td></td>
<td>3 Arable land</td>
<td>1 1 1 1</td>
</tr>
<tr>
<td>Edge habitats</td>
<td>4 Roads/tracks/paths</td>
<td>1 1 1 1</td>
</tr>
<tr>
<td></td>
<td>5 Surface waters</td>
<td>1 1 1 1</td>
</tr>
<tr>
<td></td>
<td>6 Forest edge</td>
<td>1 1 1 1</td>
</tr>
<tr>
<td>Woody habitats</td>
<td>7 Hedgerow</td>
<td>1 1 1 1</td>
</tr>
<tr>
<td></td>
<td>8 Riparian Woods</td>
<td>1 1 1 1</td>
</tr>
<tr>
<td></td>
<td>9 Other Groups of Bushes/Trees</td>
<td>1 1 1 1</td>
</tr>
<tr>
<td>(Rest )</td>
<td>(10 Buildings, Settlements)</td>
<td>1 1 1 1</td>
</tr>
</tbody>
</table>
To quantify topography at the level of the sampling station, 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 (Table 1). Because grassland was the most abundant habitat class, the sampling effort for grassland was increased and two relevées were made for each combination of grassland with the topographical clusters. 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. 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 refer to this group as “grassland habitat”.

Forty plant species relevées of 25 m² were recorded within each of the 12 local landscapes to assess species richness components. The shape of the relevées 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 recorded 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). Pairs of 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

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}:

\[ \text{Landscape (12)} \quad \alpha_3 \quad (= \text{gamma diversity}) \]

\[ \text{Habitat type (3 x 12)} \quad \alpha_2 \quad + \quad \beta_2 \]

\[ \text{Plot (40 x 12)} \quad \alpha_1 \quad + \quad \beta_1 \]

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 m²) distributed within 12 local landscapes. The number of species recorded in individual local landscapes ranged from 161 to 208.

Quantification of topographic variability

As slope was correlated with all the variability variables (Table 2), making it impossible to separate heterogeneity effects from effects of mean conditions, this variable was omitted. Combinations and subsets of the remaining four 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 (i.e. lowest value of AICc) was reached by a regression model with 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
In addition to the two candidate models that were identified, Table 3 summarizes the regression models including only one of the four topographic variables. For TV$_{SDRAD}$, the $R^2$ (0.82) was substantially higher than for the next best single variable TV$_{SDALT}$ (0.60). TV$_{SDRAD}$ was therefore used as a surrogate for topographic variability in subsequent analyses. The best model without the variable TV$_{SDRAD}$ (not shown in Table 3) had an adjusted $R^2$ of 0.72 and ranked 5 according to its AICc.

Table 2: Pearson’s correlation coefficients ($r$) between the explanatory topographic variables. Significant correlation coefficients ($p < 0.05$) were printed in bold. 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.

<table>
<thead>
<tr>
<th></th>
<th>$T_MALT$</th>
<th>$T_MALT$</th>
<th>$T_MRAD$</th>
<th>$T_MALT$</th>
<th>$T_MALT$</th>
<th>$T_MALT$</th>
<th>$T_MALT$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$T_MALT$</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$T_MSLO$</td>
<td>0.47</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$T_MRAD$</td>
<td>-0.10</td>
<td>-0.27</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>TV$_{SDALT}$</td>
<td>0.07</td>
<td>0.81</td>
<td>-0.36</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>TV$_{SDSLOP}$</td>
<td>-0.16</td>
<td>0.67</td>
<td>-0.48</td>
<td>0.78</td>
<td>1.00</td>
<td></td>
<td></td>
</tr>
<tr>
<td>TV$_{SDRAD}$</td>
<td>0.49</td>
<td>0.95</td>
<td>-0.32</td>
<td>0.78</td>
<td>0.65</td>
<td>1.00</td>
<td></td>
</tr>
</tbody>
</table>

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

<table>
<thead>
<tr>
<th>AICc rank</th>
<th>Variables included</th>
<th>Multiple R</th>
<th>Adjusted Rsquares</th>
<th>$F(1,10)$ / $F(2,9)$</th>
<th>p</th>
<th>Std. Error</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>TV$_{SDRAD}$</td>
<td>0.91</td>
<td>0.82</td>
<td>49.56</td>
<td>0.0000</td>
<td>7.34</td>
</tr>
<tr>
<td>2</td>
<td>TV$<em>{SDRAD}$/T$</em>{MRAD}$</td>
<td>0.92</td>
<td>0.80</td>
<td>23.48</td>
<td>0.0003</td>
<td>7.57</td>
</tr>
<tr>
<td>7</td>
<td>TV$_{SDALT}$</td>
<td>0.80</td>
<td>0.60</td>
<td>17.24</td>
<td>0.0020</td>
<td>10.85</td>
</tr>
<tr>
<td>9</td>
<td>TV$_{MALT}$</td>
<td>0.42</td>
<td>0.09</td>
<td>2.14</td>
<td>0.1741</td>
<td>16.25</td>
</tr>
<tr>
<td>10</td>
<td>TV$_{MRAD}$</td>
<td>0.37</td>
<td>0.05</td>
<td>1.63</td>
<td>0.2303</td>
<td>16.60</td>
</tr>
</tbody>
</table>
Effect of topographic variability on plant diversity components

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

![Figure 1: Effects of topographic variability (TVSDRAD) on species richness components at microsite level ($\alpha_1$, $\beta_1$), habitat type level ($\alpha_2$, $\beta_2$) and landscape level ($\alpha_3$). Simple linear regressions were performed based on all 40 plant species relevées within a local landscape of 1km$^2$. * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$](image)

The separate calculations 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 values of $R^2$ 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 $\beta_1$ ($R^2 = 0.29$) and $\alpha_2$ ($R^2 = 0.36$) level, but with comparably low $R^2$. There was no effect of topographic variability on the $\alpha_1$ level.

Discussion

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

The high proportion of variance in plant species richness explained by topographic variability supported our hypothesis that these 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 that represented by the local landscapes 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) have yielded contradictory results concerning the importance of topographic heterogeneity. Pausas et al. (2003, extent: 31900
km$^2$, grain size: 10 by 10 km) found that topographic heterogeneity had a significant effect on species richness, although this effect was not distinguishable from the confounded increase of area. In contrast, Moser et al. (2005, extent: 50500 km$^2$, grain size: 6 by 6 km) found that topographic heterogeneity was not important. Several factors might be responsible for these conflicting results, including differences in the quality of the floristic data, in the measures of topographic heterogeneity used, and in the model selection procedures. A more useful comparison, therefore, is between our study and that of Luoto (2002, extent: 601 km$^2$; grain size: 0.25 by 0.25 km), since both were conducted at a similar meso-scale in climatically homogeneous areas. Both studies show a strong effect of topographic variability on species richness, demonstrating that the abiotic envelope also has an important impact on local processes such as the diversity of microsite conditions and land use. They therefore challenge the common notion of the environmental envelope only being relevant 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$\text{S}$$\text{D}$RAD ($R^2 = 0.82$) as due to the additional information not represented in the parameter altitude about variability of aspect. Our results confirm the conclusion of Franklin et al. (2000) that topographic parameters related to resource or direct environmental variables (sensu Austin and Smith 1989) explain the distribution of plant species better than simple topographic variables. The best model without TV$\text{S}$$\text{D}$RAD included both $T_{\text{MALT}}$ and TV$\text{S}$$\text{D}$ALT ($R^2 = 0.72$), which suggests that by including the variability of the orientation to the sun there was a gain in variance explained of at least 10%. Nevertheless, the simple regression model including TV$\text{S}$$\text{D}$ALT ($R^2 = 0.63$) as predictor was also able to explain species richness to a considerable degree.

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

Two important points emerge from the additive partitioning of landscape species richness into $\alpha$ and $\beta$ components at the microsite and habitat levels. First, the significant increase of $\beta$ diversity (heterogeneity) between microsites with increasing topographic variability - which cannot be explained merely as a species – area effect (Forman 1995) - provides strong support for the heterogeneity hypotheses. Secondly, $\alpha$ components also increased significantly with increasing topographic variability, demonstrating that the increase of landscape species
richness was not solely due to greater diversity among habitats. The phenomenon of the landscape context or local neighbourhood affecting local $\alpha$ 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 the microsite level. For example, Kumar et al. (2006) found effects of context patch heterogeneity on local $\alpha$ diversity (species richness). Our study was conducted in a gradient dominated landscape where biotic heterogeneity could not be estimated in terms of patch heterogeneity (Cushman & Mc Garigal 2005), but we also found effects of context topographic heterogeneity on local species richness. Meta-population theory can provide a possible explanation for this phenomenon, since it would predict a higher rate of immigration in more diverse landscapes, leading to more saturated local communities (species pool effect, Hanski & Gaggiotti 2004).

In addition to meta-population effects, however, other processes could also contribute to the observed increase of microsite species richness with topographic landscape variability. For example, high topographic variability reduces the accessibility of some areas, and these are therefore likely to be use less intensively for agriculture. Abiotic site conditions were not only more variable in landscapes of higher topographic variability, as indicated by the $\beta$ species richness components, but the increase in $\alpha$ diversity components suggests in addition an ecological shift of the mean microsite conditions. The increase of $\alpha$ diversity components with topographic variability in the local landscapes investigated could be an effect of either an increasing local species pool or decreasing management intensity. Although we did not investigate these causes in the present study, the strength of the effect suggests that the underlying topographic pattern in our study area governs the most important patterns determining species richness.

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

The separate analysis of the diversity components within the three habitat types grassland, edges and woody is an important step towards understanding the effect of topographic variability. Topographic variability did not affect all habitat types equally (Figure 2a-c): thus, total species richness within habitat types ($\alpha_2$) increased strongly in grassland and woody habitats, while edges made no contribution to this effect. This is consistent with the results from earlier studies showing an effect of topography upon species composition in various types of grassland (e.g. Benayas et al. 1999, Sebastia 2004) and woody habitats (Bale et al. 1998, Ortega et al. 2004). The fact that the $\beta$ 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. However, grassland and woody habitats differed in the behaviour of the $\alpha_1$ components at the microsite level. The species richness of grasslands tends to be higher on nutrient-poor than on nutrient-rich sites (Cornwell & Grubb 2003), and in agricultural areas these less fertile conditions may persist in a few, less accessible flat areas, but are more likely to occur on steeper slopes. The $\alpha_1$ microsite components of woody habitat types did not increase with topographic variability which might indicate that for woody habitats, the increase of total species richness with topographic variability was due mainly to the heterogeneity components.

Several factors could explain higher species richness in edges compared to grassland and woody habitat types: 1) edges may contain species from two adjacent 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). Both the second and third of these possibilities could explain our results; this is because the relative contribution of edges to total species richness ($\alpha_3$) would tend to increase in topographically homogeneous and more intensively managed landscapes than in landscapes with higher environmental variability.

**Conclusions**

Abiotic heterogeneity explained high amounts of landscape species richness. This contradicts the common notion that abiotic parameters are estimators of broad species richness patterns at meso- and macro-scales, while patch heterogeneity is needed to explain species richness at finer scales. While an increase of $\beta$ 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.
Acknowledgements

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References


Chapter 2

**A sampling approach of general applicability to assess plant diversity in mountainous landscapes**

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**Abstract**

Although topography influences vegetation considerably, there are no generally applicable sampling methods integrating topography to assess plant diversity in mountainous areas. To develop such a method, we collected plant diversity data in a mountainous farming area of 250 km², applying the strategy of maximum variation sampling at both the landscape and microsite levels. Topographic variables derived from a digital elevation model were used to maximize abiotic heterogeneity between 1) twelve randomly sampled study units of 1 km² (local landscapes) and 2) 40 randomly sampled plant species relevées within each of those local landscapes (480 samples in total). Using multivariate analysis, we calculated the proportions of the species variance explained by topographic variables at both the landscape and microsite levels. In addition, we used linear regression to test the hypothesis that, with increasing topographic variability of the landscape, habitat types explain less, and topography more, of the variance in species composition of microsites.
At the landscape level, species composition changed along a gradient of topographic variability; this gradient, which explained 18% of the species variance, also correlated strongly with the ecological requirements of species, as reflected in the indicator values for nitrogen, humidity and pH. At the microsite level, the variance in species composition explained by habitat types could be increased from 11% to 17% (adjusted values) by including local and near context topographic variables. As expected, the proportion of variance explained by habitat type decreased with increasing topographic variability. However, there was no corresponding increase in the variance explained by topography; thus, although taking account of topographic variables reduced the loss in sampling efficiency in topographically variable areas, it did not completely prevent it.

By maximizing the relative topographic differences between samples, our sampling strategy eliminated some important practical constraints associated with conventional stratification approaches based on fixed topographic categories. In addition, the approach improved sampling efficiency at both the landscape and microsite levels.

**Keywords:** Maximum variation sampling strategy, topographic variability, Digital Elevation Model (DEM), biotic variability, microsite variability, plant species composition

**Introduction**

Assessing and monitoring biodiversity at landscape scale is an important issue in ecological research and conservation planning. In the last few decades in Europe, numerous monitoring schemes have been introduced in order to evaluate the effects of agri-environmental schemes and to stop further decline of biodiversity in agricultural landscapes (Kleijn & Sutherland 2003). To achieve a comprehensive sampling of biodiversity, two principles are seen as important: 1) assessment of biodiversity should be conducted at several hierarchical levels, since isolated information at one level can be misleading (Allan & Hoekstra 1992, Turner et al. 2001); and 2) a strategy of maximum variation sampling is needed so ensure that the ecological variation of a study area is adequately covered (Gillison & Brewer 1985, Austin & Heyligers 1989, Bunce et al. 1996). Because biodiversity cannot be assessed completely, indicators are needed for monitoring that are robust and equally sensitive at different hierarchical levels. In agricultural areas, higher plants are often chosen as the indicator group; this is partly
because plant diversity has been shown to correlate well with the diversity other groups of organisms (Duelli & Obrist 1998), and partly because plants are relatively easy to sample.

In numerous studies, habitat diversity metrics have been shown to be convenient and cost-efficient surrogates for plant species diversity at the landscape scale (see Benton 2003 for review). These approaches are based on a perception of the landscape as a mosaic of patches, each of which can be unambiguously assigned to a discrete habitat type. These homogeneous patches can be delineated by manual or automatic interpretation of aerial photographs or satellite imageries, and the habitat types are usually assigned by spectral interpretation, with or without ground truthing. Diversity metrics such as area and number of habitat types (e.g. semi-natural habitats) and more sophisticated measures are then calculated (e.g. McGarigal & Marks 1995). Stratified random sampling based on such habitat maps was shown to be an efficient method for assessing species diversity at the landscape level (Goedickemeier 1997, Hirzel & Guisan 2002).

It is significant that most monitoring surveys have been performed in intensively managed lowland areas (McGarigal & Cushman 2005), and the standardized indicators that have been developed can not necessarily be applied to mountainous areas, at least without modification. This is because mountainous landscapes, with their steep environmental gradients, do not fit the patch-mosaic model of landscapes well. More or less gradual transitions in vegetation types and species composition are usual in mountain areas (McGarigal & Cushman 2005), which often makes it impossible to delineate vegetation patches except at the coarsest level, for example between forest and grassland. Compared to the habitat maps of patch-mosaic landscapes, a stratified sampling based only on these coarse vegetation types is expected to be much less efficient. In mountainous areas, therefore, sampling must be based upon additional criteria that reflect the gradient dominated patterns of vegetation.

Topography influences vegetation patterns in mountainous areas in four main ways (Swanson et al. 1988): 1) it modifies broad abiotic conditions at the microsite level, 2) it affects the flow direction of biotic and abiotic quantities, 3) it influences spatial patterns of disturbance, and 4) it determines spatial patterns of various geomorphologic processes. The significance of abiotic microsite conditions for plant species composition and the link to topography are well known and extensively documented (e.g. Ellenberg 1996, Larcher 2001); and from this background we might predict that biotic variability in a landscape correlates positively with abiotic microsite variability. This hypothesis was supported by Chapter 1 of this study, which
showed that the heterogeneity/beta diversity of plant species richness at microsites increased with topographic variability, leading to an increase of species richness at the landscape level. Based on these results, we developed two predictions that are the subject of this study. First, we predict that a sampling strategy based upon habitat stratification (e.g. derived from aerial photographs) becomes less efficient with increasing microsite variability; this is because of the increasing importance of vegetation gradients that cannot be delineated. Second, we predict that topographic variables gain in significance for species composition at microsites with increasing topographic variability of the landscape; this is because of the increasing importance of environmental gradients for the vegetation. In vegetation modelling of mountainous areas, topographic variables are often used as surrogates/proxies of environmental gradients and it has been demonstrated that, combined with spectral data, topographic variables improve the predictions in spatially explicit models considerably (see Franklin 1995 for a review). A repeatable and ecologically sound method for sampling plant diversity in a mountainous landscape must therefore combine information of two kinds: information on habitats types (but only for habitats that can be reliably delineated) and information on important topographic gradients.

In view of the obvious advantages of topographic variables - ecological relevance, robustness, availability, precision and cost efficiency - it may seem surprising that a generally applicable approach to assess biodiversity in topographically complex areas has not yet been developed. One reason may be that topographic parameters are indirect variables, in contrast to direct variables such as temperature and resource variables such as solar radiation or water (Austin & Smith 1980), and they therefore serve as surrogates for particular environmental factors. This leads to two kinds of practical problem. Firstly, because one topographic variable may reflect a combination of direct and resource variables, it may be impossible to infer causality. Secondly, the ecological meaning of the same values of topographic variables can change with changing environmental conditions. Thus, in existing sampling approaches (Goedickemeier et al. 1998, Luoto et al. 2002, Sebastia 2004), topographic parameters are only appropriate for stratification within restricted areas, and special expertise may be needed to make sound topographic categories for stratification. However, a generally applicable sampling approach for the assessment of species diversity should not be dependent on regional expert knowledge and should therefore not be based upon pre-defined topographic categories. With these considerations in mind, we adopted the strategy of maximum variation sampling (Patton 1990), and used topographic variables to maximise abiotic differences among sampling sites.
In order to develop a robust and generally applicable method to assess plant diversity of topographically complex areas, we needed to answer the following questions:

What can be gained by sampling a study area by local landscapes along a gradient of topographic variability? With which of four selected measures of topographic variability is the gain highest?

Which of four measures of topographic variability correlates best with ecological variability derived from ecological indicator values at microsite level?

How much of the variance in species composition at the microsite level can be explained by habitat type and how much can be gained by including local and neighbourhood topographic variables?

Is the hypothesis supported that, with increasing topographic variability, habitat variables become less important in explaining patterns of species richness within local landscapes while topographic variables become more important?

**Methods**

**Study area**

The study area covered some 250 km$^2$ of the montane zone (from 600 to 1000 m.a.s.l.) of the UNESCO biosphere 'Entlebuch' in Switzerland. Land cover is dominated by agriculture, mostly dairy farming (53%) and forest (37%); minor cover types include woody vegetation in open landscape (4%), urban areas and buildings (4%), and water (1%) (BFS 1992/1997). The mean annual temperature is 11.3°C and the mean annual precipitation is between 1500 and 1800 mm.

**Sampling of local landscapes**

All topographic variables used in this study were derived from a Digital Elevation Model (DEM) with a resolution of 25 m (Swisstopo 2001). For each cell of a 1-km grid, three components of Topographic Variability were calculated: the Standard Deviation of ALTitude ($TV_{SDALT}$), the Standard Deviation of SLOpe ($TV_{SDSLO}$), and the Standard Deviation of potential annual solar RADiation ($TV_{SDRAD}$). The potential sum of shortwave solar radiation per year (short: radiation) was calculated based on the DEM with the software 'DiGem' (Conrad...
2002) where we assumed an atmospheric transmittance of 60 percent (standard of DiGem). The yearly sum of solar radiation was estimated in kWatt/m$^2$ based on calculations every 15 days with time steps of two hours. TV$_{SDALT}$, TV$_{SDSLO}$ and TV$_{SDRAD}$ were calculated for each of the 250 cells of 1 km$^2$ in the study area and results were ranged by constraining the observed range between zero and one (Sneath and Sokal 1973). The sum of the three components was then used to sample 12 cells along a gradient of topographic variability (TV$_{SUM}$). The cells were ranked and grouped into septiles; three 1-km$^2$ cells were then sampled randomly from the first, third, fifth and seventh septile, yielding a sample of 12 cells, called 'local landscapes'. The aim of this stratification was to make sure to cover the whole range of topographic variability in the study area. Because of our focus on agricultural landscapes, cells with less than 40 percent of agricultural land cover were excluded.

**Sampling within the local landscapes**

Within each of the 12 local landscapes, 40 points were located for plant species relevées. Because the aim was to maximize variability of vegetation types and species composition within each of the 12 study units, a stratified random sampling was used based on stratification by both habitat type and topography.

Habitat classes were digitized from true-colour ortho-photographs with a resolution of 0.5 m, and the data were extracted and calculated using ARCGIS, version 8.3.0. All elements of at least 2 m width and 100 m$^2$ area were digitized as polygons. A simple habitat classification with nine classes was applied (Table 1). The class 'Urban, buildings, settlement' was excluded, and forest was only included in the edge class. The eight remaining habitat classes were aggregated into three habitat types: grassland habitats (HAB1), edge habitats (HAB2) and woody habitats (HAB3).

To quantify topographic site conditions, a total of seven topographic variables were extracted from the DEM - four local site variables (ALT (altitude), SLO (slope), RAD (radiation) and CUR (curvature)) and three variables to characterize the topographic variability in the context (standard deviation SD) within a window of five by five cells of 25 m (SDALT, SDSLO, SDRAD). To make groups of similar abiotic site conditions, these topographic variables were clustered by k-means within each local landscape into four groups per habitat type. The four classes of topographic site conditions were crossed with the eight habitat classes, and one point was sampled for each combination (Table 1). Because grassland was the dominating
habitat class, the sampling effort for grassland was increased and three relevées were made for each combination of grassland with the topographical clusters. If a specific combination of habitat class and topographic cluster did not occur within a local landscape, an alternative sample was drawn randomly within the same habitat class, ignoring the topographical cluster class. If this failed, a sample was drawn randomly within the same habitat type. In a few cases, there were not enough woody habitats to allocate 12 relevées and they were replaced by a completely random relevée within all habitat types.

Table 1: Stratification matrix for the sampling within each of the 12 local landscapes of 1 km²: Eight habitat classes were combined with four topographic classes. In total, 40 points were sampled randomly within each local landscape. The numbers in the four columns indicate the number of samples per combination of habitat type and topographic class.

<table>
<thead>
<tr>
<th>Habitat types</th>
<th>Habitat classes</th>
<th>Topographic Clusters</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>1 2 3 4</td>
</tr>
<tr>
<td>Grassland habitats</td>
<td>Grassland</td>
<td>3 3 3 3</td>
</tr>
<tr>
<td></td>
<td>Orchards</td>
<td>1 1 1 1</td>
</tr>
<tr>
<td>Edge habitats</td>
<td>Roads/tracks/paths</td>
<td>1 1 1 1</td>
</tr>
<tr>
<td></td>
<td>Waters</td>
<td>1 1 1 1</td>
</tr>
<tr>
<td></td>
<td>Forest edge</td>
<td>1 1 1 1</td>
</tr>
<tr>
<td>Woody habitats</td>
<td>Hedgerow</td>
<td>1 1 1 1</td>
</tr>
<tr>
<td></td>
<td>Riparian Woods</td>
<td>1 1 1 1</td>
</tr>
<tr>
<td></td>
<td>Other Groups of Bushes/Trees</td>
<td>1 1 1 1</td>
</tr>
<tr>
<td>Rest</td>
<td>Buildings, Settlements</td>
<td>- - - -</td>
</tr>
</tbody>
</table>

Forty plant species relevées of 25 m² were recorded within each of the 12 local landscapes to assess species composition. As a measure of abundance (percentage of cover), we used a simple ranking of the species within each relevée from '4', '3' and '2' for the three most abundant species to '1' for all the less abundant species. The shape of the relevées was adapted to the habitat type: Grassland habitats HAB1 were sampled using 5 m by 5 m squares, while the linear habitats HAB2 and HAB3 were sampled using 1 m by 25 m rectangles.
Data analyses
The data analyses had two main objectives: 1) to determine the effects of topographic variability on total species composition of local landscapes; 2) to determine how much of the species variance in local landscapes could be explained by habitat type and topographic variables. A scaling study was performed to choose the optimal window size for topographic context variables.

For all multivariate analyses, the plant species data were Hellinger transformed and analysed by PCA (Principal Component Analyses) and RDA (ReDundancy Analyses) as suggested by Legendre and Gallagher (2001). PCA and RDA were conducted in R with the package vegan, where variance partitioning with adjustment of the multivariate $R^2$ for the number of predictor variables is implemented (Oksanen et al. 2005).

Species composition at landscape level
To explore along which ecological gradients species composition of local landscapes shifted with increasing topographic variability, species composition at landscape level was ordinated by PCA: 1) Total species lists of 40 relevées for each local landscape (HAB123) and 2) separate species lists for the three habitat types grasslands (HAB1), edges (HAB2) and woody habitats (HAB3). Ecological indicator values (nitrogen, humidity, pH, Landolt 1977) were assigned to each species and mean, weighted indicator values were calculated for each local landscape. Mean indicator values and four topographic variability measures of the 12 local landscapes were correlated with the first three axis of the PCA for better interpretation. In addition, mean indicator values were calculated separately for each microsite (nitrogen, humidity, pH), and means and standard deviations of the 40 plant species relevées per local landscapes were calculated and correlated with the four measures of topographic variability, mainly to check for high correlations of topographic and ecological variability.

The effect of topographic variability on the species composition at the landscape level was analysed by RDA for the total species list of each local landscape (HAB123) and for the three habitat types HAB1, HAB2 and HAB3 separately. Presence/absence and species lists with abundances were analysed for comparison.

Effects of habitat type and topography on species composition at microsites
The effects of habitat type and topography on species composition at microsites were analysed with the same variables used for stratification: Three habitat types (two dummy var-
ables), four variables for local topography (ALT, SLO, RAD, CUR) and three for topographic neighbourhood (SDALT, SDSLO, SDRAD) were used to explain species composition on microsite level within each of the 12 local landscapes 1) in the scaling study to optimize the window size and 2) in the variance partitioning by RDA to estimate the amount of variance explained by those variables. The optimal window size for the topographic neighbourhood was evaluated by maximizing the total variance explained while varying the window size around the sampling point from 75 by 75 meters to 1025 by 1025 meters. The $R^2$’s were adjusted by the method of Peres-Neto & Legendre (2006), but the unadjusted $R^2$’s were also shown to permit comparisons with older literature. SLO from the DEM was replaced by the estimated field values, because the correlation between those two variables was low ($r = 0.29$) and the field data were thought to be more precise. A finer resolution of the DEM would be needed to satisfy the values of SLO as microsite descriptors. The effect of topographic variability on selected fractions of the adjusted variance explained was again analysed by linear regression analyses.

**Results**

**Effects of topographic variability on species composition at landscape level**

*Ecological gradients in species compositions at landscapes level*

The first axis of the PCA of species composition at the landscape level was associated with the gradient of topographic variability and also with the plant indicator values for nitrogen, humidity and pH. These trends applied both to the total data set and to the three habitat types analysed separately: in all cases the main shifts in species composition (i.e. axis 1 of the PCA) correlated in the same direction with all topographic variability measures and with mean humidity indicator values, and in the opposite direction with nitrogen and pH indicator values. The highest correlation coefficients ($r$) of the topographic variability measures were reached by $TV_{SDRAD}$, except for edges (HAB 2, Table 2). The effect of $TV_{SDRAD}$ on species composition was then further analysed in RDA’s. Presence/absence and abundance data were analysed separately and the results are shown in Table 3. Although the abundance data increased the explained variances in species composition, the main part was explained by presence/absence data in all cases.
Table 2: Correlation Matrix (r) of the three first PCA axes with topographic and environmental variables. Mean ecological indicator values for nitrogen, humidity and pH were derived from plant species lists per local landscapes.

<table>
<thead>
<tr>
<th>N = 12</th>
<th>HAB123</th>
<th>HAB1</th>
<th>HAB2</th>
<th>HAB3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ordination Axis</td>
<td>1</td>
<td>2</td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td>TV\text{SUM}</td>
<td>0.59</td>
<td>-0.61</td>
<td>-0.07</td>
<td>0.64</td>
</tr>
<tr>
<td>TV\text{SDALT}</td>
<td>0.49</td>
<td>-0.61</td>
<td>-0.36</td>
<td>0.52</td>
</tr>
<tr>
<td>TV\text{SDSLO}</td>
<td>0.23</td>
<td>-0.61</td>
<td>0.03</td>
<td>0.28</td>
</tr>
<tr>
<td>TV\text{SDRAD}</td>
<td>0.82</td>
<td>-0.48</td>
<td>-0.02</td>
<td>0.86</td>
</tr>
<tr>
<td>Nitrogen</td>
<td>-0.91</td>
<td>-0.12</td>
<td>0.36</td>
<td>-0.92</td>
</tr>
<tr>
<td>Humidity</td>
<td>0.66</td>
<td>0.09</td>
<td>0.50</td>
<td>0.21</td>
</tr>
<tr>
<td>pH</td>
<td>-0.66</td>
<td>-0.55</td>
<td>0.14</td>
<td>-0.70</td>
</tr>
</tbody>
</table>

Table 3: Variance of species composition explained by TV\text{SDRAD} at the landscape level for all species of all 40 relevées together and for the separate species lists for each habitat type.

<table>
<thead>
<tr>
<th></th>
<th>HAB123</th>
<th>HAB1</th>
<th>HAB2</th>
<th>HAB3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Presence/absence</td>
<td>0.13</td>
<td>0.14</td>
<td>0.11</td>
<td>0.14</td>
</tr>
<tr>
<td>Including Abundances</td>
<td>0.18</td>
<td>0.18</td>
<td>0.12</td>
<td>0.15</td>
</tr>
<tr>
<td>Increase including abundance in %</td>
<td>0.38</td>
<td>0.29</td>
<td>0.09</td>
<td>0.07</td>
</tr>
</tbody>
</table>

Habitat types and topographic variables explaining species composition at microsites

Closest correlates of topographic variability with biotic microsite variability

At the microsite level, the strongest correlations between topographic variability and the ecological properties of plants were obtained using the topographic variable TV\text{SDRAD} (Table 4). This variable correlated positively with the standard deviation of the mean humidity indicator values (SD humidity) and negatively with the mean nitrogen indicator value (p < 0.05 in both cases). Therefore, in subsequent analyses of microsite species composition, TV\text{SDRAD} was selected as the measure for topographic variability.
Table 4: Correlation Matrix (Pearson’s r) of the measures of topographic variability of the landscape with means (M) and standard deviations (SD) of ecological indicator values derived from species composition. Bold correlation coefficients with p < 0.05.

<table>
<thead>
<tr>
<th></th>
<th>TV_SUM</th>
<th>TV_SDALT</th>
<th>TV_SDSLOP</th>
<th>TV_SDRAD</th>
</tr>
</thead>
<tbody>
<tr>
<td>SD humidity</td>
<td>0.56</td>
<td>0.32</td>
<td>0.43</td>
<td><strong>0.66</strong></td>
</tr>
<tr>
<td>SD pH</td>
<td>0.03</td>
<td>-0.03</td>
<td>-0.17</td>
<td>0.21</td>
</tr>
<tr>
<td>SD nitrogen</td>
<td>-0.10</td>
<td>-0.02</td>
<td>-0.14</td>
<td>-0.07</td>
</tr>
<tr>
<td>M humidity</td>
<td>0.36</td>
<td>0.30</td>
<td>0.14</td>
<td>0.50</td>
</tr>
<tr>
<td>M pH</td>
<td>0.05</td>
<td>-0.03</td>
<td>0.34</td>
<td>-0.18</td>
</tr>
<tr>
<td>M nitrogen</td>
<td>-0.50</td>
<td>-0.50</td>
<td>-0.16</td>
<td><strong>-0.68</strong></td>
</tr>
</tbody>
</table>

Scaling study for the optimal window size of topographic variability in the microsite context

Figure 1 shows how the mean total variance in species composition explained by the global RDA model changed with increasing window size for the topographic context variables (dependent variables: species; explaining variables: two dummy variables for habitat types HAB1, HAB2, HAB3; local topographic variables ALT, SLO, RAD, CUR and topographic neighbourhood variables: SDALT, SDSLO, SDRAD). The maximum variance explained was reached with a window of 125 by 125 meters (five by five pixels of 25 m), and this size was therefore used in the subsequent analyses.

Explaining microsite species composition by habitat type and topography

The results of variance partitioning among the variable groups habitat type, local topography and neighbourhood topography - are shown in Table 5. Adjusting the variance by the method of Peres-Neto & Legendre (2006) resulted in a considerable reduction in the proportion of the variance explained by these variables. Thus, 36 % of the unadjusted total variance - the value usually presented in the literature - was explained by the three variable groups, while only 17 % were explained by the adjusted variance. Including topographic variables (local and neighbourhood together) increased the variance explained from 11 to 17%, which is a relative increase of 55 % compared to using habitat type alone.
Figure 1: Total adjusted variance explained in species composition (mean ± SE) by habitat type and topography, depending on the window size of the topographic neighbourhood variables.

Table 5: Variation explained in species composition by habitat type and topography (top), analysed by RDA within each of the 12 local landscapes; these are ranked according to their TV_{SDRAD}. Unadjusted (U) and adjusted (A) $R^2$'s are indicated. The results of the linear regression analyses of the framed values (total variance explained, explained by habitat type and the gain by topography) are shown in Figure 2.

<table>
<thead>
<tr>
<th>TV_{SDRAD}</th>
<th>Total</th>
<th>Habitat Type (1)</th>
<th>Topography</th>
<th>Gain by top (2)</th>
<th>Proportion (2/1)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>U</td>
<td>A</td>
<td>U</td>
<td>A</td>
<td>U</td>
</tr>
<tr>
<td>96</td>
<td>0.37</td>
<td>0.18</td>
<td>0.19</td>
<td>0.14</td>
<td>0.26</td>
</tr>
<tr>
<td>101</td>
<td>0.38</td>
<td>0.20</td>
<td>0.15</td>
<td>0.11</td>
<td>0.26</td>
</tr>
<tr>
<td>153</td>
<td>0.37</td>
<td>0.19</td>
<td>0.18</td>
<td>0.14</td>
<td>0.26</td>
</tr>
<tr>
<td>174</td>
<td>0.36</td>
<td>0.16</td>
<td>0.18</td>
<td>0.13</td>
<td>0.23</td>
</tr>
<tr>
<td>202</td>
<td>0.39</td>
<td>0.20</td>
<td>0.20</td>
<td>0.15</td>
<td>0.30</td>
</tr>
<tr>
<td>268</td>
<td>0.35</td>
<td>0.16</td>
<td>0.14</td>
<td>0.09</td>
<td>0.23</td>
</tr>
<tr>
<td>283</td>
<td>0.36</td>
<td>0.17</td>
<td>0.13</td>
<td>0.08</td>
<td>0.27</td>
</tr>
<tr>
<td>310</td>
<td>0.35</td>
<td>0.16</td>
<td>0.13</td>
<td>0.09</td>
<td>0.27</td>
</tr>
<tr>
<td>317</td>
<td>0.35</td>
<td>0.15</td>
<td>0.16</td>
<td>0.12</td>
<td>0.23</td>
</tr>
<tr>
<td>365</td>
<td>0.33</td>
<td>0.13</td>
<td>0.14</td>
<td>0.09</td>
<td>0.23</td>
</tr>
<tr>
<td>390</td>
<td>0.38</td>
<td>0.19</td>
<td>0.15</td>
<td>0.10</td>
<td>0.30</td>
</tr>
<tr>
<td>432</td>
<td>0.36</td>
<td>0.16</td>
<td>0.16</td>
<td>0.12</td>
<td>0.23</td>
</tr>
<tr>
<td>Mean</td>
<td>0.36</td>
<td>0.17</td>
<td>0.16</td>
<td>0.11</td>
<td>0.26</td>
</tr>
<tr>
<td>SD</td>
<td>0.017</td>
<td>0.022</td>
<td>0.023</td>
<td>0.024</td>
<td>0.026</td>
</tr>
</tbody>
</table>
Effect of topographic variability on variance explained at microsite level

To test the prediction that the contribution of different variable groups to species variance changes with topographic variability, we used linear regression to analyse the effects of TV_{SDRAD} on the variance explained by habitat type and topographic variables (local and neighbourhood topography together). The variance explained by habitat type decreased significantly with increasing TV_{SDRAD}, but the variance exclusively explained by topography showed no significant trend.

**Figure 2:** Effect of topographic variability (TV_{SDRAD}) on the variance explained in species composition by redundancy analyses for each of the 12 local landscapes. Each symbol denotes the amount of explained variance 1) in total (squares), 2) by habitat type (points) and 3) the gain of including topography in addition to habitat type (triangles, local and neighbourhood together).

**Discussion**

The purpose of this study was to investigate the effect of including topographic variables in a hierarchical sampling strategy intended to maximize ecological heterogeneity among local landscapes and among microsites within those landscapes. Any additional variance in species composition that could be explained by topography was interpreted as a gain in the efficiency of the sampling.
Topographic variability affected species composition at landscape scale

The species composition at the landscape level changed with increasing topographic variability, and this changes reflected strong ecological gradients. Thus, with increasing topographic variability the mean indicator values for humidity and acidity increased, while the mean nitrogen indicator values decreased. These trends were consistent for all the three habitat types (Table 2) and were due mainly to a turnover in species, rather than to changes in relative species abundances (Table 3). Consequently, the sampling of study units along a gradient of topographic variability seemed to be an efficient way to assess the ecological spectrum of plant species in our study area. One reason for the high correlations of important ecological gradients with the main gradient in our data set might have been the choice of a climatically and biogeographically homogenous study area. According to the hierarchical approach of Klijn and DeHaes (1994), the climate sets the broad frame for ecosystems, within which geology and geomorphology constrain the properties of soils, and these in turn constrain the vegetation. In broad-scale studies covering considerable climatic gradients, different interpretations of the hierarchies of constraining factors might be one reason for different conclusions about the importance for biodiversity of topographic heterogeneity (e.g. Moser et al. 2005, Pausas et al. 2003).

Of the four measures of topographic variability investigated, the one correlating most strongly with biotic gradients was standard deviation of radiation, $TV_{SDRAD}$. This result, which applies at both the landscape and microsite levels, confirms and extends an earlier finding that $TV_{SDRAD}$ is the variable best explaining total species richness in local landscapes (Chapter 1). As reviewed by Franklin (1995), complex topographic variables like $TV_{SDRAD}$ are usually better than simple topographic variables at explaining vegetation patterns; this is probably because they represent direct or resource variables, in this case solar radiation.

The correlation between topographic variability and microsite variability in the ecological indicator values for humidity supports the hypothesis that abiotic heterogeneity influences biodiversity (Palmer & Dixon 1990). The other significant correlation was a decrease of mean nitrogen indicator values with increasing topographic variability at both landscape and microsite levels. This can probably be explained by two factors: 1) a tendency for stronger soil development and therefore more nitrogen rich conditions in flat areas than on steep slopes, and 2) farming practices that are more intensive in flat areas. However, these
hypotheses would have to be confirmed by further investigations about natural site conditions and land use intensity.

**Effects of adjusting procedure for multivariate analyses**

To allow comparison with the literature, we have presented both the unadjusted $R^2$'s of the multivariate analyses and the adjusted $R^2$'s, which deliver unbiased estimates of the real contributions of explaining variables or variable groups (Peres-Neto & Legendre 2006). The total amounts of variance in species composition explained by habitat and topography at microsite level were rather high before adjustment (mean $R^2$ of 36 %), and considerably lower afterwards (mean $R^2$ of 17 %). However, to make a proper comparison with other studies, it would be necessary to compare the adjusted $R^2$ since these take account of both the number of samples and the number of predictors; unfortunately, these values are not available before 2006.

**The gain of including topography to explain species composition at microsite level**

The mean gain in variance explained by including topography amounted to 55 % of the variance explained by habitat types, but there was considerable variation in this percentage (Table 5, Figure 2). One reason for this might be the fact that abiotic/topographic site conditions indicate a potential rather than an actual state of biodiversity, and that in our investigation area this potential was often not reached. Biodiversity in agricultural landscapes is strongly affected of agro-ecological organisation (Alard & Poudvigne 1999), which in turn is linked to land-use intensity. Wrbka et al. (2004) have shown that abiotic and biotic patterns were linked most strongly in agricultural areas of intermediate land-use intensity. Including abiotic indicators would therefore be expected to increase sampling efficiency most in such areas.

**Effects of habitat type and topographic variables along a gradient of topographic variability**

Habitat types explained less of the variance in plant species composition with increasing $TV_{SDRAD}$. This is easily understood, since the variance in species composition is expected to increase with increasing abiotic variability. With a linear increase of biotic variability with abiotic/topographic variability, we would have expected any increased variance due to topography to be matched by a corresponding decrease in the variance due to habitat type. The fact that this was not so (Figure 2) may be explained in various ways. Firstly, the deviance of the abiotic potential from the real situation may have differed, as discussed above, resulting in high variance in the data. Secondly, our sample did not include landscapes of very low
TV$_{SDRAD}$ ($< 95$) as they were not present in our study area; however, as there cannot be an effect of topography with a TV$_{SDRAD}$ of zero, it is probable that the greatest effects of changing topography are to be found below the range actually sampled. Luoto et al. (2002) showed that different vegetation types could be predicted by slope in areas with very smooth relief, which supports our assumption. Finally, we cannot exclude the possibility that there is a change in the variance due to topography across the range sampled, but we failed to detect it because of the variation in our data.

The approach – Advantages and disadvantages of general applicability

In contrast to the modelling of vegetation patterns over contiguous areas, in our approach topographic variables were used independently between the local landscapes. Topography was only used to maximize abiotic and potential biotic variability among the sampling points within each habitat type within a restricted area (1km$^2$), but not to predict defined vegetation types. The advantage of this objective use of topographic information is that it does not assume that topographical conditions reflect abiotic conditions in the same way in different sampling units. Thus, the problem that errors associated with indirect (topographic) explanatory variables increase with the size of the study area (Guisan & Zimmermann 2000) is eliminated; and a further advantage is that no expert help is needed to define categories of topographic variables. Because we were interested in developing a method that is generally applicable, we only included habitat types that can be distinguished reliably using spectral information and based on current knowledge (Dirnböck et al. 2003). However, as shown in numerous modelling studies (Guisan & Zimmermann 2000), generality is an antagonist of precision. Depending on the study area, it would certainly be possible to increase precision by defining habitats more finely. However, this would reduce the generality of the approach, which is essential for comparability between studies. Palmer et al. (2002) suggested a method to locate species-rich areas exclusively from spectral information (based on the spectral variation hypotheses, SVH, Palmer 2000), which could probably be adapted to an approach of comparable objectivity with the advantage of using only recently collected biotic data. However, some problems cannot be eliminated. Firstly, the vegetation types which could not be distinguished by high resolution infra red photographs in the study of Dirnböck et al. (2003) cannot be distinguished by this approach either. Secondly, the different phenological stages in the same vegetation types caused by land use can give different spectral information even though the vegetation type is the same; this makes the sampling of agricultural areas more complex and less efficient than the approach presented here.
Conclusions

Unlike a conventional stratification based on topographic categories defined by an expert or just by the ecological range of the investigation area, the sampling strategy presented here maximized the relative topographic differences among samples in an objective way. By doing so, the strategy eliminated some important limitations of the conventional sampling procedures. Our results suggest that, within a climatically and biogeographically homogeneous area, the presented approach can improve sampling efficiency at both the landscape and microsite level.

Acknowledgements

The authors are very grateful to I. Kump for the recording of plant species relevées and the GIS Coordination Office of the Canton Lucerne for the free use of the true-color ortho-photographs.

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Chapter 3

**Integrating topographic variability into a sampling design for assessing plant species diversity in agricultural landscapes of Switzerland**

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**Abstract**

The overall objective of the work described here was to develop an efficient sampling design to select local landscapes for monitoring landscape-level plant species diversity in agricultural landscapes in Switzerland. Theoretical considerations and the results of a local study suggest that in mountainous areas the efficiency of sampling for variability in plant species richness and composition is increased by selecting local landscapes along a gradient of topographic variability. Using plant species data from a systematic sample of 187 'local landscapes' of 1 km² from throughout Switzerland, the present study determined whether this effect also applies at a larger spatial scale. Each local landscape was assigned to one of 13 climatically and biogeographically homogeneous sub-regions, and within each sub-region the effects of using topographic variability as a surrogate for abiotic microsite variability were investigated for species richness and composition. The following measures of abiotic microsite variability were derived from a digital elevation model: standard deviations of altitude, slope and potential annual solar radiation ('radiation'), and two further measures combining these values. For
each sub-region, the effect of microsite variability was analysed using linear regression for the species richness data, and redundancy analyses for species composition data. The best measure of microsite diversity was evaluated for each sub-region by comparing Akaike’s criterion (AIC) and the generalized AIC for multivariate linear models. The expected effects of microsite variability were confirmed in two thirds of the sub-regions for plant species composition, but only one third for species richness. The standard deviation of radiation explained species composition best, while species richness showed no clear pattern. We conclude that the efficiency of a national, hierarchical sampling design can be improved by integrating the standard deviation of solar radiation as a measure of microsite variability at the landscape level.

**Key words:** topographic variability, microsite variability, plant diversity, species richness, species composition, landscape scale, abiotic gradients

**Introduction**

With numerous studies showing dramatic losses of biodiversity in agricultural regions of Europe (e.g. Korneck & Sukopp 1988, Gates & Donald 2000), assessing landscape-level species diversity in agricultural landscapes has become an important task in the past few decades. Many programmes have been launched to monitor trends in biodiversity (Bischoff & Dröschmeister 2000) while other projects have evaluated the success of measures designed to promote biodiversity (Kleijn & Sutherland 2003). As the assessment of biodiversity is complex and costly, sampling efficiency is vital both for scientific and practical reasons (Bunce et al. 1996).

All ecological patterns are scale dependent (Wiens 1989), and one scale level is often assumed to be of special importance for a particular ecological phenomenon. However, both empirical studies and theoretical considerations about the hierarchical organisation of ecosystems agree that a full understanding of the distribution of biodiversity can only be obtained by considering patterns and processes at a range of spatial scales (Allan & Hoekstra 1990, Wiens 1989, Turner 2001). For the assessment of species dynamics, for example, it is not sufficient to consider the individual habitat patch in isolation, but the landscape level must be considered to take account of processes operating at a larger scale (Wiens 1976, Franklin
1993). Consequently, numerous surveys and monitoring projects have chosen a hierarchical sampling design, where local landscapes of 0.25 to a few square kilometres represent an intermediate level (e.g. Haines-Young et al. 2000, Dramstad et al. 2001, Hintermann et al. 2002, Cooper & McCann 2002).

The structural heterogeneity in agricultural landscapes has been shown to be an important factor influencing biodiversity (see Benton et al. 2003 for review), and is theoretically formulated in the 'heterogeneity hypothesis' (Palmer & Dixon 1990). Many agricultural areas are patch-mosaic landscapes, consisting of clearly demarcated patches of contrasting land use, where measures of landscape heterogeneity based on the diversity and distribution of patches have been developed as indicators of biodiversity (McGarigal & Marks 1995, Moser et al. 2002, Benton et al. 2003). To assess landscape–level diversity in an area, landscape heterogeneity measures are therefore appropriate parameters to increase sampling efficiency by maximizing the ecological variance among sampled landscapes (Gillison & Brewer 1985, Austin & Heyligers 1989, Bunce et al. 1996, Økland et al. 2006); such a maximization process can be described as a strategy of maximum variation sampling (Patton 1990).

Not all landscapes fit the patch-mosaic model, however: in mountainous areas, borders between habitat units are often not well defined, either because the habitats are composed of similar plant life forms (e.g. various types of grassland) or because there are gradual transitions from one habitat type to another. Except at a coarse level defined by contrasting life forms (e.g. grassland and forest), the delineation of homogeneous patches in gradient dominated landscapes is therefore conceptually unsatisfying (McGarigal & Cushman 2002) and difficult to implement in a repeatable manner. Most landscape-level biodiversity indicators have been developed in patch-mosaic agricultural landscapes, and there appear to be no standardized methods for assessing biodiversity in gradient dominated landscapes such as those of mountainous areas. This is problematic, since traditionally managed mountainous agricultural areas in Europe are very rich in biodiversity, much of which is now threatened (MacDonald et al. 2000). Such areas are under intense economic pressures, and many are likely to be either abandoned or intensified, depending upon the quality and accessibility of particular sites; both types of change will have a negative effect on biodiversity.

To achieve a sampling efficiency similar to that obtained in patch-mosaic landscapes, another measure of heterogeneity is needed for situations where abiotic and biotic patterns are strongly affected by topography (Swanson et al. 1988, Dorner et al. 2002, Sebastia 2004).
One convenient measure of topographic variability is the standard deviation of altitude, which has been shown to explain patterns of species richness at both broad (e.g. Kerr & Packer 1997, Riera et al. 1998) and fine scales (Luoto et al. 2002, Dufour et al. 2006). Using data from 12 local landscapes of 1 km$^2$ in the Swiss Alps, we investigated in Chapter 1 and 2 whether topographic variability affects plant species richness and species composition in local landscapes. Because their 250 km$^2$ investigation area was climatically and biogeographically homogeneous, we could assume that all local landscapes shared a common species pool and that the species actually present reflected local abiotic conditions. The results showed that with increasing microsite variability there was an increase of species richness as well as a shift in species composition; as revealed by the species indicator values, these changes were associated with important ecological gradients of nitrogen, pH and humidity. In Chapter 1 and 2 we concluded that the most effective measure of topographic variability/microsite variability was standard deviation of potential annual solar radiation; this parameter consistently explained more of the variation in species richness and species composition than the more commonly used standard deviation of altitude.

In this chapter, we investigate whether the conclusions obtained in the first two chapters in an investigation area of 250 km$^2$ are also valid over a much larger area, so that they should be taken into consideration for developing an efficient sampling design for assessing landscape-level plant diversity in agricultural areas in the context of a national monitoring scheme. We wanted to know, if effects of topographic variability are restricted to the montane zone e.g. due to the specific combination of climate and land use, or if the findings can be extended to other sub-regions. For this purpose, we analysed a large data set on plant species richness and composition in 1km$^2$ local landscape collected within the Swiss Biodiversity Monitoring Programme (Hintermann et al. 2002), covering four altitudinal belts and seven biogeographical regions. Using these more extensive data collected over a larger area within 13 sub-regions of different climate and biogeography, we seek to answer the following questions: (1) Is the finding that plant species richness and composition in agricultural landscapes change with topographic variability confirmed in the montane and in the other altitudinal belts? (2) Is standard deviation of solar radiation the most effective measure of topographic variability for this purpose? (3) Should topographic variability be included in the sampling designs used for national monitoring schemes for biodiversity patterns?
Methods

The sampling design for assessing plant species diversity at a landscape level (Swiss Biodiversity Monitoring, BDM)

Plant species data from the indicator 'species diversity in landscapes' were available from the Swiss Biodiversity Monitoring Programme (Hintermann et al. 2002). The sampling was based on a regular grid of 1 x 1 km\(^2\) ('local landscapes') of 12 km east-west and 8 km in direction north – south, with higher sampling intensity in small biogeographical regions; in total there were 494 local landscapes available (Figure 1). As the current study was concerned with agri-environmental indicators of biodiversity, we excluded squares with less than 40 % agricultural area including mountain pastures (based on the data of the Swiss Federal Statistical Office; BFS 1992/1997), resulting in a data set of 225 local landscapes. In order to obtain homogeneous 'sub-regions', each local landscape was then assigned to one of four altitudinal belts (Szerencsits & Dietl unpublished) and these were grouped according to the Swiss biogeographical classification of Wohlgemuth 1993 (10 classes). In the subsequent analyses we only used sub-regions containing at least 8 local landscapes; this left us with 13 sub-regions of 8 – 27 local landscapes (N = 187).

The plant species data for each local landscape was recorded along a predefined transect of 2.5 km length and 5m width, which was located as closely as possible to the diagonals of the square. All higher plant species in these transects were recorded twice, once in spring and once in autumn, and the data were combined into one species list for each local landscape (for further details see Plattner et al. 2004).

Topographic variability measures derived from a Digital Elevation Model (DEM)

The topographic variables were calculated using a DEM with a resolution of 25m, resulting in 1600 points per local landscape of 1km\(^2\). The following five measures of topographic variability (MTV) were calculated for each of the 187 local landscapes:

(i) TV\(_{SDALT}\) - standard deviation of altitude; extracted directly from the DEM

(ii) TV\(_{SDSLOP}\) - standard deviation of slope; extracted directly from the DEM
(iii) TV\textsubscript{SDRAD} - standard deviation of potential annual shortwave solar radiation. This was calculated with the Arc Macro Language Code of Kumar et al. (1997) with code corrections of Zimmermann (2000).

(iv) TV\textsubscript{SUM}. The three variables TV\textsubscript{SDALT}, TV\textsubscript{SDSLOP} and TV\textsubscript{SDRAD} were each transformed to range between 0 – 1, using the formula $y_i = (x_i - \text{xmin}) / (\text{xmax} - \text{xmin})$ (Sneath & Sokal 1973), and then summed, yielding a value between 0 – 3.

(v) TV\textsubscript{PCA}. This was calculated by ordinating the variables TV\textsubscript{SDALT}, TV\textsubscript{SDSLOP} and TV\textsubscript{SDRAD} in a principal components analysis and extracting the scores of the first axis; the signs of the scores were then adjusted so that the direction from low to high variability was consistent for all sub-regions.

Figure 1: Biogeographical regions (Wohlgemuth 1993) and altitudinal belts of Switzerland (Szerencsits & Dietl, unpublished) with the sampling grid of the 1km\textsuperscript{2} local landscapes for the indicator ‘species diversity in landscapes’ from the Swiss Biodiversity Monitoring programme, BDM (Hintermann et al. 2002).
Effects of topographic variability on species richness

The data were analysed separately within each sub-region for species richness and species composition. All recorded species were included to calculate species richness of each local landscape. Species numbers were log-transformed to analyse the effect of topographic variability in five separate linear regression models per sub-region, one for each MTV. To select the MTV that best explained species richness, we applied Akaike’s Criterion (AIC, Anderson & Burnham 1998) to the simple linear regression models. In addition, null models (with $x = 1$ as the explaining variable) were calculated to show whether including MTV increased the model fit. Four criteria were used for the final selection of one measure for all the 13 sub-regions in the following order:

1) Number of sub-regions with better model fit (lower AIC) than the null model (intercept only)

2) Number of sub-regions with a tolerable difference in model fit ($AIC_{\text{deltaMIN}} < 2$) to the best fitting model

3) Number of sub-regions with best model fit (lowest AIC value = $AIC_{\text{MIN}}$)

4) Lowest Mean $AIC_{\text{deltaMIN}}$

The $AIC_{\text{deltaMIN}}$ values (Table 2) were calculated by subtracting the minimum AIC on each row (sub-region) from all AIC values of the row; as a rule of thumb, an $AIC_{\text{deltaMIN}}$ of about two indicates that alternative models have a similar likelihood (Anderson et al. 1998).

Effects of topographic variability on species composition

For the multivariate analysis of species composition, only species that had been fully identified were included in the analyses; thus, any ambiguous records such as 'Hieracium spec.' were excluded. Species that either occurred only once or were present in all local landscapes within a sub-region were also removed; this was because these species had no potential to explain gradual shifts in composition. For the analysis of species composition, we applied the procedure suggested by Legendre & Gallangher (2001), using redundancy analysis (RDA) with Hellinger transformed plant species data.

The selection of the best fitting measure of topographic variability to explain species composition was based on a comparison of a generalized 'Akaike criterion' for multivariate analyses.
(Venables & Ripley 2002) of multivariate Redundancy Analyses (RDA). For the selection of the best measure for topographic variability, the same criteria were used as for the linear regression models explaining species richness (see above).

**Results**

**Effects of topographic variability on species richness**

Within each of the 13 sub-regions, species numbers correlated positively (Spearman’s rank correlation coefficients; Rs) with all MTV (Table 1).

This analysis revealed that, with each measure of topographic variability showing the highest likelihood at least once, no measure was unambiguously the best in explaining species richness. However, based on the four criteria already described, the combined measure TV_{SUM} was chosen for investigating the effects of topographic variability on species richness.

Table 1: Spearman’s Rank correlation coefficients (Rs) of the species richness of local landscapes within sub-regions defined by biogeographical region and altitudinal belt with all the five measures of topographic variability.

<table>
<thead>
<tr>
<th>Biogeographical Region</th>
<th>Altitudinal Belt</th>
<th>N</th>
<th>TV_{SDRAD}</th>
<th>TV_{SDALT}</th>
<th>TV_{SDSLOP}</th>
<th>TV_{SUM}</th>
<th>TV_{PCA}</th>
</tr>
</thead>
<tbody>
<tr>
<td>Jura Mountains</td>
<td>colline</td>
<td>13</td>
<td>0.214</td>
<td>0.390</td>
<td>0.363</td>
<td>0.407</td>
<td>0.407</td>
</tr>
<tr>
<td>Jura Mountains</td>
<td>montane</td>
<td>27</td>
<td>0.306</td>
<td>0.419</td>
<td>0.381</td>
<td>0.422</td>
<td>0.421</td>
</tr>
<tr>
<td>Jura Mountains</td>
<td>subalpine</td>
<td>9</td>
<td>0.471</td>
<td>0.101</td>
<td>0.563</td>
<td>0.521</td>
<td>0.521</td>
</tr>
<tr>
<td>Rhine &amp; Geneva Basin</td>
<td>colline</td>
<td>9</td>
<td>0.435</td>
<td>0.485</td>
<td>0.360</td>
<td>0.435</td>
<td>0.435</td>
</tr>
<tr>
<td>Western Plateau</td>
<td>colline</td>
<td>13</td>
<td>0.390</td>
<td>0.247</td>
<td>0.533</td>
<td>0.440</td>
<td>0.429</td>
</tr>
<tr>
<td>Western Plateau</td>
<td>montane</td>
<td>26</td>
<td>0.274</td>
<td>0.278</td>
<td>0.360</td>
<td>0.398</td>
<td>0.400</td>
</tr>
<tr>
<td>Eastern Plateau</td>
<td>colline</td>
<td>19</td>
<td>0.414</td>
<td>0.293</td>
<td>0.196</td>
<td>0.307</td>
<td>0.309</td>
</tr>
<tr>
<td>Eastern Plateau</td>
<td>montane</td>
<td>9</td>
<td>0.226</td>
<td>0.243</td>
<td>0.360</td>
<td>0.385</td>
<td>0.385</td>
</tr>
<tr>
<td>pre-Alps</td>
<td>montane</td>
<td>16</td>
<td>0.221</td>
<td>0.418</td>
<td>0.390</td>
<td>0.464</td>
<td>0.477</td>
</tr>
<tr>
<td>Northern Alps</td>
<td>montane</td>
<td>12</td>
<td>0.615</td>
<td>0.378</td>
<td>0.755</td>
<td>0.776</td>
<td>0.776</td>
</tr>
<tr>
<td>Northern Alps</td>
<td>subalpine</td>
<td>15</td>
<td>0.027</td>
<td>0.536</td>
<td>0.347</td>
<td>0.409</td>
<td>0.399</td>
</tr>
<tr>
<td>Eastern inner Alps</td>
<td>subalpine</td>
<td>11</td>
<td>0.064</td>
<td>0.036</td>
<td>0.791</td>
<td>0.455</td>
<td>0.136</td>
</tr>
<tr>
<td>Eastern inner Alps</td>
<td>alpine</td>
<td>8</td>
<td>0.667</td>
<td>0.167</td>
<td>0.619</td>
<td>0.548</td>
<td>0.571</td>
</tr>
</tbody>
</table>
There were three sub-regions where topographic variability could not improve the log likelihood of the linear regression model, so that the null model had the lowest AIC value (Table 2). The effect of topographic variability on species richness in the montane zone of the pre-Alps confirmed the results for this sub-region already shown in Chapter 1. The exclusive occurrence of statistical effects in the montane belt alone did not prove a restriction to this altitude, because the number of samples in this belt was higher compared to the others (Table 3).

To determine whether the increase of species with increasing topographic variability was stronger in the montane belt compared to the rest, the slopes of the linear regression curves for the montane belt were compared with the combined samples from the other altitudinal belts with a Mann-Whitney-U test. However, the result showed no differences between the groups (n_{montane} = 5, n_{rest} = 8; rank sum \(_{montane} = 47.5\), rank sum \(_{rest} = 43.5; U = 11.5, p = 0.22\).

**Table 2**: AIC\(_{delta}\) values derived from linear regression models, explaining log(species richness) with one of five measure of topographic variability within each of the 13 sub-regions. For each sub-region (row), the minimum AIC value was subtracted, resulting in zero for the model with the best likelihood of the model (bold). In four additional rows, four criteria were applied to derive the most appropriate overall measure of topographic variability. Bold values are the best values of each row.

<table>
<thead>
<tr>
<th>Altitudinal belt</th>
<th>Biogeographical Region</th>
<th>0 model</th>
<th>Measures of topographic variability</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>(x = 1)</td>
<td>TV(_{SDALT})</td>
</tr>
<tr>
<td>Alpine</td>
<td>Eastern Internal Alps</td>
<td>1.408</td>
<td>2.671</td>
</tr>
<tr>
<td>Subalpine</td>
<td>Jura</td>
<td>0.000</td>
<td>1.888</td>
</tr>
<tr>
<td></td>
<td>Northern Alps</td>
<td>3.310</td>
<td>0.000</td>
</tr>
<tr>
<td></td>
<td>Eastern Internal Alps</td>
<td>5.158</td>
<td>6.787</td>
</tr>
<tr>
<td>Montane</td>
<td>Jura</td>
<td>4.065</td>
<td>0.835</td>
</tr>
<tr>
<td></td>
<td>Western Plateau</td>
<td>3.467</td>
<td>0.000</td>
</tr>
<tr>
<td></td>
<td>Eastern Plateau</td>
<td>0.000</td>
<td>1.999</td>
</tr>
<tr>
<td></td>
<td>pre-Alps</td>
<td>4.235</td>
<td>3.194</td>
</tr>
<tr>
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<td>Northern Alps</td>
<td>7.650</td>
<td>5.664</td>
</tr>
<tr>
<td>Colline</td>
<td>Jura</td>
<td>0.430</td>
<td>0.000</td>
</tr>
<tr>
<td></td>
<td>Rhine &amp; G. Bassin</td>
<td>0.000</td>
<td>0.942</td>
</tr>
<tr>
<td></td>
<td>Western Plateau</td>
<td>2.584</td>
<td>3.808</td>
</tr>
<tr>
<td></td>
<td>Eastern Plateau</td>
<td>1.732</td>
<td>1.700</td>
</tr>
<tr>
<td></td>
<td>4 criteria for the selection of the best overall measure of topographic variability</td>
<td>(0) model improved</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td></td>
<td>AIC(_{delta}) &lt; 2</td>
<td>6</td>
</tr>
<tr>
<td></td>
<td></td>
<td>AIC(_{MIN})</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Mean AIC(_{delta})</td>
<td>2.618</td>
</tr>
</tbody>
</table>
**Effects of topographic variability on species composition**

In contrast to species richness, species composition analyses were more sensitive to the measure of topographic variability: models using $TV_{SDALT}$ and the two combined measures ($TV_{SUM}$, $TV_{PCA}$) never achieved the best likelihood, and in five cases the log likelihood of the null model was better than any measure of topographic variability. The best measure proved to be $TV_{SDRAD}$, which fulfilled all of the criteria defined for selecting a best measure of topographic variability, and this was therefore retained for further analyses. The contribution of $TV_{SDRAD}$ to explaining species composition was calculated and tested by 1000 permutations and the results are shown in Table 5. Significant effects of topographic variability on species composition were much more frequent than for species richness, and also occurred in all altitudinal belts.

**Table 3**: Results of the linear regression models, showing the effects of $TV_{SUM}$ on log(species richness) for each of the 13 sub-regions. $R^2$, $b$ and $p$ values are indicated for each analysis. Bold values indicate $p$ values < 0.1. The average number of samples per sub-region (N) is indicated for each altitudinal belt.

<table>
<thead>
<tr>
<th>Biogeographical regions</th>
<th>Jura Mountains</th>
<th>Rhine &amp; Geneva Basin</th>
<th>Western Plateau</th>
<th>Eastern Plateau</th>
<th>pre-Alps</th>
<th>Northern Alps</th>
<th>Eastern inner Alps</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alpine (8)</td>
<td></td>
<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$R^2$</td>
<td>0.35</td>
<td>0.10</td>
<td>0.13</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$b$</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$p$</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Subalpine (12)</td>
<td></td>
<td>0.10</td>
<td>0.02</td>
<td>0.42</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$R^2$</td>
<td></td>
<td>0.18</td>
<td>0.10</td>
<td>0.08</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$b$</td>
<td></td>
<td>0.02</td>
<td>0.10</td>
<td>0.08</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$p$</td>
<td></td>
<td>0.42</td>
<td>0.08</td>
<td>0.35</td>
<td></td>
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<tr>
<td>Montane (20)</td>
<td></td>
<td>0.20</td>
<td>0.17</td>
<td>0.04</td>
<td>0.32</td>
<td>0.55</td>
<td></td>
</tr>
<tr>
<td>$R^2$</td>
<td></td>
<td>0.08</td>
<td>0.11</td>
<td>0.02</td>
<td>0.20</td>
<td>0.12</td>
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</tr>
<tr>
<td>$b$</td>
<td></td>
<td>0.02</td>
<td>0.03</td>
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<td>0.01</td>
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</tr>
<tr>
<td>$p$</td>
<td></td>
<td>0.20</td>
<td>0.05</td>
<td>0.13</td>
<td>0.12</td>
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<tr>
<td>Colline (14)</td>
<td></td>
<td>0.15</td>
<td>0.09</td>
<td>0.19</td>
<td>0.14</td>
<td></td>
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</tr>
<tr>
<td>$R^2$</td>
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<td>0.08</td>
<td>0.04</td>
<td>0.10</td>
<td>0.05</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$b$</td>
<td></td>
<td>0.19</td>
<td>0.44</td>
<td>0.13</td>
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</tr>
<tr>
<td>$p$</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 4: AIC$_{\text{delta}}$ values derived from redundancy analyses, explaining species composition with the five MTV within each of 13 sub-regions. For each sub-region (row), the minimum AIC value was subtracted, resulting in zero for the model with the best likelihood (bold) of the model. In the four additional rows, four criteria were applied to derive the most appropriate overall MTV. Bold values are the best values of the row.

<table>
<thead>
<tr>
<th>Altitudinal belt</th>
<th>Biogeographical Region</th>
<th>0 model</th>
<th>Measuring of topographic variability</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>x = 1</td>
<td>TV$_{\text{SDALT}}$</td>
<td>TV$_{\text{SDSLO}}$</td>
</tr>
<tr>
<td>Alpine</td>
<td>Eastern Internal Alps</td>
<td>15.138</td>
<td>16.202</td>
</tr>
<tr>
<td>Subalpine</td>
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4 criteria for the selection of the best overall measure of topographic variability

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Table 5: Results of the redundancy analyses for each of the 13 sub-regions. R$^2$, and p values are indicated for each analyses. Bold values indicate p values < 0.1.

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<th>Rhine &amp; Geneva Basin</th>
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Discussion

With the aim of developing an efficient sampling design for the assessment of plant diversity of agricultural landscapes at a national scale, it was investigated whether species richness and composition are affected by topographic variability within 13 climatically and biogeographically homogenous sub-regions of a wide ecological range. An additional question was which of five measures of topographic variability would be the most effective parameter to explain the expected trends. There are two reasons why decision making about the best explaining measure of topographic variability was based on the contributions to the model fits comparing AIC values, and not on statistical effects. First, the number of samples per sub-region varied between 8 - 26, which is itself a reason why significant effects of topography were detected in some cases but not in others. Second, the data set was based on a systematic random sampling at a national scale, and the local landscapes in some sub-regions may not have included an adequate range of topographic variability. Additional information about frequencies of species – which were not available for the present study - was shown to further increase the variance explained by topographic variability (Chapter 2).

Effects of topographic variability on species richness

The importance of broad scale abiotic gradients for species richness has been shown in several studies of both plants and animals (Kerr & Packer 1997, Riera et al. 1998). However, research conducted at finer scales in agricultural areas has focussed more on how species richness is affected by the mosaic structure of landscapes; thus the emphasis has been upon heterogeneity due to different types of land cover rather than to environmental gradients (Moser et al. 2002, Benton et al. 2003, Økland et al. 2006, but see Dufour et al. 2006). The consistently positive correlation coefficients of species numbers within all the 13 sub-regions and with all MTV provided strong support for the conclusion in Chapter 1 that abiotic microsite diversity does affect species richness at the landscape scale. Further support comes from the fact that topographic variability measures improved the model fit in ten out of 13 sub-regions. The combined measures (TV_{SUM}, TV_{PCA}) performed better than their components (TV_{SDALT}, TV_{SDSLO} and TV_{SDRAD}), reflecting the more or less equal distribution of low and high AIC values among the three simple measures in the 13 sub-region (Table 2). Thus, we could not confirm TV_{SDRAD} as the best explaining variable in the case of species richness, although this was predicted based on the results in Chapter 1. Although all the significant effects were in the montane belt, there was no significant difference in the slope of the regres-
sion curves between the montane and other belts, suggesting that the increase of species richness was not higher in the montane belt; once again, the absence of a statistical effect must be interpreted with care!

**Effects of topographic variability on species composition**

Although the use of generalized AIC’s for multivariate linear analysis has been criticised (Oksanen et al. 2005), the procedure delivered interpretable results about the relative value of different MTV, which largely agreed with existing knowledge from vegetation modelling studies (Franklin 1995) and our case study (Chapters 1 and 2). TV_{SDRAD} explained species composition best and had a significant effect in eight of 13 sub-regions distributed in all altitudinal belts (Tables 4 and 5). Thus, the relative superiority of TV_{SDRAD} over other measures was much clearer than that of TV_{SUM} in the case of species richness. TV_{SDALT} was never the best fitting model for species composition, and it also had the highest mean deviation (3.41) from the AIC of the best fitting models. This is remarkable, as TV_{SDALT} is probably the most commonly used measure of topographic heterogeneity, and has been widely used on both broad (Richerson & Lum 1980, Riera et al. 1998) and finer scales (Dufour et al. 2006, Luoto et al. 2002). From vegetation modelling, however, it is well known that complex topographic variables like TV_{SDRAD} are generally better at explaining vegetation patterns than simple topographic variables like TV_{SDALT} (see Franklin 1995 for review); this is probably because radiation is a resource variable of direct relevance for plant growth.

**Which measure of topographic variability should be used to sample agricultural landscapes?**

The most effective measure of topographic variability depended upon which type of floristic data was analysed. For species richness, the best overall fit of the models was reached by a combined measure of topographic variability, TV_{SUM}, while for species composition it was TV_{SDRAD}. However, to judge from the higher number of statistical effects and the clearer discrimination between the MTV, data on species composition delivered more sensitive ecological information than species richness. This is a recognised phenomenon in biodiversity research and in agricultural landscapes by Jeanneret et al. (2003) and Økland et al. (2006); Burel et al. (1998) showed that even over steep gradients of agricultural intensity, data on species richness did not reveal any clear trends, while data on species composition showed ecologically relevant shifts, for example in the proportions of generalists and specialists. In a comparison of ecological compensation areas and intensively managed controls, Jeanneret et
al. (2003) showed that there were no differences in the species richness of spiders (Arachnida) although the species composition was highly distinctive. As species composition is known to deliver ecologically relevant and necessary information for interpretation, any sampling strategy should be optimized towards an efficient assessment of species composition; for this reason, $T_{SDRAD}$ is the better measure of abiotic microsite variability.

**Should topographic variability be used at national scale to sample agricultural landscapes efficiently?**

In contrast to a stratification based on biotic criteria (e.g. habitat classification or land cover), one based on topographic or abiotic parameters works with potential rather than with actual biotic patterns. Although it is probably generally true that higher diversity of abiotic microsite conditions is associated with higher species richness and changes in relative abundance (Richerson & Lum 1980, Riera et al. 1998, Luoto et al. 2002, Dufour et al. 2006, Chapters 1 and 2), there are various reasons why the full potential of species richness may not be achieved in particular cases. For example, in agricultural landscapes, species composition may not have recovered from historical changes in management practice, or the underlying abiotic patterns may have been obscured by land use practices that homogenize site conditions, e.g. drainage (Matson et al. 1997).

To decide whether the effect of topographic variability is sufficiently important to include in a sampling design for a national biodiversity assessment, the following arguments are relevant:

In this study, statistically significant shifts in species composition along a gradient of topographic variability were shown in about two-thirds of sub-regions, even though the sampling design was not intended for this type of analysis. Considering the expected high variance and noisiness of this type of data (e.g. Bürgi & Turner 2002), this result is surprisingly clear. A maximum variation sampling design would probably further increase the number of areas with significant differences.

Topographic variability is a surrogate for environmental microsite diversity, which might be influenced by different causal factors in the different sub-regions. In an environmentally very diverse country like Switzerland, there are probably no other easily measured variables that would serve as a basis for stratified sampling. Thus, the alternative to including topographic variability is a complete or systematic random sampling, both of which are less efficient for ecological surveys (Gillison & Brewer 1985).
Our results suggest that we would lose sampling efficiency in two-thirds of sub-regions by ignoring topographic variability, but not lose anything by including it in areas with no effects. In addition, a consistent sampling design is important for comparisons between areas and makes analyses and communication easier.

Taking these considerations into account, there seems to be a clear advantage of including topographic variability (TV\textsubscript{SDRAD}) in the sampling design within climatically and biogeographically homogenous sub-regions provided that there is a minimum – yet unknown – amount of variability. This conclusion appears to contradict that of Moser et al. (2005), who considered topographic variability to be less important than we do; however, their landscape units were larger than ours (35 km\textsuperscript{2} v. 1 km\textsuperscript{2}), and there was probably more variability within landscape units but less variability among them. This suggests that the question of when topographic variability is important is a matter of scale. For monitoring topographically heterogeneous agricultural landscapes, smaller study units have the advantage that divergent processes like abandonment and intensification - which may themselves be influenced by topographic variability - can be distinguished, thus increasing the value of the survey as an early warning system. In addition, a hierarchical approach, with study sites grouped within climatically and biogeographically homogeneous sub-regions, is important in order to separate species pool and environmental effects (Klijn & De Haes 1994).

Conclusions

Using data from 13 climatically and biogeographically different sub-regions of agricultural areas in Switzerland, topographic variability was shown to explain some of the variation in plant species richness and species composition at landscape level. For species composition, topographic variability was found to be important in the majority of sub-regions, with variability of solar radiation as the best measure of topographic variability. In contrast, topographic variability was less important in explaining variation in species richness, though the results were significant for about one third of sites.

Although our strategy of maximum variation sampling in agricultural areas was originally tested in a mountainous area, the analysis presented here also shows effects of topographic variability in lowland areas of the Swiss plateau with a gentler relief. We therefore conclude that the benefit of including topographic variability in biodiversity assessments is not con-
fined to mountainous regions, though it is important that sites are nested within sub-regions of uniform climate and biogeography.

**Acknowledgement**

We are very grateful to the Swiss Biodiversity Monitoring program (BDM) of the Swiss Federal Office for the Environment (FOEN) for plant species data. A special thank goes to the BDM data coordinator, Matthias Plattner from Hintermann & Weber AG, for his support and good collaboration.

**References**


General Conclusions

The high plant diversity of mountainous farmland is recently threatened by land use change, especially by abandonment (MacDonald et al. 2000). Sensitive biodiversity indicators and efficient sampling designs are therefore needed to monitor these areas. Although topography is known to affect abiotic and biotic patterns in several ways, none of the standard approaches for assessing and monitoring habitat or plant diversity takes account of topography to improve sampling efficiency. We therefore investigated and compared effects of topographic variables derived from a digital elevation model on the variability of plant species richness and composition at several scale levels to develop a standardized and generally applicable approach for assessing plant species diversity in topographically complex areas.

The importance of topographic variability for plant diversity

Topographic variability of local landscapes was shown to affect plant species richness at landscape level, but also species richness components at habitat and microsite level. The variability of species composition between local landscapes in the montane zone of the Swiss pre-Alps was to a certain extent explained by topographic variability which correlated with ecological gradients of nitrogen, humidity and pH. At the national scale, the large environmental range over which effects or trends of topographic variability on species diversity were shown is remarkable, reaching from lowlands to the alpine zone and across seven biogeographical regions. Those results indicate that topographic variability is of high ecological significance for several aspects of plant diversity. The general superiority of the standard deviation of solar radiation (TV_{SDRAD}) in explaining botanical variability at landscape level compared to the often used standard deviation of altitude (TV_{SDRAD}) confirmed existing knowledge that aspect plays an important role for local plant species composition (Bale et al. 1998, Ortega et al. 2004) and consequently, should be considered to quantify abiotic microsite variability.

While we had expected the variance in microsite species composition explained by topography to increase steadily with increasing topographic variability, our results suggest that there may be some threshold (With & Crist 1995), with the effects of topography increasing rapidly at low levels of topographic variability but remaining rather constant in the range investi-
gated. The minimum level of topographic variability, which affects vegetation pattern, is therefore still unknown.

A sampling strategy of general applicability

There are several possibilities how to use topographic variables to sample the variability of plant species composition. Existing studies defined either categories of e.g. slope by expert knowledge (e.g. Luoto et al. 2002) or they defined categories by dividing the whole range of a parameter of a study area in a number of equally sized classes (e.g. Goedickemeier et al. 1997). Those approaches were shown to be successful in assessing the range of the variability in species composition. However, as topographic variables are surrogates and not direct measures for environmental conditions, their predictive value is best within small areas (Guisan & Zimmermann 2000) and those approaches are therefore spatially limited. Unlike a conventional stratification based on pre-defined topographic categories for the whole study area, the sampling strategy presented here maximizes in an objective way the relative topographic differences among samples within landscape units of 1 km². No expert knowledge is needed to define the topographic categories and these are independent of the total ecological range in the whole study area. In addition, rare vegetation types are more likely to be sampled which is an advantage compared to systematic or complete random sampling. In contrast to the maximum variation sampling procedure described by Patton (1990), objectivity is assured by random sampling within the individually defined topographic categories within each local landscape. Finally, and crucial for time series, the coarse habitat classification used is likely to make a robust, repeatable delineation of habitat patches possible because it is confined to a few, clearly distinguishable habitat types. All these advantages lead to the conclusion that this sampling strategy is adequate to assess botanical or habitat variability in topographically complex regions but also in areas with gentle relief in a standardized and generally applicable way.

Recommendations

The presented approach was specifically developed with respect to application, considering general applicability and cost-efficiency in addition to ecological soundness. High resolution digital elevation models are recently available for large areas in consistent quality and provide precise and cost-efficient data. I therefore recommend to consider the following points for assessing and monitoring plant species dynamics in agricultural areas:
1. For the suggested sampling strategy at micro–site level it is important that landscape units are not too large, as the predictive value of topographic variables is best within small areas (Guisan & Zimmermann 2000). Landscape units of 1 km$^2$ were shown to be a convenient compromise between numerous demands of landscape scale studies (e.g. species dynamics, habitat modelling) and are used in monitoring projects throughout Europe. As shown in the present work, the standardized landscape units make comparisons between studies possible, which are highly informative. Landscape units of 1 km$^2$ should therefore be maintained.

2. As a measure of topographic variability and a surrogate of microsite diversity, $\text{TV}_{\text{SDRAD}}$ explained several components of plant species diversity better than the usually used $\text{TV}_{\text{SDALT}}$. Local landscapes should therefore be sampled along the gradient of $\text{TV}_{\text{SDRAD}}$ to maximize sampling efficiency.

3. For the monitoring of habitats and biodiversity in gradient dominated (grassland) regions, habitat mapping is feasible for coarse land cover categories. Within the categories, point sampling could be an alternative to habitat delineation, which especially in grassland landscapes is difficult to implement in a way that criteria of objectivity and repeatability are met. The abiotic variability between points should be maximized by the clustering of a set of topographic variables.

4. The Swiss biodiversity monitoring is based on regular grid sampling. When increasing the sample size between grid points, allocating the additional samples along a gradient of topographic variability would increase cost efficiency as well as the probability to cover rare habitats and species.

It is, however important to consider the constraints in conjunction with the sampling structure, namely to separate effects of climate and biogeography from effects of topographic variability, climatically and biogeographically homogeneous environmental units must be sampled individually.

**Further research**

Topography based sampling of plant species diversity was shown to improve sampling efficiency at microsite and landscape level. The suggested sampling strategy has a high objectivity and can also improve the cost efficiency of surveys. While the sampling strategy of local landscapes has been tested on a wide ecological range and is ready for application, the
microsite sampling within local landscapes needs to be further developed and its validity confirmed for a wider range of environmental conditions. A minimum threshold of topographic variability within local landscapes should be quantified to decide whether to include topography at microsite level and a minimum range of topographic variability between local landscapes should be defined to make this decision for the sampling at landscape level.

Shifts in species composition along gradients of topographic variability may have different causes. Important factors in explaining such patterns include the type, intensity and history of land use. Further investigations of topographic variability of landscapes in the context of land use are expected to deliver a better understanding of how and why shifts in species composition and species richness occur. In particular, future patterns of land-use change can probably be predicted better by including topographic variability.

References


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And last but always first, I thank Matthias Hauck for his great round-the-clock support and his patience for endless field seasons and working evenings.
Curriculum vitae

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<td>23rd of April, 1969, Basel, Switzerland; Citizen of Muttenz (BL) and Rothrist (AG)</td>
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<td>1989-1991 Diploma for Primary School Teacher, Liestal (BL), Switzerland</td>
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<td>1991-1997 Masters in biology, University of Basel, Switzerland</td>
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<td>Diploma thesis: Cast production of earthworms and seed establishment under elevated CO₂ in a dry, calcareous grassland.</td>
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