Spatio-Temporal Patterns of Biodiversity and their Drivers - Method Development and Application

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Herrn Dipl. Ing. Gerald Jurasinski
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Gutachter:
1. Prof. Dr. Carl Beierkuhnlein
2.

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Spatio-Temporal Patterns of Biodiversity and their Drivers - Method Development and Application

By
Gerald Jurasinski
Biogeography - University of Bayreuth
Germany

There never were in the world two opinions alike, no
more than two hairs or two grains;
the most universal quality is diversity.

Michel de Montaigne

Contents

Summary

In the light of land use and climate change which rapidly alter landscapes and ecosystems worldwide there is an urgent need for standardized and comparable data in order to detect changes of biodiversity. Therefore, it is paramount to provide methods for the comprehensive assessment and evaluation of biodiversity. These methods are required to be representative as well as pragmatic due to the fact, that there is insufficient time to obtain complete data sets. If biodiversity is lost rapidly at the landscape level, frequent re-investigations have to be done in order to detect and analyze such changes. The central objective of this thesis is the development and evaluation of spatially explicit, widely applicable methods for the assessment and analysis of phytodiversity, encompassing species richness as well as spatial and temporal heterogeneity of diversity. The conceptual perspective on the one hand and the application of the methodology in order to investigate ecological phenomena on the other represent the two foci of the thesis.

A review of the terminology of biodiversity - especially 'beta-diversity' - reveals a multitude of co-existing concepts. This plethora of definitions hampers application and scientific progress. Thus, a new terminology is proposed, which, compared to Whittaker's concept of diversity (alpha, beta, gamma), provides less ambiguous terms (inventory-, differentiation-, and proportional diversity). It enables a more direct access to the underlying ecological phenomena and key questions. Hence, it can help to structure the scientific discussion and future research.

Spatial patterns of diversity may be best assessed with systematic sampling. However, square sampling grids implemented so far are exposed to the problem of distance decay and deliver indefinite values. Therefore systematic sampling in hierarchically nested equidistant grids is proposed as an appropriate methodology for the assessment of spatial patterns in vegetation.

A new coefficient of multi-plot similarity is developed for the analysis of pattern diversity. For the first time this allows the calculation of similarity between one and many plots while taking species identity into account. It performs superior to all other tested coefficients in detecting vegetation hotspots and gradients. The multi-plot similarity coefficient provides a promising tool for ecological research as well as for nature conservation and monitoring.

The developed equidistant sampling grid has been applied in a case study in Northeastern Morocco to investigate the drivers of spatial patterns of biodiversity. The nested equidistant sampling grid with hexagonal plots allows for a detailed evaluation of different aspects of biotic diversity on landscape scale. However, while disturbances play an important role in shaping the emergent patterns of species distribution, the long time disturbance regime, manifested in the coarse vegetation structure, plays an even more important role. Most notably, the relationships between spatial patterns of biodiversity and its drivers vary with

scale and exhibit considerable non-stationarity. This has important implications for ecological research. When the relation between pattern and process is under study, the sampling design should address scale issues and enable to study the variation of the relations with scale and extent.

The methodology developed for the comparison of multiple plots has been applied to a data set of vegetation on Alpine summits to evaluate whether the upward shift of mountain plants causes homogenization of the summits. The analysis reveals that this indeed is the case: The increase in species richness on the summits is accompanied by a decrease in differentiation diversity. In the context of this thesis it is to state, that the heterogeneity concept may provide an interesting tool for the evaluation of actual ecological research questions as well as for nature conservation and monitoring.

Zusammenfassung

Landnutzungsveränderungen und Klimawandel führen weltweit zu einer rapiden Veränderung von Landschaften und Ökosystemen. Es werden dringend standardisierte und vergleichbare Daten benötigt, um den damit einhergehenden Verlust von Biodiversität zu erfassen. Daher ist es überaus wichtig, Methoden für eine umfassende Erfassung und Bewertung von Biodiversität zur Verfügung zu stellen. Aufgrund der Geschwindigkeit des Biodiversitätsverlustes sollten diese ebenso repräsentativ wie pragmatisch sein. Wenn Biodiversität auf Landschaftsebene verloren geht, müssen Aufnahmen häufig wiederholt werden, um diese Veränderungen erfassen und analysieren zu können. Das Hauptziel dieser Arbeit ist die Entwicklung und Evaluierung räumlich expliziter, übertragbarer Methoden zur Erfassung und Analyse pflanzlicher Vielfalt. Dies schließt Artenreichtum ebenso ein wie die räumliche und zeitliche Heterogenität der Artenzusammensetzung. Die konzeptionelle Erarbeitung einer Methodik sowie ihre Anwendung zur Untersuchung ökologischer Fragestellungen bilden die zwei Schwerpunkte dieser Arbeit.

Eine Bewertung der bestehenden Terminologie zur biologischen Vielfalt - insbesondere bezüglich des Begriffes beta-Diversität - macht deutlich, dass eine Vielzahl konkurrierender Konzepte existiert. Diese Fülle an Definitionen verhindert die Anwendung sowie den wissenschaftlichen Fortschritt. Daher wird eine neue Terminologie vorgeschlagen, welche - im Gegensatz zu Whittakers Konzept der Vielfalt (mit den Begriffen alpha-, gamma- und beta-Diversität) - klarere Begriffe zur Verfügung stellt (Erfassungs-, Unterscheidungs- und Verhältnis-Diversität). Sie ermöglicht eine direktere Erfassung der zugrundeliegenden ökologischen Phänomene und Fragestellungen was wiederum eine effiziente Strukturierung zukünftiger Forschung und Diskussionen ermöglicht.

Räumliche Muster der Vielfalt können am ehesten mit systematischem Sampling erfasst werden. Allerdings sind rektanguläre Raster - wie sie bisher angewendet worden - nicht unproblematisch. Einerseits wird dabei die Veränderung der Ähnlichkeit von Erfassungsflächen mit der Entfernung zwischen ihnen nicht berücksichtigt. Andererseits ergeben sich uneindeutige Ähnlichkeitswerte. Daher wird das systematische Sampling in hierarchisch geschachtelten, equidistanten Rasterflächen vorgeschlagen. Es scheint eine geeignete Methode zur Untersuchung räumlicher Muster in der Vegetation zu sein.

Zur Analyse von Vielfaltsmustern wird ein neuer Koeffizient der Multi-Plot-Diversität vorgestellt. Zum ersten Mal ist damit die simultane Berechnung der Ähnlichkeit zwischen einer und mehreren Erfassungsflächen unter Berücksichtigung der Identitäten der Arten auf allen betrachteten Flächen möglich. Er erlaubt eine bessere Darstellung von

Gradienten der Artenzusammensetzung und Hotspots der Artenvielfalt als andere getestete Indizes. Damit stellt dieser Koeffizient ein viel versprechendes Werkzeug für die ökologische Forschung als auch für Naturschutzplanung und -monitoring bereit.

Das entwickelte equidistante Erfassungsraster wurde in einer Fallstudie in Nordost-Marokko angewendet, um räumliche Muster der Biodiversität und die sie bestimmenden Faktoren zu untersuchen. Das geschachtelte Raster mit hexagonalen Aufnahmeflächen ermöglicht eine detaillierte Bewertung verschiedenster Apekte der biotischen Vielfalt auf Landschaftsebene. Störungen stellen einen wichtigen Einflussfaktor in Bezug auf räumliche Muster der Artenverteilung dar. Allerdings ist das langfristige Störungsregime von noch stärkerer Bedeutung. Es manifestiert sich in der Vegetationsstruktur der Baum- und Strauchschicht. Am bedeutsamsten ist jedoch die Feststellung, dass die Beziehungen zwischen räumlichen Mustern der Biodiversität und den sie bestimmenden Einflussfaktoren erheblich mit der Maßstabsebene auf der sie erfasst werden schwanken. Sie zeigen keine Stationarität im statistischen Sinne. Für die ökologische Forschung ist dies eine bedeutende Feststellung. Wenn die Beziehungen zwischen Mustern und den sie bestimmenden Prozessen untersucht werden, muss die Erfassungsmethode dem Rechnung tragen und die Untersuchung von maßstabsabhängigen Varationen der Beziehungen zwischen Umweltvariablen ermöglichen.

Teile der für die Analyse von multiplen Untersuchungsflächen entwickelten Methodik wurden auf einen Vegetationsdatensatz von Alpengipfeln im Bernina-Gebiet (Schweiz) angewendet. Dabei wurde untersucht, ob das klimabedingte Aufwärtswandern von Arten zu einer Homogenisierung der Artenzusammensetzung auf diesen Gipfeln führt. Die Analyse zeigt, dass dies tatsächlich der Fall ist: Die Zunahme der Artenvielfalt auf den Bergspitzen geht mit einer Abnahme der Unterschiedlichkeit zwischen ihnen einher. Im Kontext der vorliegenden Arbeit ist festzustellen, dass das Heterogenitätskonzept eine interssante Möglichkeit für die Bewertung aktueller ökologischer Fragestellungen sowie für die Naturschutzplanung darstellt.

Organization of the thesis

This thesis is based on a set of manuscripts and publications that in their majority originated from research carried out in a project funded by the DFG (Be 2192/5-1,2,3). The author was the coordinator as well as the main investigator of the project "Spatio-Temporal Patterns of Biodiversity and their Relation to Disturbances in semi-arid Ecosystems of Northeastern Morocco". It was conducted from April 2003 to September 2006. The project was led by Prof. Dr. Carl Beierkuhnlein.

The thesis consists of four Chapters and an Appendix. The introduction (Chapter 1) is aimed at the development of the hypotheses as well as at the clarification of important terminology and background information which is used throughout this thesis but not addressed in detail in the single publications and manuscripts. There is an extensive part on the concepts and the measurement of ecological resemblance since it forms the basis for most of the analyses and a shorter part on disturbances because they are investigated as a driver for vegetation patterns in the central case study in Northeastern Morocco.

The thesis is largely divided into two work foci (conceptional and methodological as well as empirical work). Therefore, the further structure follows this distinction. Chapter 2 introduces the conceptional and methodological work whereas Chapter 3 gives some detail on the empirical work and the case studies including backgound information on the investigation areas which are not part of the original manuscripts. The introduction on the Morocco study is somewhat more elaborate because the majority of the fieldwork was conducted in this project.

A recapitulatory, summarizing discussion which integrates the results of the original manuscripts and publications follows in Chapter 4.

The text of the manuscripts and publications is given in the Appendix. It is directly adopted from the originals. However, the format of the references and the numbering of the figures has been unified.

List of Manuscripts and Publications

This compilation comprises the publications and manuscripts that are part of this thesis. Their order follows a logical sequence providing the way they should be read in the context of this work. Information regarding the contribution of the author to the manuscripts is given under the actual publication. Note, that manuscript 7 is a manual for a software package for the R statistics system which was developed throughout the work.

For each publication, information in parentheses indicates (in this order): Status of publication; Integration of the manuscript into the work foci of the thesis: C - Conceptual contribution, M - Methodological contribution, E - Empirical contribution; Position in the Appendix. The corresponding author is marked by an asterisk, here and in the Appendix.

Manuscript 1 (submitted; C; Appendix 1)
Jurasinski, G., Retzer, V. & *Beierkuhnlein, C. (submitted) Inventory, differentiation, and proportional diversity – a consistent terminology for quantifying biodiversity *Oikos*
Own Contribution idea (100%), writing (80%) and editing (50%) the paper

Manuscript 2 (submitted; C, M; Appendix 2)
Jurasinski, G. & *Beierkuhnlein, C. (submitted) Hexagonal grids – a new approach for quantifying spatio-temporal patterns of biodiversity. *Journal of Biogeography*
Own Contribution idea of the equidistant grid (100%), writing (100%) and editing (90%) the paper

Manuscript 3 (in preparation; M, E; Appendix 3)
*Jurasinski, G. & Retzer, V. (in prep.) Measuring multi-plot similarity with presence-absence data. *Ecology*
Own Contribution idea (70%), method development (70%), programming (70%) and data-analysis (100%), writing (50%) and editing the paper (50%)

Manuscript 4 (published; M, E; Appendix 4)
*Jurasinski, G. & Beierkuhnlein, C. (2006) Spatial patterns of biodiversity - assessing vegetation using hexagonal grids. *Proceedings of the Royal Irish Academy - Biology and Environment* 106B: 401-411.
Own Contribution idea (100%), fieldwork (100%), data analysis (100%), writing (100%) and editing (90%) the paper

Manuscript 5 (submitted; E; Appendix 5)

*Jurasinski, G. & Beierkuhnlein, C. (submitted) Distance decay and non-stationarity in a semi-arid Mediterranean ecosystem. *Journal of Vegetation Science*

Own Contribution	idea (100%), fieldwork (100%), data analysis (100%), writing (100%) and editing (80%) the paper

Manuscript 6 (accepted; E; Appendix 6)

*Jurasinski, G. & Kreyling J. (accepted) Beyond richness - Upward shift of alpine plants leads to homogenisation of mountain summits. *Journal of Vegetation Science*

Own Contribution	idea (100%), data-analysis (100%), writing (80%) and editing (60%) the paper

Manuscript 7 (published; M; Appendix 7)

*Jurasinski, G. (2007) simba - Similarity Analysis for Vegetation Ecology version 0.2-4. http://homepage.mac.com/terhorab/gerald/simba.html

Own Contribution	idea (100%), design (100%), programming (80%), writing (100%) and editing (100%) the manual

Abbreviations

CA	Correspondence Analysis
CBD	Convention on Biodiversity
CCA	Canonical Correspondence Analysis
DCA	Detrended Correspondence Analysis (sometimes also called Decorana)
DGPS	Differential Geographical Positioning System
EGNOS	European Geostationary Navigation Overlay Service
NMDS	Non-metric Multidimensional Scaling
PCA	Principal Components Analysis
UNEP	United Nations Environmental Programme
SRES	Special Report on Emission Scenarios
WAAS	Wide Area Augmentation Service

1 Introduction

1.1 Motivation

Although there is less public attention on biodiversity loss today, it is not stopped. Quite the contrary, species extinction is still accelerating (Millennium Ecosystem Assessment 2005). Furthermore, evidence accumulates that even the diversity of biotic systems of higher organisational levels (e.g. plant communities or specific habitats as i.e. raised bogs in central Europe) is decreasing on the regional scale (e.g. van der Maarel 1997; Beierkuhnlein 1998). The chief cause for this process is land-use change (e.g. Dale et al. 1994; Austrheim et al. 1999; Crist et al. 2000; Sala et al. 2000; Anon. 2001; Allan et al. 2002). Species, communities and ecosystems cannot adapt in adequate time because genetical evolution is much slower than technological evolution (Angermeier 2000) and climate change may aggravate the problems. Global warming already causes species to shift their ranges and change their phenological behavior (e.g. Theurillat & Guisan 2001; Walther et al. 2002; Thuiller et al. 2005; Walther et al. 2005b).

Newer results predict not only a general shift in climate (Anon. 2001; Arnell et al. 2004; Levy et al. 2004, see the special issue of *Global Environmental Change* 14/1) but also an increase in extreme events (droughts, floods, etc., IPCC 2001). However, very little is still known about the possible responses of ecosystems regardless of recent attempts to model the future under the various SRES scenarios (ibid.). Araújo (2004) even suggests to implement models and knowledge of climate change into the selection procedure of biosphere reserves. In general, recent literature concerning global change and ecosystem response focuses either on the human-environmental-system (very large scale and meta data analysis, e.g. Ayres & Lombardero 2000; Niemelä et al. 2000; Hannah et al. 2002; de Vries et al. 2003; Peterson et al. 2003) or on specific organisms or even organic responses to climate change (very small scale and mostly experimental, see for instance Wood et al. 1994; Constable et al. 1999; Bermejo et al. 2002; Hättenschwiler & Körner 2003; Körner 2003). Information regarding a medium scale (ecosystem, habitat, landscape) and looking for shifts in community composition is rather scarce (but see e.g. Gottfried et al. 1998) although medium scale responses are best studied in natural ecosystems.

Hence, we need spatially and temporarily explicit and widely applicable methods giving comparable results to widen our understanding of these processes as well as to monitor changes in biodiversity to predict long term responses of ecosystems to environmental change. The development of such methods and their application to actual ecological questions is addressed in the present thesis.

1.2 Background

The following chapter shall provide some background information on the measurment and analysis of similarity as well as on disturbances. Both issues are of importance in the context of this thesis but are not tackled to much detail in the original manuscripts.

Measuring and analyzing similarity

Compositional similarity or differentiation diversity between sampling plots is an important basis for most numerical analyses in vegetation ecology. It is at the heart of ordination methods and has general importance regarding the testing of ecological theory (Legendre et al. 2005). Moreover, it represents the basis for most of the analyses in the present thesis and shall therefore be discussed in some detail in this chapter.

Data on species composition is generally of multivariate character. Thus, hypothesis testing regarding the relation between species composition and its drivers can hardly be achieved with normal statistics. This led to a specific set of methods for vegetation ecologists (Sokal & Rohlf 1981; Jongman et al. 1987; Legendre & Legendre 1998; Leyer & Wesche 2007). The majority of this methods are based on the calculation of biological resemblance and ecological distance in data space. Resemblance can be calculated with a wide range of coefficients and indices, measuring similarity, dissimilarity, proximity, distance, association or correlation (Orlóci 1978; Tamas et al. 2001).

Measuring similarity

Compositional similarity measures differentiation diversity (Jurasinski et al. submitted, Appendix 1) and can be calculated with resemblance measures. These are available in two primary groups (Figure 1.1, Legendre & Legendre 1998): (1) Quantitative or distance indices are used to calculate the proximity of two samples in data space from quantitative measurements or abundance data. (2) Similarity/Dissimilarity measures can handle binary data as it is typically found in presence/absence data sets. There is a large number of different indices and coefficients available and comparative reviews can for instance be found in Cheetham & Hazel (1969), Janson & Vegelius (1981), Wolda (1981), Hubalek (1982), Shi (1993), and Koleff et al. (2003a). All binary similarity/dissimilarity measures are based on the same set of variables (Figure 1.2). Whether a coefficient measures similarity or dissimilarity, depends on the implementation of the formula. However, most of them can easily be transformed from a similarity to a dissimilarity measure by calculating 1-S (with S being similarity, Shi 1993; Legendre & Legendre 1998). From some similarity coefficients a dissimilarity measure following the Euclidean metric can be obtained by calculating $\sqrt{1-S}$ instead (for details see Legendre & Legendre 1998).

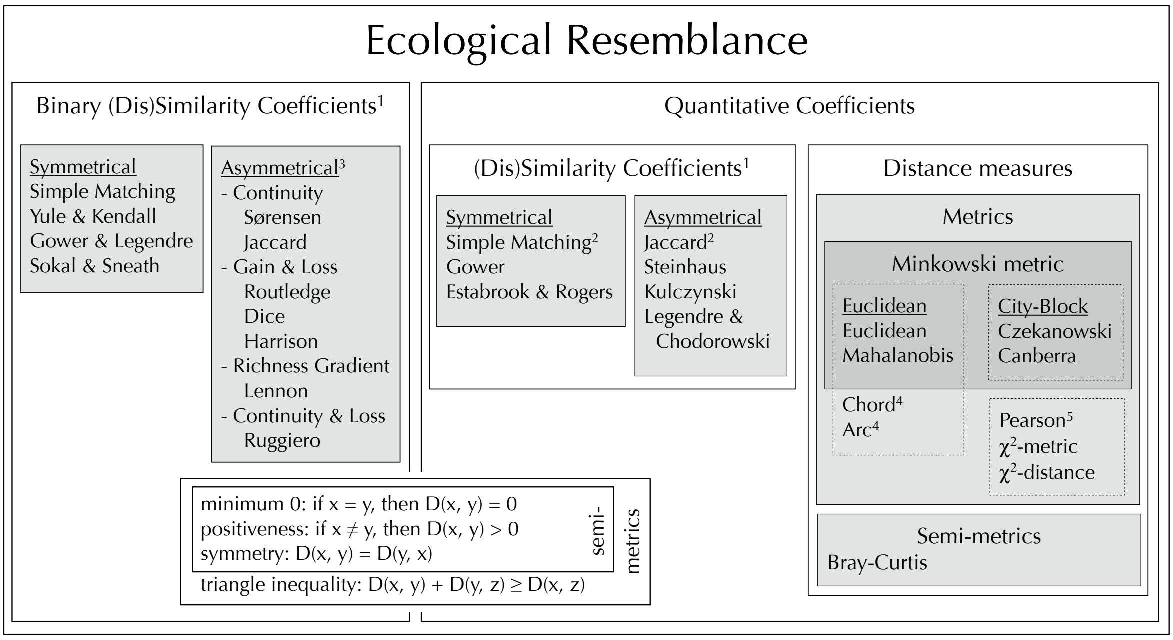

Figure 1.1. Overview regarding coefficients of ecological resemblance (mainly based on Legendre & Legendre 1998, for explanations see text). For each kind of index some examples are given. However, there are more in most cases. ¹) Binary as well as quantitative similarity coefficients (S) can be transformed to dissimilarity coefficients (D) by calculating 1-S. However, sometimes metric properties (see Figure inlay) are retained when calculating sqrt(1-S) instead. ²) From many binary coefficients quantitative indices can be derived by an extension to multi-state descriptors. ³) Subdivision follows Koleff et al. (2003, see text). ⁴) Chord- and Arc-distance derive from the Euclidean distance but are outside Euclidean space. ⁵) Coefficient of racial likeness (Pearson 1926).

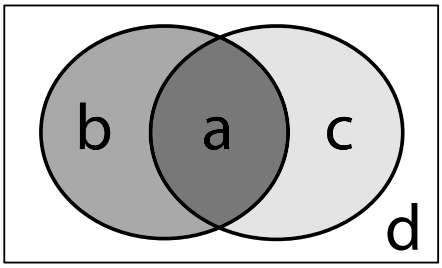

Figure 1.2. Illustration of the matching components providing the basis for binary similarity measures **a)** the number of species shared by two compared units, **b)** the number of species unique to one of the compared plots, **c)** the number of species unique to the other one of the compared plots, **d)** the number of species not found in the two compared plots but in the whole dataset (unshared species).

Indices incorporating the species not present in both of the compared samples (*d*, see Figure 1.2) are controversially discussed (e.g. Simple Matching by Sokal & Michener (1958) or the coefficient of Russel & Rao (1940)). Legendre & Legendre (1998) call these symmetrical (see Janson & Vegelius 1981 for another definition of symmetry) and discuss the "double-zero problem" at the beginning of their chapter on similarity indices, because it "is so fundamental with ecological data" (Legendre & Legendre 1998, p. 253): Species are supposed to have unimodal distributions along environmental gradients. If a species is absent from two compared sampling units (which is expressed by zeros in the species matrix), it is not discernable on which end of the gradient the both sites are with respect to a certain environmental parameter (Field 1969). Both might be above the optimal niche value for that species, or both below, or on opposite tails of the gradient. Thus, the incorporation of unshared species (*d*) might lead to wrong conclusions when the relation between environment and species composition is under study (Legendre & Legendre 1998). Additionally, Shi (1993) states that the status of *d* in similarity coefficients for paleo-ecological studies is not clear and cannot be assessed directly because of its great dependence on the less common taxa absent from both sites: "In palaeontology, absence of a taxon, particularly a rare one, […] may have been derived from differential preservation and/or sampling errors rather than some ecological […] factors". Finally, Field (1969) shall be cited as he found a very well fitting metaphor: "No marine ecologist would say that the intertidal and abyssal faunas were similar because both lacked the species found on the continental shelf".

(Dis)similarity indices which take unshared species into account mingle different ideas of differentiation diversity (additive partitioning, multiplicative partitioning, turnover, see Jurasinski et al. submitted (Appendix 1) for details). Furthermore, they tend to be less specific as the values show less variance because *d* is far bigger than *a*, *b*, or *c* for most of the datasets recorded in the field. "Including double-zeros in the comparison between sites would result in high values of similarity for the many pairs of sites holding only a few species; this would not reflect the situation adequately"(Legendre & Legendre 1998, p.254). Furthermore is the total inventory diversity (*gamma*) as a background for the calculation of *d* often difficult to define. When temporal changes are addressed, the question arises, whether the species pool of one time step or the whole species pool as recorded over several time steps should be regarded.

Because of this complications symmetric indices are not applied within this thesis. This does not mean that indices as the Simple Matching (Sokal & Michener 1958), the Margalef index (also known as Forbes 1907), or the various indices of Sokal & Sneath (1963) are of no use at all. Especially in questions of nature conservation or when regions with very different species richness are compared, they might be useful (see e.g. Retzer 1999).

Even when symmetric indices are not considered, there are still more than 30 different similarity measures known to the author. Many of these are discussed in the review-articles by Janson & Vegelius (1981), Wolda (1981), Hubalek (1982), Shi (1993), or Koleff et al. (2003a). The latter only regard asymmetric indices (in the sense of Legendre & Legendre 1998) and use ternary plots to illustrate the mathematical behavior of different similarity measures based on an artificial data set. According to Koleff et al. (2003) four types of indices can be distinguished: 'measures of continuity and loss', 'measures of species richness gradients', 'measures of continuity', and 'measures of gain and loss'. The first two are rather crude and have each only one representative. They either measure similarity only in one direction (Ruggiero et al. 1998) or are independent of the shared species of two compared samples (Lennon et al. 2001, for formulas of the indices please see the *simba* Manual in Appendix 7). The latter is best suited to test other indices regarding their dependence on *a* but it is less suited for the measurement of similarity. This should be influenced by the number of shared species (Legendre & Legendre 1998).

For each of the remaining two groups many coefficients exist. They can be distinguished by the importance given to the number of shared species. In Figure 1.3 some indices from these two groups are displayed as ternary plots. These can be used as a pre-analytical tool to decide which coefficient might be appropriate for a given data set (Koleff et al. 2003a, for details see Figure caption). If the data points are aggregated in the center (Figure 1.3 b-1) variability in similarity space is rather low. In this case the differences between the majority of the indices may be negligible (see Appendix 10 for a graphical comparison of asymmetric similarity coefficients). It is much more important to consider the mathematical behavior of the used measure if variability in similarity space is high. Then the mathematical differences between the coefficients matter and can lead to considerably different results.

Measures of continuity (Koleff et al. 2003a) almost exclusively depend on *a*: the number of shared species determines the value of the measure (see Figure 1.3 a-1,2, and Appendix 10, Figures 1-14). It only indirectly depends on *b* and *c* because high values of *b* and *c* together cause low values of *a*. Assume two sites sharing 50 species and 50 further species being present on one or the other site. The value of a *measure of continuity* will not change, no matter if one site has 1 and the other 49 or if the sites each have 25 of the unshared species. Most of the indices in this group measure dissimilarity including the - according to Koleff et al. (2003a) - most often used measure of Whittaker (1960; see Figure 1.3 a-2). Only two of the indices in this group measure similarity: The coefficients of Jaccard (1901) and Sørensen (1948; see Figure 1.3 a-1). They are mathematically simple, and differ only slightly in that Sørensen weights the shared species double which leads to a faster increase of the value of the measure with an increasing number of shared species. Both are widely used in vegetation ecology (e.g. Williams 1996, Condit et al. 2002).

Measures of gain and loss (Koleff et al. 2003a) also depend on *a*. Additionally they regard the relative importance of *b* and *c* (for examples see Figure 1.3 a 3-5). If the unshared species in a given pair of samples are distributed very uneven, the value of the indices will be lower when measuring similarity and higher when measuring dissimilarity compared to a more even distribution of unshared species. Thus, if the partitioning of the unshared species is to be included in the analysis, coefficients from this group should be implemented. These indices behave quite different depending on the relative values of *a*, *b*, and *c*. Hence, the choice is not simple (see Appendix 10, Figures 15-28 for illustrations of different patterns caused by different indices). Maybe that is the reason for their sparse implementation in ecological research (Koleff et al. 2003b). However, the measure of Simpson (1949) seems to perform best regarding the evaluated properties (ibid.). Further examples are the coefficients of Routledge (1977), Ochiai (1957), and McConnaughey (Hubalek 1982). See Figures 1.3a 3 and 4 for graphical representations.

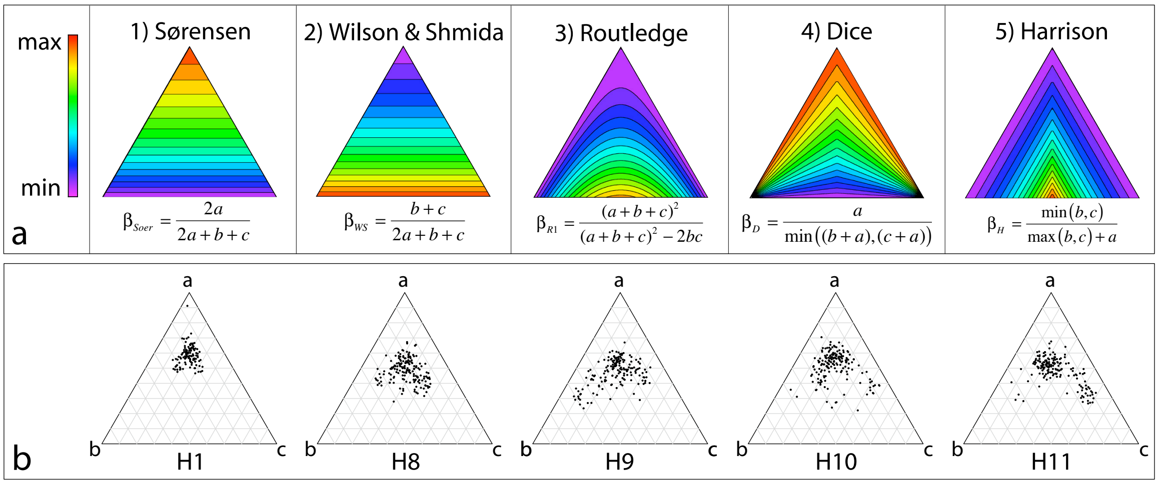

Figure 1.3. Triangular plots. **a)** They allow to display the mathematical behaviour of asymmteric binary similarity coefficients (Koleff et al. 2003). **1-2:** 'Measures of continuity' solely depend on the number of shared species, thus not taking any absences into account. This is regarded as positive when investigating the relation between species and the environment, Legendre & Legendre 1998). Most indices calculate dissimilarity (as e.g the Wilson-Shmida index **(2)**. However, Jaccard and Sørensen **(1)** calculate similarity and have often been found to be robust and reliable with vegetational data (see text). **3-5:** 'Measures of gain and loss' take the relative importance of b and c into account. However, based on the respective mathematical implementation, emphasis given to this components and therewith the shape of the ternary plot (and the calculated values) changes considerably between different measures. **b)** Ternary plots can be used as a pre-analytic tool in studies of compositional similarity (see text). Here, the three matching components calculated from different subsets of the data recorded in Morocco 2003 are displayed: The points largely concentrate in the center of the ternaries which means that the data set is less sensitive to the choice of the index. However, there are also differences between the subsets.

Shi (1993) reviewed 39 similarity measures regarding several characteristics (scaling from 0 to 1, independence from d, being metric, being symmetric (in the sense of Janson & Vegelius 1981), being not or marginally affected by sample size). They identified Jaccard 's (1901) index as the one best suited for paleontological research. It is followed closely by Sørensen (1948) and Ochiai (1957) although these are non-metric. A similarity measure is metric if it has the geometric properties of a distance measure (exhibiting triangle inequality). Pielou (1984) gives preference to this property because little distortion is caused when a metric similarity matrix is converted to a distance matrix, because both matrices have the same or very similar geometric properties (Shi 1993). The coefficients of Sørensen, Jaccard and Ochiai are also found to perform best in a comparative review by Janson & Vegelius (1981) who investigated the suitability of indices for ecological coexistence.

Throughout the present thesis Sørensen similarity is used as a binary similarity coefficient. It was introduced by Sørensen (1948) but is also known as Dice' index (1945) and sometimes falsely attributed to Czekanowski (Legendre & Legendre 1998). Sørensen does satisfy the criteria of linearity, homogeneity (the value is not changing if all values are multiplied by the same factor), and symmetry (independence from calculation direction, after Janson (1981)[1]. Its values are scaled between 0 (no species in common) and 1 (all species are the same) as many authors claim (e.g. Wolda 1981; Hubalek 1982; Shi 1993; Koleff et al. 2003a). Furthermore, Sørensen is well established and extensively used especially in vegetation ecology (e.g. Condit et al. 2002; Kluth & Bruelheide 2004). It is preferred here to Jaccard because of the double weight which is given to shared species (see Formulae 2.1 & 2.2). Legendre & Legendre (1998) argue, that the presence of a species is more informative than its absence: The latter can often not clearly be related to certain environmental parameters whereas double-presence is "as a strong indication of resemblance". This is also the reason for choosing a measure of continuity as these disregard the number of species only occurring in one of the compared units.

$$\beta_J = \frac{a}{a+b+c} \tag{2.1}$$

$$\beta_{Sør} = \frac{2a}{2a+b+c} \tag{2.2}$$

Distance indices - Euclidean vs. City-Block metrics

Distance measures are used to calculate resemblance of sampling units regarding quantitatively measured (e.g. pH, CN-ratio) or estimated (species abundances, species frequencies etc.) variables. When applied to species data they usually measure dissimilarity between sites, with values of 0 expressing complete similarity in species abundance. Upper boundaries vary between coefficients. The numerous available indices can be grouped along the following lines. Binary dissimilarity coefficients can easily be calculated from the similarity measures discussed above. Sometimes they are called 'distance measures' as well. However, the author prefers to use 'dissimilarity' in this case and preserve the term 'distance' for quantitative indices. These can generally be divided into two groups: Measures following the Euclidean metric (true metrics) and those following a City-Block metric (semi-metrics).

Euclidean distance (Formula 2.3) is the most common metric measure used for quantitative data. In a two-dimensional space, Euclidean distance is the length of the hypotenuse of a right triangle. If the space is one dimensional the Euclidean distance is simply the difference of the parameter values. In a multi-dimensional space (such as spaces unfolded by species abundances) the distance is still calculated following the

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[1] see Legendre & Legendre (1998) for a different definition of symmetry

Pythagorean theorem but in a p-dimensional space, where p is the number of species in the data set. The standard Euclidean distance has no upper limit. Therefore Legendre & Legendre (1998) propose to restrict the use of the Euclidean distance and mathematically related measures to dimensionally homogeneous data matrices (e.g. abiotic environmental data etc.). In the presented thesis it is applied in this manner that means to abiotic data only.

$$D(x_1,x_2) = \sqrt{\sum_{j=1}^{p}\left(y_{1j} + y_{2j}\right)^2} \tag{2.3}$$

A relativized version of the Euclidean distance exists. It is called Chord- or Standardized Euclidean distance and has an upper limit of √2. Standardization is obtained by dividing each value by the square root of the sum of all values of that parameter (Formula 2.4). The resulting distance corresponds to the length of a chord connecting two points of a segment of a unit sphere and is less exposed to the problems discussed with the Euclidean distance. The ecological space is than no longer Euclidean, but Riemannian, that is, a curved space (Beals 1984). A Euclidean representation of this total space has meaningless additional dimensions that simply reflect curvature. Therefore Beals (1984) argues, that it might be inappropriate to ecological phenomena because the Chord-distance "goes through a space outside vegetation space. (It is like measuring the distance from New York to Melbourne through the middle of the earth)." He proposes to use the arc distance instead, because it is the true distance between two points in a curved vegetational space (Formula 2.5). This is also called geodesic metric.

$$D(x_1,x_2) = \sqrt{\sum_{j=1}^{p}\left[\frac{y_{1j}}{\sqrt{\sum_{j=1}^{p} y_{1j}^2}} - \frac{y_{2j}}{\sqrt{\sum^{p} y_{2j}^2}}\right]} \tag{2.4}$$

$$D(x_1,x_2) = \arccos\left(\frac{-2_{Chord}^2}{\pi^2}\right) \tag{2.5}$$

Most measures closely related to the Euclidean distance (as e.g. Mahalanobis (1936) distance) are problematic as they are second degree (r = 2) of the Minkowski metric (Formula 2.6). When r > 2 too much importance may be given to the largest differences (inner term of the formula). That is why these forms of the metric are rarely used with biotic data where forms with r = 1 are more common, because the largest differences are then less emphasized (Gauch 1973; Økland 1986; Legendre & Legendre 1998). The resulting basic form is known as Manhattan metric (or City-Block distance, Formula 2.7) and several variants which shall not be discussed here in detail derive from that: mean character difference (Czekanowski 1909), index of association (Whittaker 1952), Canberra metric (Lance & Williams (1966) cited in Legendre & Legendre 1998), coefficient of divergence (Clark 1952), and the coefficient of racial likeness (Pearson 1926). In addition to the distance measures from this family there are coefficients related to χ^2 (χ^2-metric, χ^2-distance, Hellinger distance). The χ^2-distance is of particular importance because it forms the basis for ordination methods related to correspondence analysis (CA, CCA, DCA).

$$D(x_1,x_2) = \left[\sum_{j=1}^{p} \left| y_{1j} - y_{2j} \right|^r \right]^{1/r} \tag{2.6}$$

$$D(x_1,x_2) = \sum_{j=1}^{p} \left| y_{1j} - y_{2j} \right| \tag{2.7}$$

$$D(x_1,x_2) = \frac{\sum_{j=1}^{p} \left| y_{1j} - y_{2j} \right|}{\sum_{j=1}^{p} \left(y_{1j} + y_{2j} \right)} \tag{2.8}$$

All distance measures introduced so far are metric, the following is not as its values do not follow the triangle inequality axiom. The Bray-Curtis distance (Formula 2.8) represents the corresponding distance measure to the Steinhaus similarity coefficient (which is the quantitative representation of the Sørensen coefficient). Even though it is semi-metric and can thus not be used for a proper ordination in a full Euclidean space (Legendre & Legendre 1998) it has been proven as a robust and meaningful measure for ecological resemblance (Huhta 1979; Faith et al. 1987; De'ath 1999). Compared to Euclidean distance and other measures it retains sensitivity in more heterogeneous data sets and gives less weight to outliers. Faith et al. (1987) found Bray-Curtis distance (together with Kulczynski and relativized Manhattan distance) to perform best when tested with different models of species response curve shape, sampling pattern of sites, noise level of the data, species interactions, trends in total site abundance, and differentiation diversity of gradients. Moreover Bray-Curtis coefficient was most successful in clustering relevés in a comparative study of Campbell (1978).

The closely related Jaccard distance is also measured in city-block space but is a metric. It can be derived from Bray-Curtis by calculating 2B/(1+B) with B being Bray-Curtis distance. However, it performs worse compared to the Bray-Curtis index (Beals 1984) . A reason might be its metric nature. Interestingly, semi-metrics, such as Bray-Curtis, Manhattan, or Canberra distance are often found to perform best with ecological data

(Campbell 1978; Huhta 1979; Faith et al. 1987). According to Beals (1984), the advantage of measures following the City-Block metric is that all species contribute to the distance measure in proportion to their relative differences in the two samples. This weights environmental factors according to the number of species responding to it, as well as to how dramatically they respond. There is no exaggerated influence of big differences over small differences: "The city-block metric conforms to the biological fact that the difference for most if not all species reflects differences in the entire set of environmental conditions between the two samples". However, he also reveals, that binary measures (in this case Sørensen) often give even better results in ordination (Beals 1984).

Bray-Curtis distance and its one complement Steinhaus index are used in the present work to calculate resemblance based on species frequency data. As these are closely related to Sørensen similarity, which is implemented for presence/absence data, comparisons between the values are facilitated.

Similarity based on slope aspect and inclination

Slope aspect and inclination can have a significant effect on species composition especially in semi-arid vegetation (Sternberg & Shoshany 2001) and even on species richness (Badano et al. 2005). To obtain a distance measure integrating aspect and inclination a new coefficient is defined by using the model of a unit sphere and calculating great-circle distances between virtual locations (Figure A5.2 in Jurasinski & Beierkuhnlein submitted-a, Appendix4). Thus, continuous rather than class variables as e.g. found in Kjällgren (1998) can be generated. For each plot a virtual location on the sphere is defined using the values of slope aspect as longitude and 90°- slope inclination as latitude. Thus, the virtual points are located in the pole region as long as inclination is low. In this way, sites are close to each other regardless of their slope aspect. The underlying idea is that solar radiation, wind or other factors - being highly dependent on aspect and inclination (Wilkinson & Humphreys 2006) - are not considerably differing between plots with different aspect as long as the difference in slope is low. As said, the longitude values on the unit sphere derive from the directional reference made in the field. They are translated as follows: The equator of the virtual unit sphere is thought as the compass circle. The Prime Meridian of the virtual sphere is the great circle through North and South of the compass. As in geographic terms longitude counts positive in Eastern and negative in Western direction. With ϕ = latitude = 90°-inclination and λ = longitude = aspect the great-circle distance between A and B can be calculated with Formula 2.9. Because of the unit sphere, the maximum distance between two inclination/aspect pairs is ½ perimeter of the sphere which is by definition π. To scale the possible distances between 0 and 1 the values are normalized by π. Thus, a great-circle distance of 1 is rather scarce in the real world.

However, two vertical rock walls with opposite aspect would share it. Due to changes in irradiation and climatic influences with latitude this measure should be restricted to the comparison of sites within regions.

$$\zeta = \arccos(\sin(\phi_A)\cdot\sin(\phi_B)+\cos(\phi_A)\cdot\cos(\phi_B)\cdot\cos(\lambda_B-\lambda_A)) \qquad (2.9)$$

Disturbance as an ecosystem process

The perception of disturbances as an ecosystem process differed considerably between European and North American schools of vegetation scientists. The experience of European landscapes - altered and formed by man for centuries - lead to a clear focus on site conditions as the most important driver rendering species occurrence and pattern (e.g. Braun-Blanquet 1955). In North America researchers were confronted with landscapes not formed by man in which vegetation did not change with sharp borders but were dominated by gradients and considered as being dynamic (e.g. Gleason 1926; Daubenmire 1968). This might be a chief cause for the development of the different schools of vegetation ecology (Mueller-Dombois & Ellenberg 1974). This discrepancy also found expression in the differing views on disturbance. In Europe disturbaces have often been considered as of minor importance and plant sociologists simply neglected them because they interfered with their methodology and hindered the definition of associations. In North America the importance of disturbances as a process driving vegetation pattern was recognized early (Watt 1947).

Since the late seventies a multitude of hypotheses were developed, describing the role of disturbances as an important factor shaping biodiversity patterns. The Intermediate Disturbance Hypothesis (Connell 1978) and the Dynamic Equilibrium Model (Huston 1979; Huston 1994), which postulate a causal relationship between disturbance and biodiversity, are widely accepted, although they are sometimes challenged (e.g. Mackey & Currie 2000).

Based on these hypotheses the relevance of disturbances as an ecological factor has been a subject of intense debate (e.g. Grubb 1977; Sousa 1984; Pickett et al. 1989; Milton et al. 1997). Today there is a plethora of literature investigating the relation between disturbances and vegetation. The subjects are for instance functional adaptations of plants to perturbations (Pavlovic 1994; Walker et al. 1999; Garcia & Jurado 2003), the reactions of ecosystems to disturbances (Johnson et al. 1996; Engelmark et al. 1999; Fukami et al. 2001; Pakeman 2004; Quintana et al. 2004; Stampfli & Zeiter 2004), and the characteristics of disturbance regimes (Goldberg & Gross 1988; Turner et al. 1993; Bornette & Amoros 1996; White et al. 1999; Whelan 2002; Puettmann & Ammer 2005).

The impact of natural perturbations, most notably fire and storms, and their relevance for forest ecosystems are well covered (e.g. Denslow 1995; Vetaas 1997; Thiollay 1998; Frelich & Reich 1999; Loehle 2000; Puettmann & Ammer 2005; Sibold et al. 2006). The investigation of the effects of anthropogenic disturbance in contrast concentrates on grasslands and heaths (Leps et al. 1982; McNaughton 1985; Tilman 1996; Osem et al. 2004; Manier et al. 2005). However, the impact of disturbances on spatial patterns of differentiation diversity has been widely neglected, although some studies consider disturbances as one factor shaping spatial patterns (Bobiec 1998; Pitkänen 2000; Izcak & Price 2001; Samuelson & Rood 2004; Harrison et al. 2006). In the present work it is hypothesized that patterns of differentiation diversity can be explained by disturbance effects. The explicit consideration of disturbances in the analysis of compositional similarity is scarce (but see e.g. Ali et al. 2000; Harrison et al. 2006). This is surprising with regard to the importance of disturbances as a process generating pattern especially in Mediterranean ecosystems (Naveh & Whittaker 1979; Lavorel 1999; Osem et al. 2002).

The evolution of Mediterranean ecosystems as they are today, was highly influenced by man (Pignatti 1978; Ajbilou et al. 2006; Beierkuhnlein 2006). Therefore, they are fairly well adapted to disturbances such as fire, soil disturbance or grazing (Lavorel & Richardson 1999). Often disturbances rather modify species' relative abundances than composition (Fernández-Alès et al. 1993). Furthermore, many species developed efficient strategies that allow recovery from dormant seeds, buds or resprouting (Malanson & Trabaud 1987; Keeley 1992). Beside fires, grazing - and closely related soil disturbance - are important factors in shaping vegetation patterns in the Mediterranean (Naveh, Zev & Whittaker 1979; Carmel & Kadmon 1999). Grazing may inhibit the development and growth of woody vegetation, and, depending on intensity, even reverse the successional pathway (Callaway & Davis 1993; Carmel & Kadmon 1999). However, grazing also contributes considerably to the distribution of diaspores (e.g. Shmida & Ellner 1983; Fischer et al. 1996; Couvreur et al. 2004) and might therefore support woody succession by opening niches throgh the reduction of the biomass of competing herbaceous vegetation (Mitchell & Kirby 1990; Alon & Kadmon 1996).

After all, it is apparent that disturbances play a major role in shaping Mediterranean ecosystems. This suggests, that they are also important for the characteristics of differentiation diversity. Therefore, their importance as a driver of spatial patterns is addressed in Jurasinski & Beierkuhnlein (submitted-a, Appendix 5).

In this thesis, disturbances are understood as temporarily limited events, which affect particular organisms or communities by changing spatial patterns, temporal dynamics, physical environment or the flow of information (Pickett & White 1985; White & Jentsch

2001). Hence, they can be understood as ecosystem functions (Beierkuhnlein & Schulte 2001). Their impact on the diversity of ecosystems is long but not conclusively discussed (Huston, M.A. 1994; Mackey & Currie 2000; Hastwell & Huston 2001). As a whole they establish a characteristic disturbance regime. This can show both sudden and gradual developments. For substantial compilations and evaluation of the relevant literature see e.g. White & Jentsch (2001) or Malkinson & Kadmon (2006).

1.3 Hypotheses

In the light of land use and climate change which rapidly alter landscapes and ecosystems worldwide (e.g. Meyer & Turner 1992; Millennium Ecosystem Assessment 2005) there is an urgent need for standardized and comparable data in order to detect changes of biodiversity (e.g. Tilman et al. 2001; Wallace et al. 2004; Balmford & Bond 2005; Hanski 2005). Such methods are required to be representative as well as pragmatic due to the simple fact, that there is insufficient time to obtain complete data sets relating to temporal trends. If biodiversity is lost rapidly at the landscape level, frequent re-investigations have to be done in order to detect and analyse such changes. Therefore, the central objective of this work is the development and evaluation of spatially explicit, widely applicable methods for the assessment and analysis of phytodiversity, encompassing species richness as well as spatial and temporal heterogeneity. This methodology should provide for various possibilities to the analysis of the drivers of emerging patterns in vegetation in space and time. Furthermore, it should enable to track changes in biodiversity at the landscape scale.

The methodology of grid based biodiversity analysis (Beierkuhnlein 1999) was taken as a starting point and further developed (Jurasinski & Beierkuhnlein submitted-b, Appendix 2) and applied in a case study in Northeastern Morocco (Jurasinski & Beierkuhnlein 2006, Appendix 4; Jurasinski & Beierkuhnlein submitted-a, Appendix 5). In addition, conceptual work has been submitted (Jurasinski et al. submitted,, Appendix 1; Jurasinski & Beierkuhnlein submitted-b, Appendix 4). Moreover, parts of the methodology have been applied to foreign data (Jurasinski & Kreyling accepted, Appendix 6) and to artificial data sets (Jurasinski & Retzer in prep., Appendix 3). The conceptual perspective on the one hand and the application of the methodology to the investigation of ecological phenomena on the other represent the two foci of the thesis. The conceptual work follows the paradigm that terminology should be as clear as possible and the design principle that form follows function. In the empirical work specific hypotheses related to the ecosystems under study are formulated and tested with the proposed methodology.

Conceptual and methodological aspects

A key element of scientific progress is communication (Kuhn 1976; Jain 2007). Therefore it is important to employ a clear, unambiguous terminology (Loehle 1987) especially in the light of the increasing number of ecological publications and specialization (Graham & Dayton 2002). The term which is central to the present work - 'beta-diversity' - is not clearly defined. Therefore a new terminology is proposed in Jurasinski et al. (submitted, Appendix 1). Another conceptual contribution suggests the employment of equidistant regular sampling grids for the analysis of spatial patterns of biodiversity based on a short literature review (Jurasinski & Beierkuhnlein submitted-b, Appendix 2). This manuscript already contains a methodological component. The methodological aspect is further extended in Jurasinski & Retzer (in prep., Appendix 3). In this contribution a new coefficient for similarity measurement is developed because there are no measures available that enable the comparison of more than two sampling units whilst taking species identity into account. The performance of the coefficient and its ability to reveal gradients in species composition are evaluated. Therefore hypotheses regarding the performance of the measure have been formulated and tested in the original contribution (Jurasinski & Retzer in prep., Appendix 3)

Empirical aspects

The sampling design developed in Jurasinski & Beierkuhnlein (submitted-b, Appendix 2) was implemented to investigate spatial patterns of phytodiversity in a Mediterranean ecosystem in Northeastern Morocco. The investigated ecosystem is governed by strong climatic variability and the influence of man (Naveh 1975; Naveh & Whittaker 1979; Osem et al. 2004). Both together lead to a vegetation defined by gradual transitions from scattered forests to open steppe-like ecosystems. Therefore, it was hypothesized that the spatial patterns in vegetation in this ecosystem are primarily driven by disturbance. However, recent studies suggest that such relations often change with scale (e.g. Lichstein et al. 2002; Wagner & Fortin 2005). The same holds for the similarity of species composition between sampling units (distance decay after Nekola & White 1999; Steinitz et al. 2005). These considerations lead to the following hypotheses which were tested in the Morocco case study. The corresponding publications/manuscripts are given in parentheses.

(1) Similarity in plant species composition decreases continuously with distance. Due to the small scale of the study (largest geographical distance covered is 6 km) the rate of distance decay will be relatively low compared to large scale studies (Jurasinski & Beierkuhnlein submitted-a, Appendix 5).

(2) The correlation between compositional similarity of vegetation and the dissimilarity of predictor variables (disturbance, vegetation structure, abiotic environmental conditions) changes with geographical distance between plots. Based on findings of Jones et al. (2006) and Duque et al. (2002) the correlation is expected to increase with spatial scale/distance between sampling units because the sampled environmental gradient is likely to increase as well (Jurasinski & Beierkuhnlein submitted-a, Appendix 5).

(3) Disturbance is the main driver of vegetation patterns in the regarded transitional ecosystem (Jurasinski & Beierkuhnlein submitted-a, Appendix 5). The incorporation of areas with varying disturbance severity and intensity (see e.g. Svenning 1998; Thiollay 1998) enables the evaluation of the importance of disturbances as a driver of phytodiversity.

Based on the central aim of method development further methodological questions were tested empirically as well. They follow from the sampling design which is deduced in Jurasinski & Beierkuhnlein (submitted-b, Appendix 2). Features of the nested equidistant sampling grid and of the hexagonal plot have been evaluated. In this regard, the following hypotheses apply:

(4) Data recording for spatial analysis is often tedious. Therefore it is crucial to minimize sampling effort on the single sites. Closely related to this problem, is the question of frequency versus presence/absence data as a basis for the assessment of spatial patterns in vegetation. Most species in the field layer of the investigated Mediterranean ecosystem occur with low abundances. Therefore presence/absence data will be equally qualified compared to frequency data to reveal spatial pattern and investigate the relation between vegetation and environement (Jurasinski & Beierkuhnlein 2006, Appendix 3).

(5) The equidistant sampling grid, developed in Jurasinski & Beierkuhnlein (submitted-b, Appendix 2) consist of hexagonal cells. Therefore the sampling sites are as well hexagonal in shape. The crossing radii of the hexagonal plot are used to assess data on vegetation structure or similar features. It is hypothesized that the values for bush and tree cover assessed with the line intercept method on the marking ropes closely resemble the ‘real’ cover values (Jurasinski & Beierkuhnlein 2006, Appendix 3). If this is true, the hexagonal plot could be implemented for an efficient assessment of structural variables.

(6) Parts of the developed concept have been applied to published data to investigate homogenization in the species composition of mountain summits (Jurasinski & Kreyling accept., Appendix 6). Based on Walther et al. (2005a) and related publications (Kjällgren & Kullman 1998; Klanderud & Birks 2003) it is hypothesized that the upward shift oft mountain plants due to climate warming leads to a homogenization of Alpine summits. Thus, increasing ‘alpha-diversity’ might be accompanied by decreasing ‘beta-diversity’.

2 Conceptional and methodological contributions

2.1 A new terminology for biodiversity

A new terminology for the measurement and analysis of biodiversity has been proposed in Jurasinski et al. (submitted). It is used throughout this thesis document. However, due to the fact that it has been released later than some of the papers, it is not used in all of the publications/manuscripts. Please refer to **Appendix 1** for the original text**.**

2.2 Sampling spatial patterns with hexagonal grids

The foundations of sampling in equidistant grids are comprehensively discussed in Jurasinski & Beierkuhnlein (submitted). It is a conceptional contribution in which systematic sampling on equidistant grids is deduced from a literature review on sampling for the analysis of spatial patterns. Please refer to **Appendix 2** for the original manuscript.

2.3 The coefficient of multi-plot similarity

Introduction

The heterogeneity concept (Jurasinski & Kreyling accepted, Appendix 5) was established to enable the assignment of a reasonable measure of differentiation diversity to a focal sampling unit. However, similarly to other approaches implemented so far (e.g. Williams 1996; Lennon et al. 2001), species identities are not respected when the similarity values calculated between a focal plot and its neighbors are simply averaged. Therefore a further step was taken and a new measure of multi-plot similarity was developed. To test its behavior and performance against other measures of differentiation diversity, data from a case study recorded in a diploma thesis (Rettenmaier 2004) supervised at the Department of Biogeography has been utilized. Furthermore, artificial data sets with known properties (species occurrence follows gradients and hotspots) have been created based on the general characteristics (species number, plot number, approximate shape of the species accumulation curve) of these field data. This offers the possibility to test the performance of the multi-plot similarity measure and its ability to detect gradients and hotspots under various conditions.

The data of Rettenmaier (2004) was preferred over data from Morocco because the extent of the implemented grid was larger on one scale level. Due to the hierarchical nesting and the implementation of three different scale levels the maximum number of sampling units on one scale and grid amounts to 19 in the Morocco data (see Chapter 3.1). There are many different grids, but all of them are constituted of 19 units only. Although the data of Rettenmaier (2004) covers a smaller area (about 34 ha), a much larger number of sampling units (61 plots) is arranged in one regular hexagonal grid on one scale level. This provided better possibilities for the creation of the artificial data and allowed for the analysis of the performance of the measure with a variety of data sets (random, gradient, hotspot, real, …) whilst sampling on the same grid.

Northern Sweden - Tundra in the Stordalen Nature Reserve

The data of Rettenmaier (2004) was recorded in a Tundra ecosystem Southeast of Abisko, Sweden. Abisko is situated about 200 km North of the Polar Circle at 68°21′N and 18°49′E in the Swedish province Norrbotten at lake Torneträsk (ibid., Figure A3.1 in Jurasinski & Retzer in preparation, Appendix 3). Already in 1912 a research station (Abisko Naturvetenskapliga Station, ANS) was established and even before (1909) a large National Park was founded South of Abisko (ibid.). Throughout the years more and more area has been taken under protection and because of the ANS the natural ecosystems of the region are relatively well studied. The climatic conditions around Abisko are special contrasted to places on the same latitude. An open "window to the Atlantic" due to a discontinuity of the Skandes causes mild winters and cool summers. The large lake Torneträsk adds to the atlantic conditions with a cooling effect in summer and a wetting effect (fog) in winter and autumn. However, precipitation is exceptionally low (304 mm/a) because of the position West of the Skandes. Mean annual temperature is 0.5°C. Mean Juli temperature is 11°C. The coldest month (January) exhibits -11.9°C mean temperature.

Data was recorded on a Northwest oriented gentle slope which is mainly covered by heath. There are also wetter places where shrubberies composed of different *Salix* (Willow) species, *Betula nana* L. (Dwarf Birch) and *Juniperus communis* L. (Common Juniper) are dominating. Small fragments of birch forest occur in depressions providing protection from the harsh climate conditions. Based on the small scale relief the soils reflect a characteristic moisture gradient from wet depressions to moist banks to dry humps (Billings 1973) which leads to a small scale mosaic of soil types. Vegetation structure is considerably influenced by micro-topographic features as these - in combination with slope aspect - control the snow distribution and the length of the snow covering period. Species data originally has been recorded in frequencies regarding occurrence in the six triangles which made up each hexagonal plot (Rettenmaier 2004). For the analyses in Jurasinski & Retzer (in prep.) only presence/absence on each plot of the primary grid was taken into account.

Measuring multi-plot similarity with presence/absence data

See original manuscript in **Appendix 3**.

2.4 simba - Similarity analysis for vegetation ecology

All analyses carried out and the majority of the illustrations shown in this thesis can be accomplished using a single software package. The R statistics system (in the following shortly referred to as 'R') is an implementation of the S language developed at Bell Laboratories which also forms the basis of the S-Plus systems. The main difference is that it is in the public domain (R Development Core Team 2005). Due to its open source character and the possibility to write and provide additional packages with useful functions it has a fast growing user basis.

In addition to the use of available packages an own package for R was developed. It is called *simba* and will soon be available on CRAN (Comprehensive R Archive Network, http://cran.r-project.org/). Until then it can be downloaded from http://homepage.mac.com/terhorab/simba/. The documentation of the package is added as an appendix (**Appendix 7**; Jurasinski 2007) because it is considered a direct outcome of the work on this thesis. It provides details on the functions contained. The majority of the analyses implemented in analysing the data for this work can be carried out using functions available in the package *simba*. Others use functions of the packages *vegan*, *base*, *stats*, and *geoR*. Throughout the thesis the following p-levels apply: *** for $p < 0.001$, ** for $p < 0.01$, * for $p < 0.05$, ns or no indication for non-significant relationships. Deviations from this scheme are indicated.

3 Empirical contributions

3.1 Spatial patterns of phytodiversity in a Mediterranean ecosystem

Introduction

Investigation area

Rationale The investigation area of the central case study is located in Northeastern Morocco. This region offers several features important in the context of the general questions of the work. The vegetation mosaic is highly diverse and primarily ruled by gradual transition from scattered forest to open steppe-like ecosystems. Garrigue - sometimes tending to Maquis-like thickness - occurs beside open, wood-free, and sparsely vegetated areas. Furthermore, Savanna-like vegetation (comparable to the vegetation of Spanish dehesa or Portuguese montado) with relatively large and widely scattered Holm Oak trees (*Quercus rotundifolia* L.) and a rather closed field layer mainly build up by grasses completes the mosaic. It is shaped by the influence of man and his livestock for centuries. The intensity of the marginally controlled land-use is increasing due to fast population growth and the growing demand for food throughout the Southern Mediterranean (Lavorel 1999). The peripheral region is largely decoupled from economic growth in the urban centers of Morocco. Conclusively, we find a region subjected to land-use change which will most likely suffer from global warming, paired with a highly diverse vegetation mosaic difficult to assess with standard vegetation ecological methodology (but see Müller-Hohenstein 1978 for an intensive phytosociological coverage of the region). Therefore, the area is especially suited to test the methodology of grid based vegetation assessment.

Geology The high plateaus in Northeastern Morocco can be delimited by the different landscapes which adjoin them in the North, West and South (to the East their is gradual transition to the Sahara). In the river valleys in the North, paleozoic schists, riddled with granite, are to be found. Upon the basement jurassic layers build a heavily dissected cuesta which towers more than 1000 m above the basins and plains of the forelands to the North filled with tertiary and quaternary sediments (Müller-Hohenstein 1978). West of the plateaus the landscape has been shaped by the Moulouya river. Its tributaries carved canyons into the overlying rock and formed buttes and mesas (Raynal 1961). On the Southern side of the high plateaus small massifs of cretaceous, jurassic and triassic sediments build the border to the Saharan landscape of South Morocco (Müller-Hohenstein 1978). The basement of the cuesta is build up by a monotonous series of argillaceous schists, which rarely alternate with small banks of arkosic sandstones (Medioni 1977). The sandstones contain muscovite and plagioclase. Thus, they have an intermediate position between arkosic sandstones and graywacke (Beierkuhnlein & Weber 1992). The overlying rock consists of middle and late jurassic sediments. On the plateau the calcareous and dolomite cover is often present at the surface in large plates and coarse boulders. This is also reflected in a fairly high pH-value (7.1-8) throughout the investigation area.

Orography and climate The geographic position of the investigated area is at about 34° North and 3°West at the escarpment of the Northeastern Moroccan High Plateaus (Plateau du Rekkam) about 100 km South of the Mediterranean Sea and East of the Algerian border (Figure 3.1). The cuesta at the elevation of the Plateau du Rekkam from the Moulouya valley is called Gaada de Debdou and inhabits an exceptional orographic position compared to its surroundings. Here is the highest point of the whole plateaus (1675 m) which are widely stretching to the Southeast until they reach the Sahara. The Gaada functions as a natural barrier to the clouds approaching from the Northwest. Therefore, it receives far more precipitation (about 500mm/a) than the plateaus or the plains of the Moulouya valley (about 200mm/a). More details regarding the climatic situation in the investigation area can be found in Appendix 9.

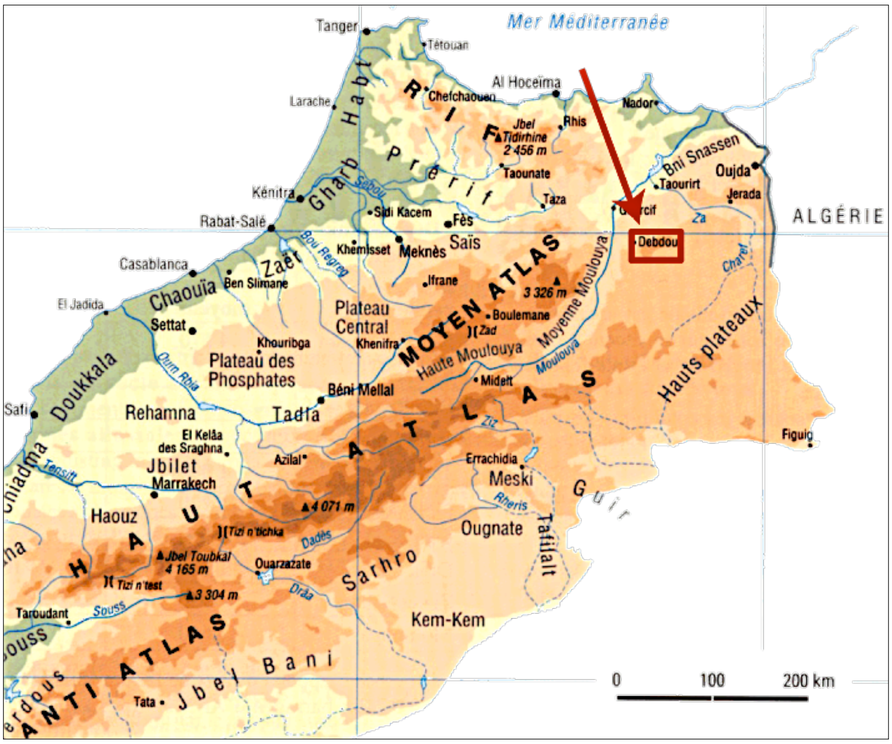

Figure 3.1. Location of the investigation area for the case study in Northeastern Morocco. The investigation area is marked by the red rectangle. Map source: Pigeonniere 2002

Vegetation It has to be stated, that inter-annual variability in precipitation is very high. Therefore, the actual climatic conditions vary heavily between years (see Figure 3.5 c).

However, the generally more favorable climatic conditions (compared to the surroundings) allow for the growth of evergreen Holm Oak (*Quercus rotundifolia* L.)[1] forests. On the steep slopes of the Gaada the Oaks are accompanied by *Pinus halepensis* Mill. (Aleppo Pine) and *Tetraclinis articulata* (Vahl) Masters (Gum Juniper). On the plateau, where most of the sampling was conducted, only *Juniperus oxycedrus* L. *ssp. oxycedrus* (Prickly Juniper) occurs with the Holm Oak. On the slopes these main species are accompanied by a variety of woody species growing as trees or shrubs (e.g. *Pistacia lentiscus* L. (Mastic), *Jasminum fruticans* L. (Jasmine Bush), *Rhamnus lycioides* L. (Buckthorn), *Phillyrea angustifolia* L. (mainly *ssp. intermedia*, Narrow-Leaved Phillyrea)).

Semi-nomadic pastoralism with sheep and goats is the primary anthropogenic influence. Owing to the favorable climatic conditions the herds can graze over a long period even when in regions further east on the plateau (Dahara) or in the western plains (Moulouya-Valley) fodder becomes sparse. Thus, there are tendencies to settlement because the nomads remain longer at the Gaada than elsewhere in the region (as long as conditions allow for effective grazing, Steinmann 1998). This leads to a relatively high grazing pressure. However, due to accessibility and preferences regarding tent sites, disturbance intensity and severity is not uniform throughout the investigation area. In addition to the pastoralists there are settlers who do mixed farming and gain additional income from growing cereals (rainfall-dependent agriculture), fruits and vegetables. Another important plant resource is Rosemary (*Rosmarinus officinalis* L.). It is exploited under supervision of the forest service for the distillation of oil which is sold worldwide for medicinal and cosmetic use. In summer several temporary distilleries supplement the stationary distilleries on the Gaada and in the Debdou valley and many people from elsewhere come to the region for a temporary job of 'harvesting' rosemary. Rosemary oil production is a considerable source of income for the Ministére Delegue des Eaux et Forets (Ministry of Water and Forestry, Bezzot pers. comm.).

Sampling design

Sampling grid A hierarchically nested, equidistant sampling grid covering three spatial scales was implemented in the Morocco study (see Jurasinski & Beierkuhnlein submitted-b, Appendix 2 for the background regarding equidistant sampling grids). Throughout the three years of fieldwork the grid has been developed and sampled to various extents (see Table 3.1 for an overview). The initial sampling grid as utilized in the first field period (2003) consisted of a regular array of 19 *large plots* and covered a total area of about 23.4 km^2 (see Fig. 3.2 for an explanation of the hierarchical nesting and the associated terminology). In the first year of fieldwork the variability of environmental conditions

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[1] The nomenclature of the plants follows Valdés et al. 2002

was fairly restricted since sampling only took place on the plateau at altitudes between 1550 and 1670 m. Therefore, bedrock as well as soil and climatic conditions were relatively constant (see Fig. A5.2 in Jurasinski & Beierkuhnlein submitted-a (Appendix 5) for the ranges of recorded predictor variables). Please note, that the nomenclature for the sampling units of the three scale levels changed during the study (large plots = Plots, plots = Sample-Plots, sub-plots=Sub-Plots). The grids on the largest scale (large plots) are called 'primary grid' in the following.

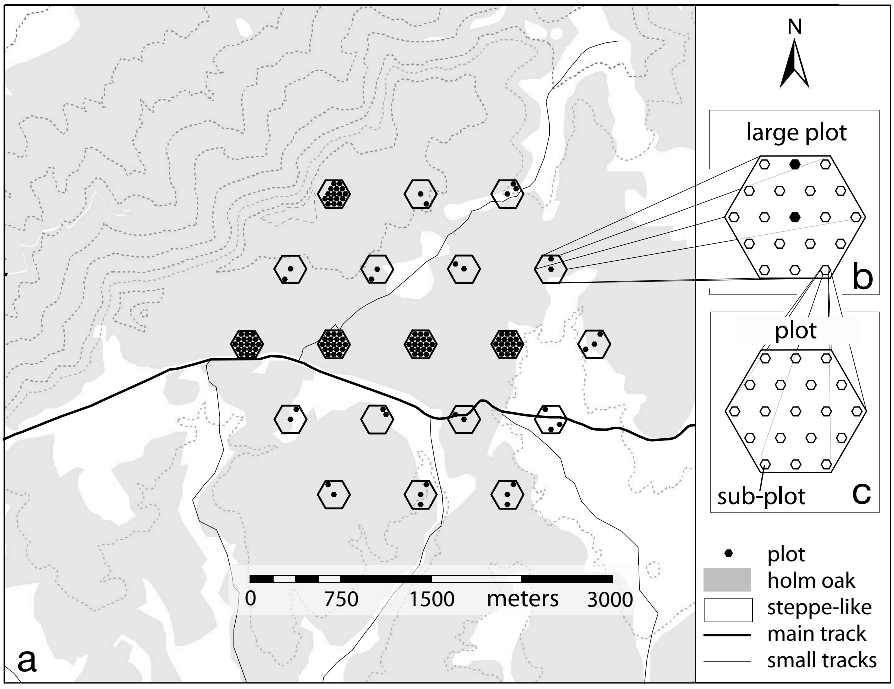

Figure 3.2. Equidistant hierarchically nested sampling grid as implemented in 2003. **a)** Geographical positions of *large plots* and sampled *plots* on the map. **b)** The 19 *large plots* which make up the primary grid each contain a regular grid of 19 *plots*: **c)** The *plots* contain again a regular grid of 19 *sub-plots*. Sampling took place on semi-randomly selected *plots* in each *large plot* (5 *large plots* were sampled completely) as well as on *sub-plots* within the *plots*. On one *plot* in each *large plot sub-plots* were sampled completely, on the others only partially. **Note**, that the terminology changed during the work: *large plot = Plot, plot = Sample-Plot, sub-plot = Sub-Plot*

Extension of the grid In 2004 the primary grid (*large plots*) was extended for two reasons. (1) Different distance levels ought to be implemented. Therfore further *large plots* were added in the center and at the margins of the initial grid. This resulted in three partially overlapping primary grids of 19 *large plots* with varying distance between neighboring *large plots*. Figure A5.1 (Appendix 5) explains this design in detail and shows the geographical positions of the plots sampled in 2004 on the map (distance level 2 represents the initial grid and areal extent as sampled in 2003). (2) A wider range of environmental gradients ought to be covered. This was realized through the extension of the grid to regions at the slopes of the Gaada (Figure A5.1, Jurasinski & Beierkuhnlein submitted-a). Altitudes now ranged between 1130 and 1670 m. Therefore the ranges of most of the recorded variables extended as well (see Figure A5.2, Appendix 5).

Sampled units In the first year of study the grid has been sampled two-fold (Figure 3.2): In some of the large plots the whole grid of plots has been sampled. In others data was only recorded on 2 to 3 semi-randomly chosen plots. Semi-random means that at first always the central plot was sampled and then further, randomly chosen plots. In 2004 plots were selected for sampling with a stratified random algorithm: 2 to 4 plots of each large plot have been chosen randomly for sampling depending on the number of plots which were already sampled in 2003. In the context of the presented thesis, the plot was the main level where sampling took place. However, for some analyses data from the plots was scaled up to provide information on the large-plot. Furthermore sub-plots were sampled by students acquiring data for their associated diploma thesis or term paper. A dismountable hexagonal frame was designed by the author and manufactured by the University workshop to facilitate data recording on this scale level (Figure 3.3). The implemented sampling schemes were developed together with the students depending on the specific research questions (see Lerche 2004, Gohlke 2006 for details).

Table 3.1. Overview over the units sampled during the course of the project. For further explanation see notes and text.

	sampling scale		
	large plot	plot	sub-plot
radius	120 m	8 m	0.6 m
area	3.74 ha	166 m^2	0.94 m^2
n in 2003	19	125	566 (205)[1]
n in 2004	43	143 (24)[2]	715
n in 2005	11	15[3]	285[4]

1) In 19 plots all 19 sub-plots have been sampled (n=361). In further 41 plots transects of 5 sub-plots were sampled (n=205).

2) 24 of the 143 plots were already sampled in 2003.

3) The 15 plots were sampled twice during the vegetation period.

4) The value results from 19 sub-plots sampled in each of the 15 plots. However, as these have been sampled three times during the vegetation period, the total number of sub-plots sampled in 2005 amounts to 855.

Recorded data

Vegetation On plot scale the presence of vascular plants was recorded, unknown species were collected for later determination. At the department of Biogeography in Bayreuth a comprehensive herbaria of the region was established throughout the last 30 years. It was used to identify critical species. For efficiency and in order to keep it simple, species abundance was not recorded. This means less but more reliable information because the estimation of abundance might be vulnerable to subjective errors (Tüxen 1972; Leps 1992). More exact approaches, such as the point quadrat method, are too time-consuming, especially for species with low abundance (Goodall 1952; Everson et al. 1990) which make up the majority of the species in the Morocco samples.

Environmental paramters At first visit a comprehensive description of the plot was denoted. The severity of disturbance was categorized based on hoof marks, feces of goats and sheep, grazing signs, fire scars and ash, and logging signs. These six parameters have been recorded as percentages. For aggregation the percentages were taken as values between 0 and 1 and simply added. So the maximal disturbance value is 6. In some of the analyses the distance to tracks and tents (using GIS) were additionally considered as disturbance parameters.. Slope aspect, slope inclination, elevation, and relief were denoted. The soil was classified with field methodology (see Jurasinski & Beierkuhnlein 2006 (Appendix 4) for details) and a soil sample was taken for later analysis of pH, CN ratio, and conductivity. The depth of the A horizon, soil type, stone and gravel content, presence of roots and humus, bulk density and topsoil texture were recorded as well (see Jurasinski & Beierkuhnlein submitted-a (Appendix 5) and Jurasinski & Beierkuhnlein submitted-b (Appendix 4) for details).

On plot and sub-plot scale features of the sampling units have been utilized to obtain quantitative and reproducible estimates of variables describing vegetation structure and disturbance. In hexagonal plots the ropes which are used to mark out the plot in the field can be used to assess quantitative data on cover (see Jurasinski & Beierkuhnlein submitted-b, Appendix 2; Jurasinski & Beierkuhnlein 2006, Appendix 3)

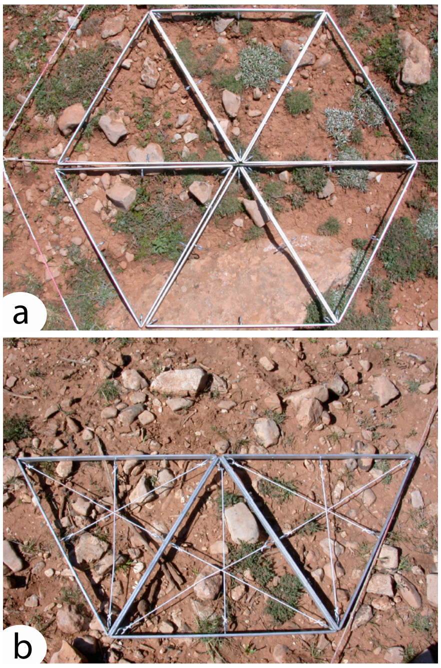

Figure 3.3. Aluminium-frame for data recording on sub-plot scale. **a)** The dismountable frame consists of 6 equilateral triangles. **b)** The equilateral triangles can be further divided with rubber straps to allow for a finer resolution of frequency values.

The line intercept method has been implemented on the marking ropes to assess data on the cover of bushes, trees and *Asphodelus microcarpus* DC. as well as on the proportion of bare soil and stones (for the reasons regarding the consideration of *Asphodelus* cover see Jurasinski & Beierkuhnlein 2006, Appendix 3). In 2003 extensive, detailed sketches of the position and cover of bushes, trees and other features have been made. The cover values obtained from these drawings were then compared to the cover values based on the line intercept recording to evaluate the quality of the line intercept recordings (see Jurasinski & Beierkuhnlein 2006, Appendix 3). On sub-plot scale the segmentation of the sampling frame (Figure 3.3 b) was used to obtain frequencies of parameters describing structure and disturbance parameters as e.g. cover of bushes, bare soil, and feces of animals (Lerche 2004; Gohlke 2006).

General Results

During the three years of fieldwork a total of 366 species have been recorded on 244 plots (complete species list in Appendix 8). Some plots have been sampled repeatedly. Therefore the number of sampled plots amounts to 298 when each sampling time is taken into account separately (see Table 3.1). Three plots sampled in 2004 have been omitted from all further analyses as they were situated in or very close to an episodic lake. The lake just has retracted before sampling and thus this plots contained almost no species (see Jurasinski & Beierkuhnlein submitted-a, Appendix 5). The inclusion would have caused compositional similarity between these and all other plots to be very low and not comparable to the other data. Thus, data from 241 plots (295 sample dates) is used in the analyses. However, rarely all data has been analyzed together because subsets have been investigated in the light of different questions.

Of the total inventory diversity, 11 species are woody, growing mainly as trees in their adult phase. Most of these only occur on the slopes of the Gaada with the exceptions of *Quercus rotundifolia* L. and *Juncus oxycederus* ssp. *oxycedrus* L. which make up the shrub and tree layers on the plateau. Throughout all field periods average inventory diversity per plot amounts to approximately 81 species (76±14 in 2003, 84±15 in 2004, 91±12 in 2005). The overall maximum species number per plot is 112, the minimum species number equals 39. About half of the species can be considered as rare (recorded on less than 20 plots) whereas a third is very rare (recorded on less than 10 plots) throughout the area. This corresponds to general ecological theory regarding the distribution of species in samples (Preston 1948; Harte et al. 1999, see also species frequency distribution curves in Jurasinski & Retzer in prep., Appendix 6). Total inventory diversity varies from year to year. This is not surprising when regarding the different numbers of plots being sampled (Table 3.1). However, a relatively large fraction was recorded in 2004 only (Figure 3.4). This may be mainly be attributed to the extension of the sampling area to the slopes of the Gaada and to totally wood-free, open steppe-like areas on the plateau.

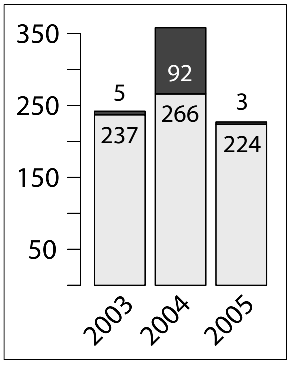

Figure 3.4. Total inventory diversity for the three field campaigns in Northeastern Morocco Height of bars = number of species recorded in respective year. Lower part denotes the number of species also recorded in other years (light grey), the upper, black ,part represents the number of species found exclusively in that year.

This also extended the ranges of the environmental variables, which before were relatively narrow (distance level 1 and 2 in Figure A5.2, Jurasinski & Beierkuhnlein submitted-a). This holds especially for pH, altitude and slope inclination. Climatic conditions varied considerably between years with 2005 being much warmer and drier than the years before. The year 2004 has been the wettest and coldest during the field work. For more climate data see Appendix 9.

Discussion

Species Almost 100 species (92) were recorded exclusively in 2004. One reason for this can be seen in the expansion of the investigation area which now comprised parts of the slopes down to debdou valley: Many of the adventitious species were encountered there which indicates the difference in vegetation. Furthermore a large amount of those species belong to steppe vegetation and were encountered on plots close to agriculture further to the Southeast in direction of the Dahara. Another reason might be the increasing knowledge about the species on the Gaada, and some did simply not occur in 2003. A reason for the latter could also be the continuing good climatic situation. From 2002 to 2004 the precipitation increased each year. This can be reproduced with the data recorded by the climate-loggers which were installed throughout the investigation area as well as with the precipitation data of the station Ayn el Kbira (Figure 3.5 and Appendix 9).

Considering the fact that the 366 species have been recorded in the field layer on a total area of approximately 4 ha (resulting from 241 plots with about 166 m^2 each) Total inventory diversity is relatively high. This is in accordance with the literature (Naveh, Zev & Whittaker 1979; Lavorel & Richardson 1999; Osem et al. 2002). However, also rare species have been encountered. Regardless of the relatively high grazing pressure, two Orchid species (*Orchis langei* Richter and *Ophrys tenthredinifera* Willd.) have been recorded. They were found in 2004 each on one single plot with 3-4 individuals inside humble oak bushes (*Quercus rotundifolia* L.). *Fritillaria lusitanica* Wikstr. ssp. *lusitanica* was also quite rare. All these species do not have special adaptations or protections against grazing and spoil disturbance and all individuals were encountered only within protecting shrubs.

The probability to find such rare species with a preferential sampling design tends to zero. Comparably Beierkuhnlein (1999) reports high species numbers from grid based sampling. In a study focussing on spatial pattern of forest vegetation on landscape scale the author encountered that the number of species recorded was higher than it could be expected. On 0,04% of the area covered by a German topographical map sheet (1:25.000) more than 60% of the plant species of the whole map sheet was found. This illustrates that systematic sampling designs enable to detect a large portion of the species richness with a comparatively low intensity survey. Accordingly Palmer & White (1994) "believe that, in general, the probability of encountering unusual microsites (of any sort) […] is close to unity" when sampling systematically. They come to this conclusion in an extensive study on the influence of scale on species richness through sampling on differently sized plots arranged in a square grid.

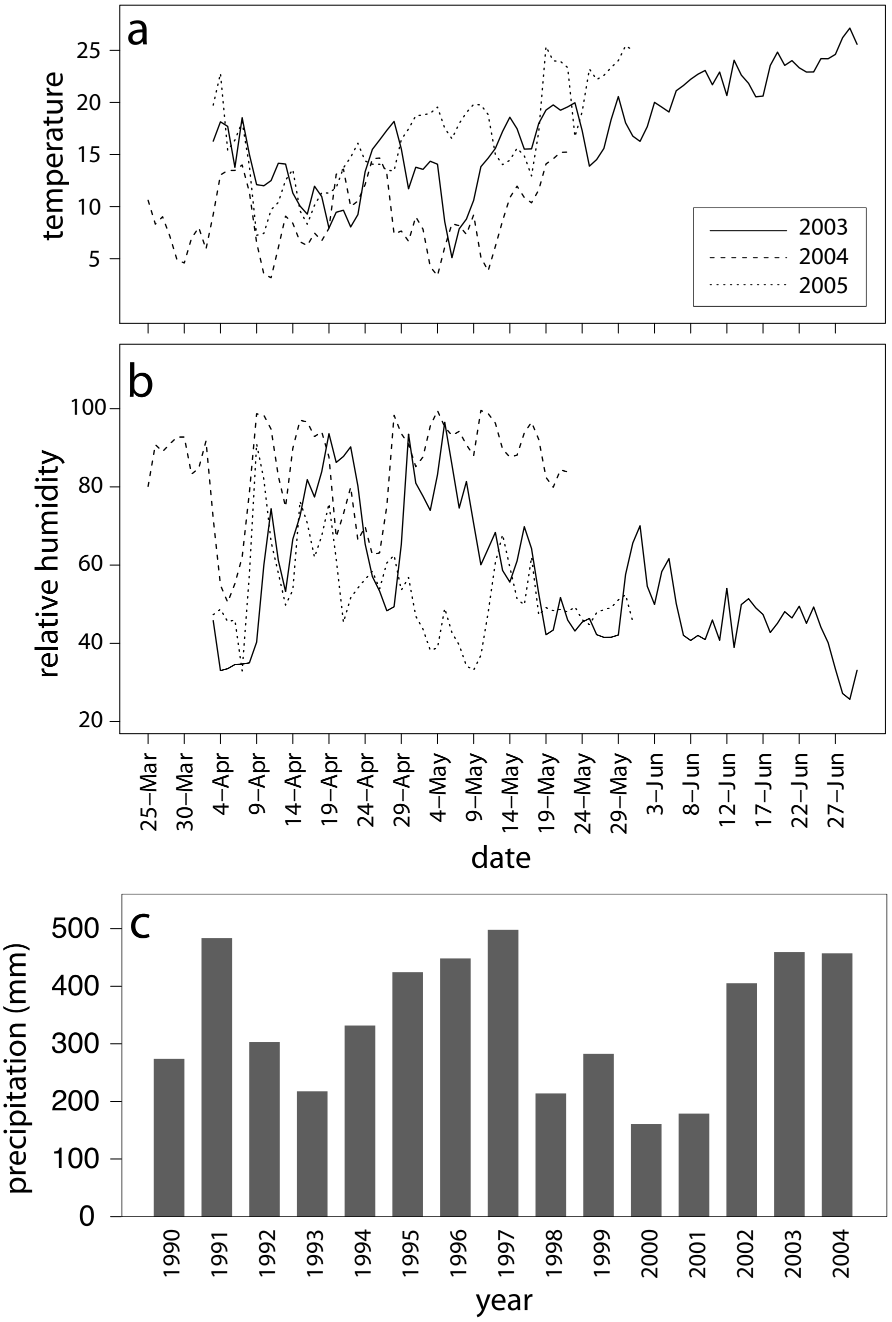

Figure 3.5. Climate data. **a-b)** Logger-data (daily averages from 4 loggers distributed throughout the investigation area) for the three years of field work (see legend).The loggers have been installed for different time spans covering the time of the field periods. **a)** Temperature. **b)** Relative humidity. Values above 90 indicate precipitation (rain and fog). **c)** Annual sums of precipitation from 1990 - 2004 (Data from the Forestry Ayn El Kbira, no recordings available for 2005).

Generally, the species recorded on the Gaada can be divided into three groups regarding the frequency of occurrence. (1) Species, which occur very frequent throughout the investigation area and can be found on the majority of the plots (e.g. *Erodium cicutarium* (L.) L'Her, *Medicago minima* (L.) Barthal, *Picnomon acarna* (L.) Cass.). (2) Species whith a medium chance of occurrence (e.g. *Brachyapium pomelianum* Maire, *Galium parisiense* L., *Carduncellus pinnatus* (Desf.) DC. which are often bound to certain structural features or perturbations. For example is *Carduncellus pinnatus* very tolerant against hoof tread. Contrarily *Brachyapium pomelianum* and *Galium parisiense* predominantly grow in the shelter of bushes or shrubs. (3) This group of species is relatively large. Its representatives can only be found on few to very few of the plots. Among these are many species which only have been recorded in 2004. This is due to the fact that they grow on the slopes of the Gaada. Some examples are *Melica uniflora* Retz., *Leuzea conifera* DC., *Verbascum sinuatum* L., *Urginea maritima* (L.) Baker and - apparently closely tied to the edge of the Plateau - *Crupina crupinastrum* (Moris) Vis..

The high inventory diversity on the plots is astonishing in face of the relatively high grazing pressure. However, most species only low abundances thus competition for space is low. Available space and resources can be used by stress tolerators which are able to cope with the harsh conditions (Sax 2002; Casado et al. 2004). Also geophytes with narrow leaves and adapted phenology are quite common. Noy-Meir & Oron (2001) found, that they might even be supported by grazing. However, if vegetation structure is more heterogeneous, more species find their niche. A linear multiple regression with backward selection of the environmental variables against the number of species reveals that the best model predicting species richness often contains all structural variables but *Asphodelus* cover (Table 3.2).

Table 3.2. Models and model parameters of linear multiple regression for subsets of the data[1] and all plot data together, explaining the species richness on the plots. Although different models result depending on data subset it is apparent that the structural variables, especially tree and bush cover are important predictors for inventory diversity on the plots.

All data from all years combined:
best model (only significant predictors, $R^2_{adj}= 0.36$, $P < 0.001$)
n.spec ~ altitude*** + conductivity*** + bush cover*** + tree cover** + bare soil*** + stones*** + disturbance1***

2003
best model (only significant predictors, $R^2_{adj}= 0.40$, $P < 0.001$)
n.spec ~ fine roots*** + bush cover*** + tree cover*** + stones**

2004
best model (only significant predictors, $R^2_{adj}= 0.49$, $P < 0.001$)
n.spec ~ altitude*** + slope* + bush cover*** + soil cover** + stones***

[1]) Data of 2005 was not considered separately because there were not enough datapoints compared to the number of variables. However 2005 data is included in 'All data'.

Environment The variability in the sampled environmental parameters is relatively low (Figure A5.2, Jurasinski & Beierkuhnlein submitted-a). Especially pH and conductivity exhibited very narrow ranges. For all environmental variables ranges increased by extending the sampling grid (in 2004). The primary aim of the extension was to obtain several distance levels (see Jurasinski & Beierkuhnlein submitted-a, Appendix 4).

However, different gradient lengths resulted as well. This increased the interpretability of the findings related to distance decay and non-stationarity (ibid.). Given results of Duque et al. (2002) and Jones et al. (2006) as well as own findings (Appendix 4) the primary intention to keep certain environmental variables relatively stable seems questionable. The longer the gradients covered, the more likely are significant relationships. To a certain part this might be of pure mathematical reason. However, only when long gradients are covered the importance of variables can be evaluated reliably (see Jurasinski & Beierkuhnlein submitted-a, Appendix 5).

Spatial patterns of biodiversity - assessing vegetation using hexagonal grids

Methodological issues of sampling vegetation with hexagonal grids are evaluated and discussed in Jurasinski & Beierkuhnlein (2006). The questions investigated in this contribution are if frequency data is better suited to describe patterns than presence/ absence data, and whether the hexagonal plot can serve as an efficient tool to assess reliable quantitative data on vegetation structure. Please refer to the original publication which is given in **Appendix 4** for details.

Distance decay and non-stationarity in a semi-arid Mediterranean ecosystem

Questions of distance decay and non-stationarity in the Mediterranean Ecosystem investigated in Northeastern Morocco are investigated in Jurasinski & Beierkuhnlein (submitted-a). The decrease of compositional similarity with distance and the change in the relation between species composition and environmental drivers is evaluated. Special focus is on disturbances as an important factor in the investigated ecosystem. See **Appendix 5** for the text of the original manuscript.

3.2 Homogenization of Alpine summits

Introduction

In the general context of the research project (DFG Be 2192/5-1,2,3) a heterogeneity concept was developed (see also Jurasinski & Retzer in prep., Appendix 3) and applied to compare subsets of the data and different structural types (see also Gohlke 2006). Furthermore, it has been adapted to another data set to test its power regarding the examination and understanding of current ecological key questions. Although developed for regular grids, the heterogeneity concept can be utilized also on irregularly spaced sampling units. In this case spatial auto-correlation may overlay relations between species composition and environmental variables. However, as the comparison of heterogeneity at different points in time is in focus it is not important how much of it is explained by spatial configuration and how much by environmental parameters. The spatial configuration is not changing which suggests that any detected change is very likely caused by altered environmental conditions alone.

Swiss Alps - Summits of the Bernina region

The data set was assembled by Walther et al. (2005). They resurveyed mountain summits which had been studied prior to 1907 (Rübel 1912) and in 1985 (Hofer 1992) and investigated whether an upward shift of plants caused by climate warming can be detected. This analysis included ten summits of the Bernina Group in the Swiss Alps which were among a set of summits well investigated by the originators of European plant sociology as Rübel and Braun-Blanquet (Rübel 1912; Braun-Blanquet 1955). The geographical position of the Bernina region is marked in Figure 3.6, the actual positions of the single summits are shown in Figure A6.4 (Jurasinski & Kreyling accepted, App. 6).

Thanks to the resurvey of Walther et al. (2005) data from three time steps were available. This allowed for an evaluation of temporal trends. Generally such appropriate long-term data sets are sparse as most long-term data covers only two points in time (Walther, pers. comm.). In all three surveys, the uppermost 10m of each summit was searched in detail and the presence of vascular plant species was recorded. One exception was Piz Languard where 30m was searched (for details see Walther et al. 2005). Because of its temporal resolution the data was apparently useful to test the heterogeneity concept. The analysis largely relied on the species lists and further information provided by Walter et al. (2005). Additionally a digital map has been retrieved from the internet (http://www.swisstopo.ch) and a coarse representation of the region was digitized (valleys and ridges, positions of the summits) to enable a discussion of the results in the actual geographic context (for details see Appendix 6, especially Figure A6.4).

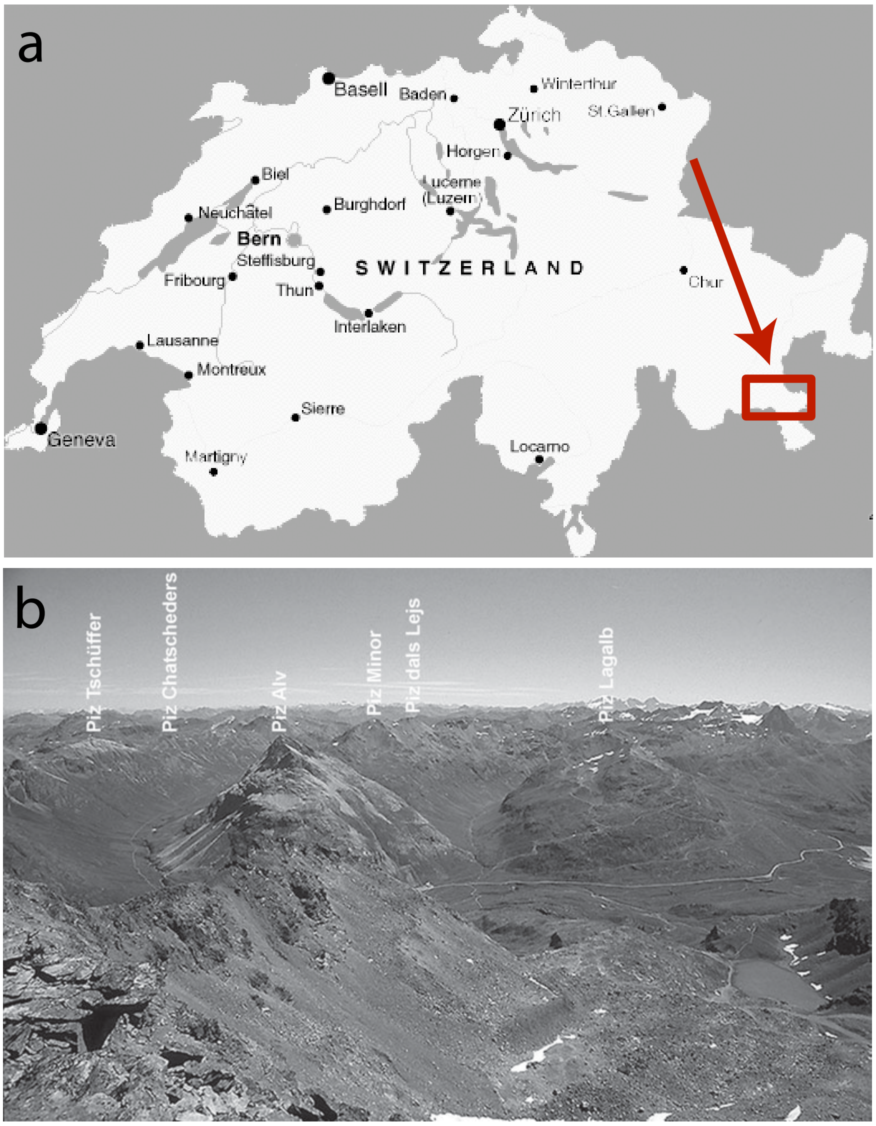

Figure 3.6. a) Location of the Bernina region in canton Graubünden in Switzerland. Swiss map adapted from www.capexil.com/swiss/ **b)** Subset of the investigated mountain summits in the Bernina region as seen from Munt Pers (3207 m, from Walther et al. 2005)

Upward shift of alpine plants and homogenization of mountain summits.

Homogenization of Alpine summits due to the upward shift of plants has been addressed in Jurasinski & Kreyling (accepted). In the context of the thesis this contribution stands for the application of the concept of spatial heterogeneity to a current ecological research question which receives considerable attention with regard to the discussion about global warming. See **Appendix 6** for the original manuscript.

4 Summarizing Discussion

4.1 Conceptional issues

Sampling Design

Theoretical and conceptional issues regarding the implemented sampling design are intensively discussed in Jurasinski & Beierkuhnlein submitted-b (Appendix 2). Because of the modifiable area unit problem (MAUP, Openshaw & Taylor 1979) it is not trivial to determine a proper grain (cell size) and extent (distance between cells, or in a continuous array the number of left out cells between sampled cells). Possible solutions are pre-investigations with cyclic sampling in transects in different directions and test samplings with different plot sizes to obtain species accumulation curves. But it remains a catch 22 problem: To examine a proper distance one has to know a proper plot area which can only be determined reliably when the 'appropriate' distance has been determined. Usually one would first determine the size of the plots with species area curves. Then, cyclic sampling for the determination of the grid extent would follow (Jurasinski & Beierkuhnlein submitted-b, Appendix 2). This approach was e.g. used by Rettenmaier (2004).

However, this does not prevent from finding the 'wrong' pattern. The species area curve approach is a method of the classical vegetation ecology (Mueller-Dombois & Ellenberg 1974; Dierschke 1994; Frey & Lösch 2004) and its ultimate goal is the determination of a plot size allowing for the sampling of vegetation to determine plant sociological associations (van der Maarel 1982; van der Maarel 2005). If patterns on a higher scale (and organizational) level are addressed, a plot size incorporating the variation of plant sociological association might be too large (or too small). As the relationships between ecological response (species composition or other parameters of interest) and predicting variables (whatever is under study) will most likely vary with scale in every field study (Reed et al. 1993; Dale et al. 2002; Wagner 2003), the question arises, which relationship is most important on which scale. In most cases this will not be known beforehand and a determination according to ecological common sense might fail. Therefore a hierarchically nested approach is suggested in Jurasinski & Beierkuhnlein submitted-b (Appendix 2) and applied in the Morocco case study. This allows for the evaluation of relationships on different scale levels (Jurasinski & Beierkuhnlein submitted-a, Appendix 4) but increases sampling effort considerably. Therefore the thorough recording on different scales is often bound to methodological work (Palmer & White 1994; Stohlgren et al. 1997) and rarely implemented in conservation monitoring or general ecological research (but see e.g. Lennon et al. 2001; Gering et al. 2003).

Due to the hierarchical nesting, the sampling grids as implemented in 2004, contain a total of 16383 potential sampling locations (15523 sub-plots, 817 plots, and 43 large plots). It is impossible to sample them completely. Therefore, only parts of the grid have been sampled entirely on all levels (i.e. all plots in a large plot and all sub-plots in a plot) to enable the analysis of spatial patterns at these scales. Elsewhere only randomly chosen plots inside the bigger units have been sampled. Thus, the advantages of equidistant sampling units (no spatial auto-correlation, see Jurasinski & Beierkuhnlein 2006; Jurasinski & Beierkuhnlein submitted-b, Appendices 3 and 2) could be combined with a thorough analysis regarding the influence of scale. With the implemented sampling design different issues regarding spatial patterns of phytodiversity have been addressed. And there are still interesting questions which not have been touched yet but can and will be investigated with these data (see Chapter 4.4).

Alternatives to 'beta'

A new terminology for the assessment and measurement of diversity is developed in Jurasinski et al. (submitted, Appendix 1). From the beginning, the concept 'beta-diversity' was at the heart of this thesis (namely in the notion of differentiation). When an anonymous reviewer returned a submitted manuscript stating that "… beta-diversity is such a nebulous and difficult concept …", it became obvious that clarification is needed. The ambiguity of Whittaker's definition (1960; 1972) might have caused such perceptions and the confusion around 'beta-diversity' (Jurasinski et al. submitted). On the other hand Whittaker (1960; 1972) was very clear with 'alpha' and 'gamma' which both describe the same quality of diversity but on different scale levels. The concept proposed in Jurasinski et al. (Appendix 1) takes the opposite direction suggesting one term for the similar meanings 'alpha' and 'gamma' (inventory diversity) and splitting 'beta' according to the general question whether the utilized coefficients preserve species identity or not (differentiation and proportional diversity, Jurasinski et al. submitted) because this distinction is crucial. Discussions about clear terminology are necessary and can yield a better understanding and therefore drive scientific progress.

Multi-plot similarity

In Jurasinski & Retzer (in prep., Appendix 3) a new coefficient for the measurement of similarity is proposed. It is the first to take species identity into account when calculating the differentiation diversity between one and many plots. Therefore it can be seen as 'ordination on the spot', especially when not the similarity to the direct neighbors but the similarity to all other plots in the data set is calculated. It is to be noted that the latter is subject to the problem of distance decay because more distant plots are likely to be less similar. However it remains a method with interesting possibilities, especially for nature conservation and biodiversity assessment. The coefficient of multi-plot similarity allows for the identification of hotspots of dissimilarity even on small scales. Under modern process oriented paradigms of conservation (see e.g. Berger 2003; Opdam & Wascher 2004; Whittaker et al. 2005) it can be an interesting tool to evaluate regions regarding their suitabilty as nature reserves and to monitor conservation success.

4.2 Methodological issues

Structure assessment

The hexagonal plot provides for a reliable and efficient assessment of vegetation structure (Jurasinski & Beierkuhnlein 2006 (Appendix 4), see also Rettenmaier 2004). However, this alone is not a strong argument for hexagonal sampling units, because in square or rectangular plots lines can be drawn as well to intersect the plot and to record data with the line intercept method (e.g. Lee et al. 1997; Schmiedinger & Beierkuhnlein 2004). But in the square or rectangular case they have to be installed additionally. Anyway, this is only one aspect. More interesting is the combination of features: The hexagonal plot features a lower perimeter area ratio, it is easily to be marked out beginning from the center, offers a good option to assess structural features, and fits into the equidistant grid. Therefore it offers interesting possibilities for sampling the spatial variation in phytodiversity.

Frequency vs. abundance data

It has been shown, that resemblance values calculated from frequency data differ only slightly from those based on presence/absence data (Jurasinski & Beierkuhnlein 2006, Appendix 4). For a great part this is due to mathematical implementation. The smaller the variation in the sampled abundance or frequency data the closer related are the similarities based on presence/absence and abundance or frequency data. This can easily be tested empirically. For instance with the aggregated frequency data from plots where all sub-plots have been sampled. When the (dis)similarity between all possible pairs of plots (49 plots result in 1176 pairs) is calculated based on presence/absence data derived from the pure plot data as well as based on the frequency data the Pearson product moment correlation between the resulting matrices amounts to -0.886. When the range of frequencies is artificially decreased from the initial 19 classes (based on 19 sub-plots) and dissimilarity and correlation are recalculated r equals -0.913 (10 classes), -0.933 (7 classes), -0.950 (5 classes), and -0.960 (4 classes) respectively. This means, that the higher the resolution of the frequency (or abundance) data, the more the results of the two methods might differ.

Campbell (1978) that quantitative data may increase the ability of differentiation of phytosociological data when the variation in species occurrence is low (see also Williams et al. 1973). However, when the differences in species composition are only of quantitative nature qualitative indices will fail. Especially when the classification into associations is intended quantitative data might be more appropriate. However, this was not the aim in the present case. In the investigated Mediterranean ecosystem (Northeastern Morocco) estimating abundances would be prone to errors because most species occur with low abundances and are rather small. In this case frequency data might offer a good compromise between the reproduction of the variation in species composition and the required sampling effort. Frequency data showed a slightly higher correlation to vegetation structure than presence/absence data (Jurasinski & Beierkuhnlein 2006, Appendix 4). Nevertheless, frequency does not measure abundance because plants are usually contagiously distributed (Greig-Smith 1983). Therefore it rather gives information on the uniformity of distribution (Mueller-Dombois & Ellenberg 1974). Thus, it is useful in the Morocco case, because it describes whether relatively randomly distributed species occur in all triangles or only in some. This in turn might be based on certain disturbances or structural configurations of the plot. Presumably the correlation between compositional similarity and the distance of environmental variables could even be improved with a higher resolution of frequencies. However, this would have increased sampling effort as well.

Disturbance classification

The issues accompanying the disturbance classification are discussed in Jurasinski & Beierkuhnlein (submitted-a, Appendix 5). Generally it is difficult to obtain a standardized disturbance classification. However, as long as no reliable or easily accessible data on land use and disturbances exist, the utilization of feces counts, hoof marks and grazing signs have to be used as proxies. The definition of reproducible disturbance categories which than can be taken as dummy variables into the analysis might be an alternative solution (Buhk et al. submitted), but its application will largely be reserved to ‘organized’ and ‘planned’ landscapes were such data is readily available. In large scale studies remote sensing data might offer an interesting possibility to classify disturbance regimes spatially (Carmel & Kadmon 1999) but such data are rarely available. Thus, exclosures might be the most appropriate way to study the effect of disturbances in terms of grazing on vegetation (see e.g. in Stohlgren et al. 1999; Osem et al. 2002; Pakeman et al. 2003; Retzer 2007). However, results have to be interpreted cautiously because other variables might change as well when exclosures are set up (e.g. insect herbivory, insect reproduction, changing of dispersal regime due to then changing (insects) and missing (grazers) dispersers…).

4.3 Empirical results

In the following, the central information of the hypotheses from Chapter 1.3 is repeated before the respective paragraphs to recall the origin of the questions and to enable an easier contextualization.

Distance decay

(1) Similarity in plant species composition decreases continuously with distance. Due to the small scale of the study the rate of distance decay will be relatively low compared to large scale studies

In the Morocco case study similarity decreases relatively fast with distance (Jurasinski & Beierkuhnlein submitted-a, Appendix 4) which leads to the rejection of the second part of hypothesis 1. Furthermore the decay is not homogeneous with distance. In related studies researchers often sought to find a proper regression model which best describes the distance decay relation (ibid.). Large scale studies most often identified the model with log-similarity as the most appropriate (e.g. Qian et al. 1998; Nekola & White 1999; Qian et al. 2005) whereas the model with log-distance often performed best with data from medium scales and from the Tropics (e.g. Condit et al. 2002; Phillips et al. 2003; Jones et al. 2006). The mutual validity of niche-based processes, spatial configuration, and dispersal is also emphasized by Soininen et al. (2007) who conducted a quantitative meta-analysis of distance decay relationship across organisms and environments.

Soininen et al. (2007) use the halving distance, that is, the distance at which the initial similarity value is halved, instead of the slope, to compare different distance decay relationships with each other. The advantage is, that it can be calculated for any type of regression. They state that a high halving distance refers to a slow turnover in species composition. Thus it measures the scale dependency of differentiation diversity. Accordingly, it is apparent from the Morocco data that relationships heavily depend on scale. If sampling is constrained to one of the distance levels only, the slope changes (which would also cause different halving distances). The enlargement of the investigation area in 2004 led to an increase in the ranges of altitude (Jurasinski & Beierkuhnlein submitted-a, Appendix 4). Thus, the increase in scale dependency of the differentiation diversity with the inclusion of different scale levels supports the long known clear relations between altitude and species composition (Beals 1984).

Usually linear regressions are relatively rough approximations of distance decay relationships, and the fits are not very good (e.g. Nekola & White 1999; Condit et al. 2002; Jones et al. 2006). When compared to spline regressions it is apparent, that often the decline is much more pronounced for the very short distances (Figure A5.5 in Jurasinski & Beierkuhnlein (submitted-a, Appendix 5); see also Jones et al. 2006). This leads to the suggestion, that it might be a general characteristic of distance decay, that the log-distance model is most appropriate for short distances, followed by a regression model with untransformed distance and similarity for medium distances which is replaced by a model with log-similarity for very large distances. According to the ongoing discussion of dispersal based versus niche based community assembly (e.g. Hubbell 2001; Condit et al. 2002; Svenning & Skov 2002; Chust et al. 2006; Steinitz et al. 2006) a generalized model would presumably include both. Therefore fat-tailed dispersal kernels fit better to field data from small to medium scale studies and neutral models alone are implausible (Chave & Leigh 2002). Furthermore, the patterns of distance decay observed in large scale studies (Nekola & White 1999; Condit et al. 2002; Chust et al. 2006) reflect niche differentiation due to specific traits of species and environmental heterogeneity.

The fast decay for short distances is found in all data subsets of the Morocco data. This is relatively surprising because sheep and goats are known to excessively contribute to dispersal (e.g. Shmida & Ellner 1983; Fischer et al. 1996; Osem et al. 2002; Couvreur et al. 2004). The different dispersal strategies of the plants as well as the grazing patterns defined by the migration of the nomads might contribute to this fast distance decay under relatively constant environmental conditions. The ranges of environmental variables are much smaller when only distance levels 1 and 2 are taken into account compared to the whole data set (Figure A5.2 in Jurasinski & Beierkuhnlein submitted-a, Appendix 5). The niches are rather defined by disturbance and the ability of the plant species to tolerate stress and harsh conditions than by abiotic environmental constraints. Due to the structural configuration of the trees and bushes the micro-climatic and disturbance conditions show a high variability which increases species richness on structurally variable plots.

Non-stationarity

(2) Correlation between compositional similarity of vegetation and the dissimilarity of predictor variables is likely changing with geographical distance between plots.

The correlation between species compositional similarity and the dissimilarity of predictor variables is indeed changing with scale (Jurasinski & Beierkuhnlein submitted-a, Appendix 5). This is called non-stationarity (Legendre & Legendre 1998; Wagner 2004; Wagner & Fortin 2005) and has been found in recent studies elsewhere as well (e.g. Foody 2004). Based on the insight that space matters, methods are proposed to account for the variation in the data which is caused by the spatial configuration of sampling units (Borcard & Legendre 2002; Lichstein et al. 2002; Dray et al. 2006). Although space as such explains very little, this makes sense because space can be understood as a surrogate for all variables not measured explicitly. Directional correlograms, as suggested by Oden &

Sokal (1986) might support the identification of hidden relations which in turn can help to reveal the variables and processes behind. A further publication addressing issues of anisotropy and directional differences is in preparation.

The presented data and analyses also support the finding that the correlation increases when the sampled environmental gradient is longer (e.g. Jones et al. 2006; Jurasinski & Beierkuhnlein submitted-a, Appendix 5). Beals (1984) formulated it the other way around: "As environmental distance increases, sociological distance becomes less sensitive to environmental differences". Thus, we should aim to cover the largest possible gradient when the relationship between species compositional patterns and driving variables is under study.

Disturbance

(3) Disturbance is the main driver of vegetation patterns in the regarded transitional ecosystem.

Disturbance drives pattern (Lavorel & Richardson 1999). Especially in Mediterranean communities (Naveh 1975; Osem et al. 2004). However, the magnitude of the contribution clearly depends on spatial scale. On smaller scales, Lerche (2004) found a relatively strong correlation between disturbance and species composition even though the results were inconsistent throughout the investigation area. On plot scale, the correlation is higher when more plots are included and when the sampling covers a larger extent (Table A5.2 in Jurasinski & Beierkuhnlein submitted-a, Appendix 5).

If the relatively deficient disturbance classification is taken alone (variable 'disturbance 1' in Table A5.2) relations are lower in most cases than with the variable 'disturbance 2', which incorporates the distances to tracks, tents and the road as an indicator of disturbance regime. The closer a plot is located to these, the more often the herds will come along. Especially the distance to tents seems to be a good estimator, as the nomads always walk in circles around their homes.

The problems with the disturbance classification in the field have already been discussed above. It is to add that the sampled vegetation structure is formed by former disturbances. When trees are cut, there is often heavy resprout (Keeley 1992, Keeley et al. 2005, Lloret et al. 2004), which, in concert with heavy grazing, leads to dense dwarf shrubs. If grazing pressure is lower, less dense shrub vegetation results. The actual vegetation structure can therefore be seen as an integrating variable describing the past and actual disturbance regime (Jurasinski & Beierkuhnlein submitted-a, Appendix 5) and can be included into the analysis through the characterization of vegetation structure. However, it is to admit that this involves the risk of circular arguments, especially when the whole vegetation is taken as the response, and not only the field layer like in the present case.

Homogenization

(6) The upward shift oft mountain plants due to climate warming leads to a homogenization of Alpine summits.

This hypothesis has been confirmed by the analysis in Jurasinski & Kreyling (accepted, Appendix 6). Nevertheless it is to emphasize that the general pattern is accompanied by individual developments on single summits. This is not surprising, because historical issues, dispersal pathways and vector characteristics might play an important role as well (ibid.). After all, it is very likely, that homogenization due to climate warming occurs. In the actual debate about climate change the homogenization in species composition of Alpine summits will not be of major concern to the public. But these summits can serve as a model for other, less geographically distinct ecosystems (Walther, et al. 2005a), and they show that differentiation diversity might being lost when inventory diversity is increasing. When biodiversity is more than species richness (UNEP 1992, Beierkuhnlein 1999) this has important implications for nature conservation and future adaptations to climate change and it would be very interesting to know if this happens in other ecosystems as well. Therefore, long-time monitoring sites are an indispensible prerequisite (Kullman 2002; Cousins 2004).

In the context of this work it is even more interesting that the concept of spatial heterogeneity can be applied to recent ecological questions. In an upcoming paper which will be based on Gohlke (2006) and further data from plot scale level, it will be shown that it can be of use not only for temporal comparisons but for spatial comparisons as well. The variation of the similarities calculated between a focal plot and its neighbors or other plots in the data set does explain spatial heterogeneity of differentiation diversity and might therefore be a valuable tool in conservation monitoring and success control (although it is not a measure of differentiation diversity, see Jurasinski & Retzer (in prep., Appendix 3) as well as Legendre et al. 2005).

4.4 Conclusions and Outlook

The loss of biodiversity calls our attention and drives our research. Land-use change and global warming in concert increasingly change the face of this planet. On the other hand might diversity be the best insurance for our ecosystems. Therefore it is paramount to provide methodologies with which biodiversity can be assessed and evaluated comprehensively. The different analyses introduced in the present thesis show that hierarchically nested, equidistant sampling grids allow for a detailed evaluation of different aspects of biotic diversity on landscape scale.

The importance of drivers of ecological pattern can only be assessed when multiple scales are taken into account. Biogeographical and vegetation ecological analyses should therefore be always spatially and temporally explicit and cover multiple scales. The analysis of the spatial and temporal variation in the relationships between processes and patterns caused by these processes is an important tool to better understand ecological phenomena.

The developed coefficients of multi-plot similarity and spatial heterogeneity can be valuable tools in conservation planning and monitoring as well as in ecological research, for instance when the change of diversity under climate change is addressed. The latter has been applied to investigate the upward shift of Alpine plants as a cause for homogenization of summits and the performance of the first was found to be superior compared to similar coefficients regarding the detection of gradients and hotspots in species composition. For the future it is planned to test these coefficients with further field data to evaluate their usability in a general context.

Based on the multi-scale characteristics of the Morocco data, further questions, as the temporal variation of spatial patterns, the reliability and scalability of data from lower scale levels to provide information on higher scales, as well as the directional variation of the relations between predictor variables and the vegetational response are already investigated and will be addressed in upcoming publications.

The R package *simba* for the calculation and analysis of similarity which results from the work on the this thesis, provided the basis for most of the data processing and analysis. It is released to the public domain and can be a useful tool for other ecologists working on differentiation diversity and patterns in space and time.

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Appendices

Appendix 1 Inventory, differentiation, and proportional diversity – a consistent terminology for quantifying biodiversity. *Oikos* (submitted)

*Jurasinski, Gerald (gerald.jurasinski@uni-bayreuth.de); Retzer, Vroni (vroni.retzer@uni-bayreuth.de); Beierkuhnlein Carl (carl.beierkuhnlein@uni-bayreuth.de)

Address (all authors):
Biogeography, School of Biology, Chemistry and Earth Sciences, University of Bayreuth,
95440 Bayreuth, Germany

Abstract

To resolve the confusion surrounding the concept of 'beta-diversity', a more consistent terminology is proposed. Almost 50 years ago, Whittaker (1960) suggested a concept for biodiversity measurement. He formulated the terms 'alpha-', 'beta-' and 'gamma-diversity', which have been widely applied since. However, there is no agreement between ecologists on the definition of the terms - especially regarding 'beta-diversity'. A multitude of different definitions hamper application and scientific progress. As the importance of variability of species composition in space and time becomes more and more evident, a concise terminology is urgently needed. On basis of a review of the existing concepts we propose a less ambiguous, clear terminology: 'inventory diversity' for describing within sample diversity, 'differentiation diversity' for compositional similarity between samples and 'proportional diversity' for the comparison of inventory diversity across spatial and temporal scales.

Keywords

alpha-diversity, beta-diversity, gamma-diversity, Whittaker, diversity concept

Introduction

> *"List(s) of the actual species […].are needed, not estimates of beta-diversity which can be estimated in many ways because no two ecologists can agree on what beta-diversity is!"*
>
> Anonymous Reviewer

Ecologists today widely agree that biodiversity is more than species richness (for exceptions see e.g. Olszewski 2004). After intense debate in the 1970s and 1980s (e.g. Allan 1975; Pielou 1975; Connell 1978; Lovejoy 1980) about the nature, measurement and loss of biotic diversity (Ehrlich & Ehrlich 1981; Wilson 1985; Wilson 1989), intensified research and discussion about biodiversity lead to increasing political awareness. As a consequence the Convention on Biodiversity was adopted (UNEP 1992). Here, for the first time a widely accepted comprehensive definition on biological diversity was formulated which included diversity within and between species as well as of ecosystems. This definition is rather vague -but gave rise to further discussion on the term in the scientific community which in turn increased the diversity of concepts and approaches (e.g. Gaston 1996; van der Maarel 1997; Beierkuhnlein 2001; Su et al. 2004).

However, the idea that biotic diversity should be more than mere species richness is much older: Whittaker (1956, 1960) was the first to develop a framework incorporating different aspects of biotic diversity. In his groundbreaking work on the vegetation of the Siskyou Mountains Whittaker (1960) developed a terminology for the measurement and comparison of vegetation diversity:

> *"The two phenomena involved suggest the need for distinguishing three aspects or levels of species-diversity in natural communities: (1) The richness in species of a particular stand or community, or a given stratum or group of organisms in a stand. Fisher's (1943) alpha index is one means of measuring this, which may be designated primary or 'alpha' diversity. (2) The extent of change of community composition, or degree of community differentiation, in relation to a complex gradient of environment, or a pattern of environments, which may be designated secondary or 'beta' diversity. (3) The species-diversity of a number of community samples, for some range of environments, which have been combined, so that the diversity value is a resultant of both alpha and beta diversities of these samples. […] The same types of measurements may be applied to 'gamma' as to 'alpha' diversity; 'beta' diversity represents a different problem […]."*
>
> Whittaker 1960, p.320

Within the same paper Whittaker also laid the foundation for future confusion (see Box A1.1) as he proposed two different notions of the new term 'beta-diversity'. Both are related to the idea that the heterogeneity of an ecosystem or a landscape can be based on the analysis of single observations within this landscape/ecosystem. This measure can be used to compare ecosystems or landscapes. Nonetheless, Whittaker was not clear in its definition. On the one hand he defined 'beta-diversity' as the average proportion of species, which can be found on a single site in relation to the whole investigation area. On the other hand he termed the turnover of species along a gradient as 'beta-diversity', expressed through the resemblance of sites in species composition. These definitions differ considerably insofar that the first considers only species numbers whereas the second takes species identity into account.

In most cases, expressions of beta-diversity have been used to test niche-based models against neutral models of species assembly (e.g. Ruokolainen et al. 1997; Condit et al.

2002; Tuomisto et al. 2003a; Chust et al. 2006) and - to a smaller extent - in conservation related studies (e.g. Steinitz et al. 2005; Wiersma & Urban 2005), or in studies on biological homogenization (e.g. McKinney 2004; Olden et al. 2006). Furthermore, some large scale - studies have been published (Bobiec 1998; Nekola & White 1999; Izcak & Price 2001; Couteron & Pelissier 2004; Kluth & Bruelheide 2004).

Recently, the importance of beta-diversity as "a key concept for understanding the functioning of ecosystems, for the conservation of biodiversity, and for ecosystem management" has been emphasized (Legendre et al. 2005) and scientist call for a stronger incorporation into ecological research (e.g. Condit et al. 2002; Olden & Rooney 2006) and in conservation planning (e.g. Srivastava 2002; Wiersma & Urban 2005). However, implementation is still scarce compared to alpha-diversity.

The studies cited above mostly apply the 'turnover perspective' of Whittaker, but over the years other perspectives and approaches to 'beta-diversity' have been defined as well (e.g. Lande 1996; Izcak and Price 2001; Vellend 2001; Chave & Leigh 2002; Veech et al. 2002; Couteron & Pelissier 2004; Qian et al. 2005; Veech 2005). Unclear terms are always problematic (Loehle 1987) but obviously hard to avoid in ecology (e.g. biodiversity, heterogeneity, stability and so forth (see e.g. Kolasa & Rollo 1991; Dutilleul & Legendre 1993; Jurasinski & Kreyling accepted). The confusion caused by the multiple meanings of 'beta-diversity' (see opening quote and Box A1.1) may be the reason for the sparse application which is in contrast to the importance of the concept.

Even authors applying the concept(s) of 'beta-diversity' often criticize the ambiguity (see e.g. Vellend 2002; Lorance et al. 2002; Koleff et al. 2003). Thus, clarification is necessary. Therefore we short review of the different notions of Whittaker's concept with a strong emphasis on 'beta-diversity' and on this basis develop and discuss an alternative terminology for the measurement and analysis of diversity. This paper shall be seen as an invitation to further discussion.

Methods

This paper is based on recent and classic literature regarding 'beta-diversity' of which we learned about during our work on spatial pattern in species composition and the environment (e.g. Beierkuhnlein 2000, Jurasinski & Beierkuhnlein 2006). To quantify the usage of different beta-diversity concepts in the literature a search in the 'Web of Science' was conducted. All 73 papers with 'beta' and 'diversity' or 'diversities' in the title were screened manually and all non-ecological papers have been skipped. Five papers were not considered in the analyses: one could not be accessed, three were only comments and one mentioned 'beta-diversity' solely in the title. The resulting 71 papers were analyzed systematically regarding type of study and the kind of 'beta'-concept employed.

Alpha, beta, gamma and their development

Alpha and gamma-diversity

As Whittaker noted (1960), alpha and gamma diversity are descriptors of species within one certain area, but differ in the units considered. Alpha diversity is measured within a sample (in Whittaker's original notion a stand or community, also frequently used terms are: site, sampling unit, plot, etc. - in the following named 'sample'), while gamma diversity refers to the species richness on a higher aggregational level: usually a combination of different samples (or stands / communities) within the investigation area (landscape). Whittaker (1956) suggested the term 'alpha-diversity' as he suggested Fisher's alpha parameter of the log-series species-abundance distribution as a useful measure. There are basically two different measures for alpha/gamma diversity: 1) Sampled species richness or estimated species richness using sample or individual based rarefaction (species-accumulation curves; e.g. Gotelli & Colwell 200;, Chao 2005), and their extension to animals (e.g. Brose & Martinez 2004). 2) descriptors of species-abundance distribution such as the indices of Simpson (1949) or Shannon-Weaver (1949).

Box A1.1. Confusion surrounding diversity concepts - especially 'beta-diversity'

There exists a substantial ambiguity among ecologists as far as biodiversity conceptualization and evaluation is concerned. (Ricotta, 2005)

The related concepts of 'beta-diversity' and 'species turnover', often used interchangeably in the ecological literature […], require clarification. and *'Beta-diversity' is an abstract concept whose utility needs to be limited if it is to retain meaning.* (Vellend, 2001)

'Beta-diversity' is a more abstruse concept measuring change in species composition between communities. (Novotny & Weiblen, 2005)

'Beta-diversity' has grown to incorporate a range of concepts but is generally regarded as referring to some component of how two or more sampling units vary across spatial or temporal axes. (Harborne et al., 2006)

Comparisons between the results of different studies may be hindered severely by the variety of measures that have been used to quantify beta diversity and by the variety of ways in which these measures have been applied. (Koleff et al. 2003)

The different notions of 'beta-diversity'

'Beta-diversity' is frequently used in a very general sense of differentiation between units (e.g. Balvanera et al. 2002; Condit et al. 2002; Duivenvoorden et al. 2002; Ruokolainen et al. 2002; Koleff et al. 2003b; Alonso and McKane 2004; Chave 2004; Kluth & Bruelheide 2004; Sætersdal et al. 2004; Chust et al. 2006; Olden & Rooney 2006). In 2001 Vellend tried to clarify terminology by distinguishing between 'beta-diversity' (relation in species richness or representatives of species richness of different scale levels) and 'species turnover' (compositional similarity). This is an important line of thought as Vellend's

(2001) 'beta diversity' examines changes in species richness while his idea of 'species turnover' deals with the variation in species composition. This distinction is crucial and can systematically be applied to the different notions of 'beta-diversity'. In the following the different concepts found in the literature are arranged along this separation.

Concepts of 'beta-diversity' examining the variation in species richness

Multiplicative partitioning. In his original paper Whittaker (1960) defined 'beta-diversity' as the relation between 'gamma-' and average 'alpha-diversity':

> *"The simplest measurement of beta diversity may be the relation,* $\beta = \gamma / \alpha$*, in which* α *is the diversity value for an individual sample and* γ *that for the sample resulting from merging a number of individual samples from a community pattern or coenocline."*
>
> Whittaker 1960, p.321

Species identification is not necessary to calculate this coefficient, which expresses a kind of heterogeneity and implicitly takes the number of communities as a measure of beta-diversity (Routledge 1977). The reciprocal value of this coefficient can be directly explained as the average proportion of species richness found in an average sample. This value generally decreases with heterogeneity of the samples (but also depends on plot number and size in relation to the investigated area). It indirectly measures similarity of species composition as it approaches 1/n if the single plots share no species at all and 1 if all plots contain the same species. For any value between these extremes the origin of the heterogeneity between the plots cannot be distinguished: Imagine a data set with 10 plots where 8 plots have an identical species composition and 2 plots differ totally from all others. The resulting value of 'beta-diversity' would be the same as for a data set with 10 plots of moderate similarity. Although Whittaker did rarely implement this definition of beta-diversity in practice (Veech et al. 2002), it is taught (Brown & Lomolino 1998; Gaston & Blackburn 2000) and applied (Harrison et al. 1992; Gaston et al. 2001; Lennon et al. 2001; Wiersma & Urban 2005) in ecology.

Additive partitioning. Recently, Veech et al. (2002) published a paper reviewing an additive notion of 'beta-diversity' closely related to Whittakers (1960, 1972) original idea. They refer to Lande (1996) who proposed to partition 'gamma-diversity' into additively combined components of 'alpha'- and 'beta-diversity' (Formula 1.1). Lande (ibid.) was the first to use Whittakers (1960, 1972) terminology (alpha, beta, gamma) in this context but the conceptual idea of partitioning diversity into additive components is much older (MacArthur et al. 1966; Levins 1968). In 'additive partitioning' 'beta-diversity' is defined as the average amount of diversity not found in a single, randomly chosen sample (Veech et al. 2002). However, it "does not explicitly recognize differences among samples or communities, which, after all, is the original intent of beta-diversity" (ibid.).

$$\beta = \gamma - \bar{\alpha} \tag{1.1}$$

Concepts of 'beta-diversity' examining the variation in species composition

Resemblance expressed by similarity/dissimilarity coefficients. The second definition of Whittaker (1956, 1960) is that of 'beta-diversity' as the turnover in species composition along a gradient. He suggested to use available indices of compositional similarity, such as coefficient of community (Jaccard 1901), coincidence index (Sørensen 1948), or percentage difference (Bray & Curtis 1957). This understanding of 'beta-diversity' is the most widespread one. Therefore, a multitude of coefficients Is available. Several comparative reviews have tested features and performance of similarity and distance coefficients (e.g. Cheetham & Hazel 1969; Janson & Vegelius 1981; Wolda 1981; Hubalek 1982; Shi 1993; Koleff et al. 2003a; Clarke et al. 2006).

Two relatively recent and interesting approaches are worth mentioning: Chao et al. (2005) show, that similarity is frequently underestimated because the coefficients do not account for "unseen" shared species. To solve that problem they propose a probabilistic extension to the existing coefficients of Jaccard (1901) and Sørensen (1948). A similar approach is that of Plotkin & Muller-Landau (2002) for a Sørensen-type similarity index for abundance counts that relies on a gamma distribution to characterize "real" species abundance structure.

Condit et al. (2002; see also Chave & Leigh 2002, 2002) propose to use the codominance index of Leigh et al. (1993) as a similarity measure. It is based on the probability of joint occurrences of species in compared sampling units (Palmer 2005). The measure is defined as the probability F(r) that two randomly chosen individuals a distance r apart belong to the same species (Chave & Leigh 2002).

As the results of ecological studies depend on the coefficient applied, the multitude of available indices may affect the clarity of statements, the reproducibility of findings, and inter-study comparison.

Multivariate dispersion. Lately Anderson et al. (2006) proposed to calculate beta-diversity "as the average distance (or dissimilarity) from an individual sample to the group centroid" of a (dis)similarity matrix. It can be computed with any appropriate resemblance coefficient.

Slope of the distance decay relationship. This approach to 'beta-diversity' was formulated by Condit et al. (2002) and independently by Qian et al. (2005). The latter propose to use the slope of the distance decay relationship as a measure of beta-diversity because it "is a measure of the exponential rate of increase in dissimilarity with distance." Distance decay is a general geographical phenomenon (Tobler 1970): The similarity of samples - independent of variables used for evaluation - is likely to decrease with geographical separation. Ecologists have studied distance decay previously, but did not regard it explicitly as a measure of beta-diversity (e.g. Qian et al. 1998, Nekola & White 1999, Tuomisto et al. 2003b). The reason might be, that the slope of the distance decay relationship is based on a measure of 'beta-diversity' itself, which in the cited works always is regarded in the turnover sense and calculated with coefficients of compositional similarity.

Closely related to this concept of 'beta-diversity' is the suggestion of Beals (1984) who plots similarity against environmental distance (expressed by an elevational gradient). This leads to specific curvatures depending on the coefficient used and Beals (1984) suggests that the curvature can be interpreted directly as a function of the length of the environmental gradient which he calls 'beta-diversity'.

The sum of squares of a species matrix. In a recent paper, Legendre et al. (2005) argue, that the variance of a community composition table is a measure of 'beta-diversity'. They show that the total beta-diversity of a data set can be derived from a dissimilarity matrix or the original species matrix alike. However, the "raw-data approach" provides more statistical power and should be preferred when the variation in species composition among samples is addressed. Legendre et al. (2005) state that variance partitioning based on the regression of distance matrices (Legendre et al. 1994) "is inappropriate when the hypothesis to be tested concerns […] the variation in species compositions among sites", as it partitions the variation of a dissimilarity matrix but not the variation of the species matrix. Although the mean of the squared dissimilarities is a measure of 'beta-diversity', the variation (sum of squares) of the dissimilarities is not, because the variation is not a simple function of the variation in the original data table.

Gradient length in ordination space. Distance along gradients in ordination space was relatively early used as a proxy for 'beta-diversity': Already Whittaker introduced the "half changes (HC)" to overcome the problem that the similarity of two samples from different ends of a gradient often equals zero as they have no species in common (Whittaker 1956, p.321; Whittaker 1960, p.39). Therefore, Whittaker (1956) recommends to calculate the percentage similarity between successive plots along a gradient. At the point where percentage similarity reaches 50 %, the calculation is stopped, and started anew from that point until either a new stopping point is found, or the end of the gradient is reached. The number of "half-changes" - determined by this method - "may thus indicate the extent of change in species populations along the gradient" (Whittaker 1956) and therefore is a measure of 'beta-diversity' (Whittaker 1960).

With the upcoming of ordination techniques, ordination axes were used to detect thegradients. Already Gauch (1972, 1976) defined "Z units" of species turnover as the "axis length (100) divided by the average standard deviation of species distributions". The term "Z unit" was rarely used and renamed to "sd units" by Hill (1980) and a gradient length of 4 sd units represents a complete species turnover. Closely related is the concept of the mean range of species "R" (Minchin 1987): "These are computed as 100/r, where r is the mean range of the physiological response functions along a given gradient". While half changes and sd / z units are almost equivalent (1 HC = 1.349 Z; Hill 1980), there is no simple relationship between those two and R; however, in practice 1 R approximates 6 sd units (Minchin 1987).

A simple direct measure of the turnover is the gradient length in DCA, as this ordination method directly scales the axes in sd units (Hill 1980). Based on a critique of available measures of floristic resemblance also Økland (1986) proposes to use DCA axes length as a measure of 'beta-diversity'. In a slightly different approach Ohmann & Spies (1998) used the "total variation (TV) from stepwise CCA" as a measure of beta-diversity.

Discussion

Alpha and gamma diversity

Generally, alpha and gamma diversity do not differ in their quality but in the spatial extent over which data is recorded. Beierkuhnlein (2001) termed both 'quantitative diversity' because they base on counts of variables (e.g. species, or genera). There are several problems associated with determining gamma-diversity. First, it is mostly calculated from the species found within individual samples, which rarely is a true representation of the species richness in the total area, as usually only small portions of the area are actually investigated. Second, although Whittaker (1960) explicitly defined gamma diversity as the diversity of a landscape - the perception of an appropriate 'landscape-scale' is extremely variable (see Table A1.1). Third, there is a specific problem in temporal studies or monitoring: Should the species richness of all inventory years together be seen as gamma or the total species richness of one year of study. Especially in regions with large inter-annual changes such as semi-arid or Mediterranean ecosystems, this might change results considerably.

Whittaker (1977) suggested an extended classification with seven diversity levels to account for the nested hierarchy of scales - which is even more confusing than the three level concept considered here - and cannot solve any of the problems discussed. However, he also applied alpha and beta at different scales, thus indirectly acknowledging the superfluity of the 'gamma' concept, as 'gamma' can easily become 'alpha' on a higher spatial level.

Table A1.1. Overview of the size of the study area for ecological investigations at 'landscape scale'. This list is not intended to be comprehensive but illustrative for the variability of the term 'landscape scale' employed in ecology. Data is derived from a search in the Web of Science (TI="landscape scale AND (biology OR diversity OR ecology OR vegetation OR animal)") and subsequent manual evaluation.

Source	Landscape scale
Pregitzer et al. (2000) J.Ecol. 88:45-53	0.026 km^2
Corney et al. (2004) Biol.Conserv. 120:491-505	0,04 km^2
Holland & Fahrig (2000) Agr.Ecosys. & Environ. 78:115-122	4 km^2
Wills & Abbott (2003) Biol. & Fert.Soils 39:94-102	26 km^2
Pierce et al. (2005) Lands.Ecol. 20:137-147	64-75 km^2
Potter et al. (1998) Lands.Ecol. 13:203-214	140 km^2
Higgins et al. (1999) Conserv.Biol. 13:303-313	471 km^2
Hester et al. (1996) Biol.Conserv. 77:41-51	1000 km^2

K. B. Pierce, T. Lookingbill, and D. Urban. A simple method for estimating potential relative radiation (PRR) for landscape-scale vegetation analysis. Landscape Ecology 20 (2):137-147, 2005.

P. M. Corney, M. G. Le Duc, S. M. Smart, K. J. Kirby, R. G. H. Bunce, and R. H. Marrs. The effect of landscape-scale environmental drivers on the vegetation composition of British woodlands. Biol.Conserv. 120 (4):491-505, 2004.

A. Wills and I. Abbott. Landscape-scale species richness of earthworms in the Porongurup Range, Western Australia: influence of aspect, soil fertility, and vegetation type. Biology and Fertility of Soils 39 (2):94-102, 2003.

K. S. Pregitzer, D. D. Reed, T. J. Bornhorst, D. R. Foster, G. D. Mroz, J. S. Mclachlan, P. E. Laks, D. D. Stokke, P. E. Martin, and S. E. Brown. A buried spruce forest provides evidence at the stand and landscape scale for the effects of environment on vegetation at the Pleistocene/Holocene boundary. J.Ecol. 88 (1):45-53, 2000.

J. Holland and L. Fahrig. Effect of woody borders on insect density and diversity in crop fields: a landscape-scale analysis. Agriculture Ecosystems & Environment 78 (2):115-122, 2000.

D. U. Potter, J. R. Gosz, M. C. Molles, and L. A. Scuderi. Lightning, precipitation and vegetation at landscape scale. Landscape Ecology 13 (4):203-214, 1998.

S. I. Higgins, D. M. Richardson, R. M. Cowling, and T. H. Trinder-Smith. Predicting the landscape-scale distribution of alien plants and their threat to plant diversity. Conserv.Biol. 13 (2):303-313, 1999.

A. J. Hester, D. R. Miller, and W. Towers. Landscape-scale vegetation change in the Cairngorms, Scotland, 1946-1988: Implications for land management. Biol.Conserv. 77 (1):41-51, 1996.

Beta diversity

Although the term 'beta-diversity' is closely associated with Whittaker's name, he was not the first to investigate the heterogeneity of samples. The idea to use the relation between species richness of larger and smaller scale levels as a measure of heterogeneity was already expressed by Williams (1950) and the first coefficients of compositional similarity were developed as soon as 1884 (Peirce) and 1901 (Jaccard). However, Whittaker was the first to set up a comprehensive framework of biodiversity measurement. But with his work he also caused some confusion and lead to questionable definitions of further levels of biodiversity; e.g. 'delta', 'omega' (van der Maarel 1997). The literature review shows that only slightly more than 50% (38 out of 71) of all studies are pure applied studies, while the other 33 are reviews, theoretical and methodological (often with applied examples) papers related to the concept and its measurement. This indicates that the theoretical foundation of 'beta-diversity' still requires a lot of input.

Concepts of 'beta-diversity' examining the variation in species richness

Two measures fall into the group of concepts disregarding species identity, namely Whittaker's multiplicative 'beta-diversity' (see above, 1960; Whittaker 1972) and the additive partitioning approach (Formula 1.1, Lande 1996; Veech et al. 2002). Veech et al. (2002) argue to use additive partitioning instead of the multiplicative approach, because 'alpha', 'beta' and 'gamma' are then measured in the same units. This allows to compare of the contributions of alpha and gamma to total species richness across spatial or temporal scales (DeVries et al. 1997; Summerville & Crist 2002; Crist et al. 2003). Consequently, it is mainly implemented to study e.g. the organization of species richness across scales (Wagner et al. 2000; Gering et al. 2003) and to monitor restoration success (Martin et al. 2005). Veech et al. (2002) recommend this methodology especially for conservation planning and reserve design and state that there is increasing use since Lande's paper (1996) because of "growing acceptance among ecologists for defining beta-diversity as the diversity among samples".

Nonetheless, as only average species numbers or respective diversity values are taken into account, both concepts do not allow for hypotheses testing regarding the drivers of species composition whereas hypotheses on the spatial distribution of species richness across scales can be addressed (Loreau 2000; Crist et al. 2003). However, Kiflawi & Spencer (2004) show that the additive and multiplicative perspectives are directly related. They convert Whittaker's (1972) modification of the original notation that expresses the number of "full changes" in species composition among sampled sites (Formula 2) to the general formula of additive partitioning. Thus, the multiplicative measure is simply a summary statistic of the relation between the additive components.

$$\beta = \frac{\gamma}{\bar{\alpha}} \tag{1.2}$$

Loreau (2000) argues that the additive approach has a greater potential in terms of consistency (Lande 1996) and application to multiple scales. The additive partitioning between 'alpha' and 'beta' is solely a matter of scale. Thus, their respective values heavily depend on the scale of recording ('grain' of the investigation sensu Palmer & White 1994).

Kiflawi & Spencer (2004) present an interesting statistical tool for testing hypothesis with measures of additive and multiplicative partitioning. Similarly, Couteron et al. (2004) integrate additive partitioning and distance based approaches into the well known concept of ANOVA and ANCOVA. This can be of great value when investigating the organization of species in space and time. As their approach relies on the sampling of individuals or fine scaled frequencies it is restricted to species occurring with few, clearly separable, individuals. Furthermore the approach implicitly assumes mutually exclusive sets of plots which cannot be achieved with nested sampling design (e.g. Stohlgren et al. 1995; Kluth & Bruelheide 2004; Jurasinski & Beierkuhnlein 2006).

Concepts of 'beta-diversity' examining variation in species composition

The most frequently applied method to measure the variation in species composition is the calculation of similarity or distance coefficients. In this case species identity is preserved and the calculated value is either determined by the species' presence and absence or by their relative abundances.

Recently proposed coefficients including a probability term estimate the "true" diversity of two compared plots from the whole sampled population. This might increase the performance of the indices (Chao et al. 2005), but does not change their general properties. Chao et al. (2005) also mention the approach of Condit et al. (2002, see also Leigh et al. 1993, 2002) and state that codominance is not a statistically valid index of similarity because for two identical assemblages with many species, F tends to 0. Moreover, two identical assemblages may result in different values of F, depending on species richness and relative abundance patterns. It is possible, however, to normalize F to produce a valid similarity index.

Chave & Leigh (2002) acknowledge as well, that "F(r) is a crude measure of species turnover, or beta-diversity" as it depends "disproportionately on the more common species, whereas turnover may be more rapid among rare species" (Pitman et al. 2001). The codominance index implicitly takes the geographic distance between samples into account. Therefore it is not a measure of differentiation between sampling units but a measure of spatial organization of species in the ecosystem.

Økland (1986) argues that measures of floristic relationships are generally problematic to describe ecological relationships. First, they use noisy field data directly. Thus they are not able to describe short ecological distances adequately (Gauch & Whittaker 1972). Second, they are cannot be determined for very long gradients because two distant samples then may not share any species (ibid.). Third, sample dissimilarity as a function of gradient separation describes an S-shaped curve (Bray & Curtis 1957), due to the non-linear relationships of species space and ecological space (Gauch 1973; but see Beals 1984).

Analyses based on resemblance measures

Similarity (or distance) is usually calculated between a pair of samples, but Whittaker (1960, 1972) suggested that the mean similarity calculated between samples may represent a measure of 'beta-diversity' as well. Legendre et al. (2005) emphasize that this is true, but state, that the variance of the similarities is not a measure of 'beta-diversity'. We would like to add that neither the mean nor the variance take species identities into account. In both cases, indices calculated from the raw data, are aggregated on a higher level to examine heterogeneity. Closely related is the multivariate dispersion of Anderson et al. (2006).

Both methods of aggregation neglect the phenomenon of distance decay. Because the similarity of objects is likely to decrease with distance (Tobler 1970), it is not clear how much of the variation is explained by geographical distance and how much by environmental difference. The alternative is to take the geographical distance between samples explicitly into account (Condit et al. 2002; Qian et al. 2005) but still species identities are neglected. Condit et al. (2002) state that they "lose information by averaging all pairs of plots (at a given distance); this allows the data to be smoothed and provides theoretically relevant numbers, but abrupt transitions due to habitat change would be missed."

The slope of the distance decay relationship depends on the properties of the similarity coefficient (problems discussed) and on the regression model used. There is no general agreement regarding the best fitting model for the distance decay relationship. Whereas in large-scale studies the regression of the logarithmic similarity against geographical distance described the relationship best (Qian et al. 1998; Nekola & White 1999, Qian et al. 2005), the best model in medium scale studies in the tropics was obtained by regressing the untransformed similarity against log-distance (e.g. Condit et al. 2002, Duivenvoorden et al. 2002, Phillips et al. 2003). In a recent small scale study (unpublished), we found that the best fitting model changes with scale. Additionally the models usually fit relatively poor (Jones et al. 2006). Thus, slopes of distance decay relationship should be evaluated with care and with the goodness of fit and the appropriate scale in mind.

Soininen et al. (2007) recently argue that the best regression model often depends on the ecosystem and organisms under study. They propose to use the 'halving distance' instead of the slope of the distance decay relationship. The 'halving distance' can be constructed independent from the regression model and therefore allows for comparisons across organisms and ecosystems . The 'halving distance' is defined as the geographical distance at which the initial similarity S reaches S/2. Although the problem regarding the regression model can be solved, another parameter: initial similarity has to be defined rather arbitrarily (Soininen et al. 2007 use the similarity at a distance of 1km).

The slope of the distance decay rate or the 'halving distance' is a measure of spatial heterogeneity in species composition and a true measure of species turnover. In every case it is a subsequent analysis, based on the calculation of differentiation diversity. It is relevant for conservation (Ferrier et al. 2002; Wiersma & Urban 2005), as well as for the investigation of pattern and process in ecological communities (e.g. Podani et al. 1993; Garcillán & Ezcurra 2003; McDonald et al. 2005) and community assembly (dispersal versus niche Condit et al. 2002; Gilbert & Lechowicz 2004; Jones et al. 2006).

The similarity-distance function might predict the slope of a power-law species area curve (Condit et al. 2002). Based on this characteristic the authors conclude that it is an appropriate measure of beta-diversity. Already MacArthur (1965) proposed to use species-area curves as an analytical tool to diversity taking the intercept of the curve as a measure of 'alpha-diversity' and the slope parameter as a measure of 'beta-diversity' (see also Caswell & Cohen 1993; Ricotta et al. 2002). However, Connor & McCoy (1979) show that this is mathematically not valid, because the slope and intercept of the power-function are interdependent parameters. Additionally, there is empirical critique. Even for simple systems some component of the slope is probably due to within-habitat diversity so the slope cannot serve as a measure of 'beta-diversity'. Furthermore, it requires to know the true area of the community being sampled (Veech et al. 2002).

The suggestion of Legendre et al. (2005) to measure 'beta-diversity' as the sum of squares of the original species matrix provides a more direct way to assess the variation in species composition. Legendre et al. (2005) argue to use rather canonical partitioning than Mantel tests of dissimilarity matrices for "partitioning the spatial variation of community composition data among environmental and spatial components, and for testing hypotheses about the origin and maintenance of variation in community composition among sites". Ordination methods can be very helpful as they have the power to identify the major structure (gradients) in the data set and reduce noise by relegating it to axes of lower rank (Gauch 1982). However, in principle the length of the ordination gradient as a proxy for 'beta-diversity' is related to calculating similarity indices, because ordinations represent intrinsic (e.g. Euclidian distance in PCA or Chi-square distance in CA - see e.g. Legendre & Legendre, 1998) or specifically chosen distance or (dis)similarity indices (NMDS) in low-dimensional space. Thus, the problem of zero similarity between plots from the extreme ends of the gradient remains unsolved. Nonlinear ordination methods such as isomap by Tenenbaum et al. (2000) or De'ath's extended dissimilarities (De'ath 1999) are promising approaches to deal with this problem. Also the multivariate dispersion as proposed by Anderson et al. (2006) overcomes this problem. Although DCA results depend on the detrending method applied (Legendre & Legendre 1998), the appealing feature of DCA scores is clearly the scaling in standard deviations, which facilitates comparison of results between different data sets. Therefore, the dimensionality reduction obtained in ordination is a powerful tool to extract gradients and reduce data complexity and thus to estimate the variation in species composition. Such methods have been successfully applied by different authors (e.g. Økland 1990; Rydgren et al. 1998; Pitkänen 2000; Svenning et al. 2004).

A new, more descriptive terminology

A clear terminology, which researchers agree upon, is an important basis for intensive discussion within a field of research (Kuhn 1976; Loehle 1987). In 1984, Beals criticized Whittaker (1967) for bringing the vague terms 'direct gradient analysis' for ordination by environmental factors and 'indirect gradient analysis' for ordination by sociological factors into the discussion and called for more descriptive terms ('environmental ordination' and 'sociological ordination'). Nevertheless, the vague terms made it into the plant sociological terminology. Similarly the abstract terms 'alpha-', 'beta-', and 'gamma-diversity' made it in the biogeographical terminology.

Here, we advocate the use of descriptive terms instead: the Greek letters should be avoided and replaced by a more meaningful and unambiguous terminology. We do not agree with Veech et al. (2002), that 'beta-diversity' should be further used by ecologists in a broad sense. It is not very helpful to apply the term 'beta-diversity' to all concepts which somehow investigate the variation in species composition because this requires every scientist to sort out which notion of 'beta-diversity" the author(s) use. However, we do agree with Veech et al. (2002), that 'beta-diversity' should not be seen "just as change along an environmental gradient". Therefore, we propose an alternative terminology to avoid confusion and gain clarification of the concepts. Three primary levels of diversity can be distinguished in this alternative framework: 'Inventory diversity', 'differentiation diversity' and 'proportional diversity' (see Box A1.2). The variants and approaches discussed above fit into these levels as follows (see Table A1.2).

Box A1.2. The proposed terminological concept

Inventory diversity - within sampling diversity (abundance, frequency or presence/absence) - no matter which spatial or temporal scale is regarded.

Differentiation diversity - compositional similarity between samples - no matter which spatial or temporal scale is regarded.

Proportional diversity - relative distribution of 'inventory diversity' across spatial and temporal scales.

Inventory diversity largely refers to Whittaker's 'alpha' and 'gamma' and should be used for the species data assessed within sampling units (abundance, frequency or presence/ absence). It does not matter whether 'inventory diversity' is expressed as recorded species richness in the field or as 'true' species richness estimated from the sampled data (Colwell & Coddington 1994; Chao et al. 2005), nor on which scale inventory diversity is assessed ('alpha' or 'gamma-diversity' in the sense of Whittaker (1960, 1972)): it remains **inventory diversity**. Because of the importance of scale (Dale et al. 2002; Legendre et al. 2002; Rahbek 2005) the term 'inventory diversity' should always be used with a reference to the scale on which it was recorded. The quality remains the same whilst the spatial and temporal reference changes.

Table A1.2. A new terminology for the measurement and analysis of diversity (first column). Existing concepts are sorted according to the proposed new terminology (second column). The third column gives the number of studies (of 73 analyzed) in which the existing concepts have been employed (only for 'beta' concepts).

New terms	Available concepts	NoS[1]	Whittaker
inventory diversity	species richness, Shannon, Simpson		alpha, gamma
differentiation diversity	resemblance (compositional (dis)similarity, distance)	38	beta
	sum of squares of species matrix	3	
turnover[2]	gradient length in ordination	12	
	slope of distance decay relationship / halving distance	7	
proportional diversity	additive partitioning	12	
	multiplicative partitioning	20	
	slope of species-area curve	3	

[1]) Numbers are based on a literature review on 'beta-diversity' in the ISI web of science (see methods).

[2]) Turnover is a subordinate category which is based on the calculation of differentiation, therefore it is filed under this category. However, species identities are then skipped an data is aggregated. This may lead to an increase in insight but it means loss of information as well.

Differentiation diversity results from the comparison of samples whilst taking species composition (frequency, abundance or presence/absence) into account -again - no matter which spatial or temporal scale is regarded. Usually two distinct units are compared because most of the available indices can handle only this. Recent studies, which emphasize the importance of 'beta-diversity' often use this 'resemblance' notion (e.g. Condit et al. 2002; Srivastava 2002; Gering et al. 2003; Sax & Gaines 2003; Olden et al. 2006). The sum of squares of a species matrix is provides a global measure of 'differentiation diversity' whilst taking the species identity into account (Legendre et al.

2005). Compositional similarity is thought to be determined by ecological processes. Thus, compositional similarity (or differentiation diversity) can be used to study the drivers of species compositions.

The variation of species composition in space is a major concern in vegetation ecology and biogeography. Sometimes measurements of ‘differentiation diversity’ are pooled to express a mean ‘differentiation diversity’ for an area (Lennon et al. 2001; Koleff et al. 2003b; Anderson et al. 2006). However, this approach neglects distance decay. The slope of the distance decay relationship addresses this issue. It investigates the spatial organization of ‘differentiation diversity’. Therefore it is related to the spatial heterogeneity of species composition and a true measurement of **turnover**. So why not call it ‘turnover’?

This renders the slope of the distance decay relationship or the ‘halving distance’ an ideal tool for the investigation of spatial patterns in species distribution and their drivers. Similarly, ordination methods depend on underlying similarity or distance coefficients as well. In his original paper (Hill 1980) already stresses that DCA offers a unique possibility to measure species turnover. Thus, gradient length in ordination space is also a measurement of ‘turnover’. Within the proposed concept ‘turnover’ is always determined in a subsequent analysis of ‘differentiation diversity’ describing their spatial organization.

Proportional diversity Proportional diversity does not account for species identity but expresses the relative distribution of ’inventory diversity’ across spatial and temporal scales. The concepts of multiplicative (Whittaker 1960) and additive partitioning (Lande 1996; Loreau 2000; Veech et al. 2002) both express ‘proportional diversity’, they just differ in their mathematical concept and are more related than it seems from first sight (Kiflawi & Spencer 2004). The term ‘proportional diversity’ has already been used by Bambach (2000) in a similar notion and we think that it expresses the concept quite clearly.

We agree with Crist et al. (2000) that the provision of methods to obtain statistical inference whether the observed patterns of diversity are significantly different from random might support the development of these concepts. However, we’d like to emphasize that additionally a crisp terminology is needed (Beals 1984) which spares the explanations which notion of ‘beta’ is addressed in a certain study. The additive partitioning of ‘inventory diversity’ into the average diversity found within scales and the average difference in diversity between scales is the appropriate technique to evaluate the distribution of ‘inventory diversity’ across scales and thus a measure of ‘proportional diversity’.

In the rare cases where exactly two samples are compared, ‘proportional diversity’ may come close to a measure of ‘differentiation diversity’ (dependent on the coefficient used to calculate the compositional similarity). However, as long as the identity of species is taken into account we refer to the measure as a coefficient of 'differentiation diversity'. does not account for species identity but expresses the relative distribution of inventory diversity across spatial and temporal scales. The concepts of multiplicative (Whittaker 1960) and additive partitioning (Lande 1996; Loreau 2000; Veech et al. 2002) both express 'proportional diversity', they just differ in their mathematical concept and are more related than it seems from first sight (Kiflawi & Spencer 2004).

Conclusion

Whittaker's (1960) concept for assessing diversity has triggered a lot of development in ecology. However, especially the term 'beta-diversity' has begun to take on relatively different meanings and thus is a rather confusing concept. The terminological ambiguity is an obstacle to the development in all fields requiring more than inventory data ('alpha' or 'gamma-diversity' sensu Whittaker). Compositional (dis)similarity between samples ('differentiation diversity') and the variation of inventory diversity across scales ('proportional diversity') are important fields for future research, which should not be neglected due to unclear concepts. Thus, we hope to contribute to the discussion by offering a clear terminology as a basis for scientific communication.

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Appendix 2 Hexagonal grids - an alternative for quantifying spatio-temporal patterns of biodiversity. *Journal of Biogeography*, submitted

*Jurasinski, Gerald (gerald.jurasinski@uni-bayreuth.de); Beierkuhnlein Carl
(carl.beierkuhnlein@uni-bayreuth.de)

Address (both authors):
Biogeography, School of Biology, Chemistry and Earth Sciences, University of Bayreuth,
95440 Bayreuth, Germany

Abstract

Aim Quantitative and comprehensive methods to assess spatio-temporal changes in biodiversity, especially on the landscape and ecosystem scale, are scarce. However, despite a few positive examples of reverted extinction or increasing population sizes, species still go extinct at an increasing rate. Land-use change, climate change and invasive species are major causes for biodiversity loss. Therefore we urgently need standardized and comparable data in order to detect changes of biodiversity. We propose a widely applicable, transferable and reproducible method to reveal spatio-temporal patterns in vegetation and to relate them to ecosystem processes.

Methods We shortly review the methodology to detect, analyze and explain spatial patterns in vegetation. From this we deduce an alternative methodology for biodiversity assessment.

Results A hierarchically nested systematic grid of hexagonal plots is a promising approach to investigate spatio-temporal patterns of biodiversity from landscape to ecosystem scale.

Main Conclusions Despite on very large scales equidistant systematic grids are rarely used in biodiversity assessment. They are common in environmental research and management but can be also of benefit for conservation and in biogeographical research.

Keywords

spatial pattern, beta-diversity, global change, conservation monitoring, grid-based sampling, similarity, scale issues

Introduction

Despite from large mammals or other species of economic interest the most species go extinct because their habitat is altered by man (e.g. Grime 2002; Duffy 2003). Land-use and land-use change are amongst the main drivers of biodiversity loss (Crist et al. 2000; Sala et al. 2000; Millennium Ecosystem Assessment 2005). Often populations first change their geographic occurrence or their density in a given region before they vanish. Alas, there are hardly any reliable methods to assess and track such changes at ecosystem or landscape scale. In order to detect these changes quantitatively and qualitatively, standardised and comparable data on regional patterns of biodiversity are needed. Frequent re-investigations have to be carried out (Balmford & Bond 2005). Methods to obtain these are required to be representative as well as pragmatic due to the simple fact that there is no time to achieve complete data sets when ongoing temporal trends are addressed. They need to be repeatable after short periods of time, they have to enable us to cover large areas with low effort whilst assuring an adequate reliability, and should allow for the application of a comprehensive biodiversity concept.

Such a comprehensive concept of biodiversity was first brought to a wider public with the Convention on Biodiversity (UNEP 1992; for further developments see e.g. Setælæ et al. 1998; Beierkuhnlein 2001; Su et al. 2004). Although it encompasses more than mere species diversity, a lot of research is still based on species richness (alpha diversity) as a measure of diversity (e.g. Tilman & Elhaddi 1992; Schulze & Mooney 1993; Krishnamani et al. 2004). Even the numerous projects addressing the implications of biodiversity for ecosystem function (e.g. Grime 1998; Bednekoff 2001; Hart et al. 2001) largely concentrate on alpha-diversity. The same holds for papers on emerging patterns of vegetation (e.g. Cracraft 1992; Araújo 1999; Lister et al. 2000). The concentration on alpha diversity as a measure of biodiversity indicates a lack of methodological applications of an extended biodiversity concept (for exceptions see Pitkänen 1998; De'ath 1999; Kluth & Bruelheide 2004).

Furthermore, recent literature with respect to the influence of global change on biodiversity generally focuses either on the human-environmental-system (very large scale and meta data analysis, (e.g. in Ayres & Lombardero 2000; Hannah et al. 2002; de Vries et al. 2003) or on specific organisms or even organic responses to climate change (very small scale and mostly experimental (e.g. Wood et al. 1994; Constable et al. 1999; Bermejo et al. 2002; Körner 2003)). Information regarding a medium scale (landscape, ecosystem, habitat) and focusing on shifts in community composition is rather scarce (e.g. Gottfried et al. 1998). This might be due to missing methodology.

Based on a short review of ideas on sampling design we deduce a new systematic sampling approach for the assessment and monitoring of biodiversity which is suitable for studies on different scales (from patch to landscape). It allows for the incorporated assessment of alpha- and beta-diversity and spatial pattern. We will discuss the advantages and prospects of the implementation of equidistant sampling grids with hexagonal plots and give some ideas of application.

Sampling design - form follows function

It is my belief that it is of the very essence of every problem that it contains and suggests its own solution. This I believe to be natural law. Let us examine, then, carefully the elements, let us search out this contained suggestion, this essence of the problem.

Louis Sullivan 1896

The paradigm of "form follows function" which was proposed by Sullivan in 1896 as the inherent standard of every design problem is also applicable to the question of sampling design. In this case the function can be understood as the purpose of the sampling. In our case, the aim is the comprehensive description and analysis of spatial patterns of phyto-diversity. This provides the preliminaries for the appropriate sampling design.

From preferential to systematic sampling

Various sampling schemes and designs have evolved in plant ecology. Preferentially located plots are the classical solution and have "often been used in vegetation sampling in Central Europe" (Mueller-Dombois & Ellenberg 1974). Preferential sampling without preconceived bias does not deserve the criticism which considers all subjective sampling as unscientific because it differs from preferential sampling with preconceived bias in a major aspect: "The investigator approaches his study object with a negative hypothesis in mind" (ibid.). However, this approach requires a good reconnaissance and subsequent knowledge of the area of investigation to determine the "best" locations for investigation and therefore the results will differ remarkably between scientists, working groups or scientific schools. So it is not appropriate either if the transfer of results and reproducibility are desired or if the monitoring of long-term changes is the objective. Furthermore it does not allow for covering a larger area or investigating spatio-temporal patterns.

Random or systematic sampling might be suitable if one is looking for variation across vegetation in space (Mueller-Dombois & Ellenberg 1974). However, because truly random distribution does not exist in nature, Greig-Smith (1964) suggests that random sampling may often be inappropriate. Plant populations are rather clumped or contagiously dispersed which is the major problem when applying statistics that are based on random distribution (Palmer & van der Maarel 1995). Hence random sampling can hardly be used to assess them sufficiently. Reiter (1993) states that the effort of random sampling is very high and it easily leads to over or under sampling of parts of the investigated area. Similar findings regarding the inefficiency of random sampling are reflected in different studies (Kipfmueller & Baker 1998; Singer et al. 2002; Higgins & Ruokolainen 2004). Austin (1981) experienced that more plots need to be sampled in random sampling to attain the same statistical significance compared to a systematic design. He adds that spatio-temporal changes are not detectable and only mean variations can be displayed. Colbach et al. (2000) state that a systematic sampling minimises the failure of choosing preferentially in the field, as is often the case in random sampling. Though the place of sampling is determined in the laboratory and transferred to a map or a satellite navigation device humans tend to adjust it in the field unintentionally when sampling randomly. Because of the stronger constraints this tendency is much weaker in systematic sampling.

When sampling systematically, a regular grid is projected on the region of interest, so that the variation in vegetation can be recorded objectively because plots are not subjectively chosen (Traxler 1998). This approach may suffer from inflexibility but objective (and systematic) location of sampling plots is an important preliminary when assessing spatial pattern. Cole et al. (2001) state that "the prime advantage of systematic sampling [...] is the efficient description of spatial pattern". However, systematic grid-based sampling might be exposed to the problem of spatial auto-correlation (Wildi 1986; Fortin 1999; Rahbek & Graves 2001; van Rensburg et al. 2002). The question is wether spatial auto-correlation is a paradigm or a problem when investigating vegetation (Legendre 1993). Accepting it as an intrinsic property of ecosystems and adapting this knowledge in ecological studies may provide a broader understanding of patterns and processes in vegetation (Legendre & Legendre 1998). Much more variance in a data set might be explained when spatial structure is included into the analysis (Legendre 1993). Cole et al. (2001) assume that one of the reasons for the lack of familiarity with grid-based sampling schemes may be the widespread availability of computer packages to compute analyses of variance, but lack of software to analyse spatial auto-correlation. However, there are know a range of possibilities available (e.g. packages geoR, sp and gstat for the R statistics system (R Development Core Team 2005), SAM, ArcGIS©).

On larger scales - especially on national or continental levels - grid based methods are widely adopted and successfully used to characterise and monitor biodiversity (e.g. Tutin et al. 1980; White et al. 1992; Diniz-Filho et al. 2003; Gaston & Rodriguez 2003; Hortal et al. 2004). The grids are often very large (e.g. spanning a continent or whole countries). Data are accumulated and generally several data sources have to be tuned to a shared level of grain (size of the sampling units) and extent (area over which observations are made, e.g.

Rahbek & Graves 2001; Araújo 2003; Thuiller et al. 2004). For a thorough discussion of the terms grain and extent see Gustafson (1998).

In the case of large scale studies grid cell size is often arbitrary or based on the structure of already available data or on cartographic grid systems. At the other extreme are studies with micro-grids such as those of Wiens & Milne (1989) who used a 5*5 m plot with different levels of subdivision to investigate beetle movement and its relation to micro-structures. Another study assessing logging and burning impacts on arthropods was carried out by Abbott et al. (2003). Within preferentially located plots 20*20m large grids, consisting of 4*4 pitfall traps with 5m spacing, were established.

The implementation of systematic grids at landscape or ecosystem scale is scarce. However, some examples can be found in recent literature: Schmidtlein (2003) used a systematic triangular grid consisting of circular, overlapping plots to assess patterns of vegetation at landscape scale. Titus et al. (2004) monitored submersed vegetation at two spatio-temporal scales inside an alkaline lake. Bowman et al. (2000) implemented nested rectangular grids on three spatial scales to determine which scales were relevant to demographic variability of small mammals. We infer that systematic sampling is an appropriate choice when looking for spatial patterns also on the landscape and ecosystem scale. But which is the grid form best suited for a comprehensive analysis of biodiversity?

Systematic grids - optimising cell arrangement

Squared or rectangular grids of varying size and extent are applied in ecological research and implemented to study different problems (see above). However, whereas in environmental research equidistant sampling grids (as hexagonal or triangular grids) are more common (Yfantis et al. 1987; Van Groeningen 2000; Zio et al. 2004) they are hardly used in ecology even though the hexagonal grid provides several advantages. These are discussed in the following.

Beierkuhnlein (1999) applied regular rectangular grids at landscape scale to characterise spatial pattern in vegetation through the calculation of resemblance measures between neighbouring plots. The author faced the following problems. First, adjacent plots are not equidistant (Fig. A2.1a). This is problematic if distance or similarity measures (such as Euclidean, Bray-Curtis, ChiSquare distance or Sørensen, Jaccard and Ochiai indices) are computed between adjacent cells in the grid to describe spatial pattern, because they calculate a similarity/distance in data space. Therefore the results can only be taken and displayed consistently if the compared plots all share the same geographic distance. The reason is that similarity is likely to decrease with distance. This phenomenon of distance decay was first published by Tobler (1970) and has been reformulated in an ecological context by (Nekola & White 1999). In a square grid it is unclear how much of the variation in similarity is explained by spatial configuration alone, when the similarity values between neighbours in the horizontal and vertical direction are compared with the values in diagonal direction. Second, if the similarities are calculated between one plot and all its neighbours, two results in the diagonal between two adjacent plots (see Fig. A2.1a) will be created. It is not feasible to calculate their mean because the results derive from two different pairs of plots. Beierkuhnlein (1999) suggested that this problem may be overcome by using a moving window technique. A different approach is implemented by Lennon et al. (2001; see also Williams 1996 and Gaston et al. 2001) who average the (dis) similarities between a focal cell of a square grid to the eight surrounding cells, thus disregarding the problem of distance decay. When implementing hexagonal (triangular) grids, the mentioned problems do not apply because every pair of neighbouring cells is unique and all cells are equidistant (see Fig. A2.1b).

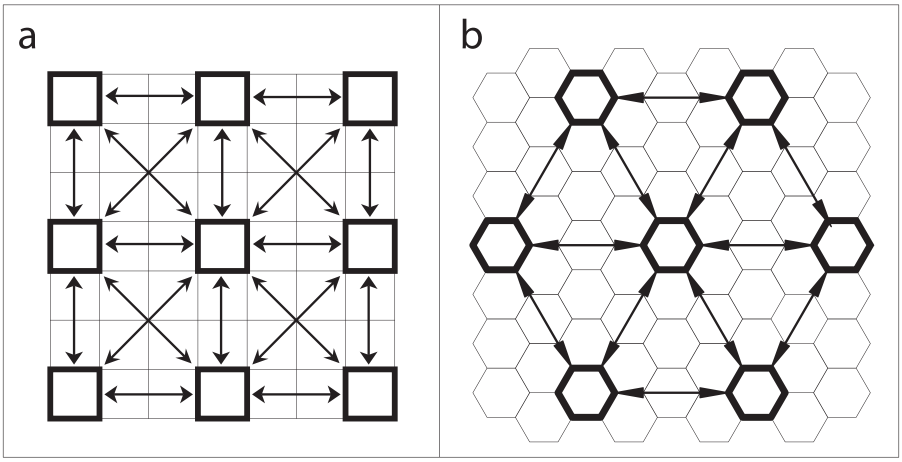

Figure A2.1. a) In a square grid the adjacent plots are not equidistant. Furthermore similarities calculated between different plots occur in one place (crossing diagonals). Calculating an average of those is not acceptable. **b)** In a hexagonal (or triangular) grid all adjacent neighbours are equidistant. All calculated similarity/dissimilarity values are unique.

A further argument supporting the application of hexagonal grids can be seen in cartography. White et al. (1992) developed the EPA (Environmental Protection Agency of the US) EMAP (Environmental Monitoring and Assessment Programme) grid, which is hexagonal, through consequent deduction following cartographic principles and trying to realise the least possible deviation in area when subdivided as a spherical tessellation. Furthermore distortion in shape is kept low over the extent of a face when hexagons are used for a projection surface. Following this implementation of a large scale hexagonal grid for monitoring purposes in the U.S. a project for vegetation mapping and monitoring in Hungary is under way. It is called MÉTA and is as well based on a hexagonal grid which covers the whole country with a resolution of 35 ha (http://www.novenyzetiterkep .hu/meta/en/index.shtml). Another project applying a large scale hexagonal grid for monitoring purposes was conducted in Flanders, Belgium by De Clercq & De Wulf (2004). The main purpose of such large scale projects is mapping. These can be realised in well developed countries and for long term inventories where educated staff (although often linked with voluntary work) as well as the institutional support is given, but they face many technical restrictions in less developed regions. However, those regions may experience the most serious and rapid changes in land-use and hence in biodiversity during the next decades (Balmford & Bond 2005; Millennium Ecosystem Assessment 2005; Secretariat of the Convention on Biological Diversity 2006). Pragmatic methods for medium scale studies, with relatively low resource demands, are therefore urgently needed (UNEP 2004).

The implementation of equidistant grids for modelling purposes may as well bear some advantages. The spatio-temporal changes in spatial patterns of biodiversity as well as in range sizes and geographical distributions in relation to global change (comprising land-use and climate change) are an issue of major interest (e.g. Theurillat & Guisan 2001; Walther et al. 2002; Thuiller 2003). But beyond monitoring, science and the public is interested to know what might happen in the future. Modelling can be used to estimate future developments. Beside studies which model physiological changes under climate change (e.g. Delucia et al. 2000; Dullinger et al. 2004) or the various FACE experiments which investigate physiological response to climate change (e.g. Warwick et al. 1998; Spinnler et al. 2002; Nowak et al. 2004) there are studies which implement systematic grids to model variation in spatial pattern (e.g. Hovestadt et al. 2000; Parrott 2004). The grids used in those models are still mostly squared. However, hexagonal grids might be very well suited for the modelling of change in vegetation pattern because every cell has six equidistant neighbours with which it shares the same length so migrating moves can be computed directly (Beecham & Farnsworth 1998; Oom et al. 2004). Furthermore shared length with adjacent cells (and therewith connectivity) is maximal in the hexagonal grid (Pagnutti et al. 2005).

Surprisingly hexagonal grids are rarely to be found in ecological field studies despite of papers communicating research for which field data was recorded based on the EPA EMAP grid (e.g. Stapanian et al. 1997; Polasky et al. 2000; Lawler et al. 2003). Apart from the EPA EMAP grid in only few studies hexagonal grid designs are applied (e.g. Hobson et al. 2002). In contrary to the low number of applications of hexagonal grids, Noss (2003) suggests that planning units for reserve design should preferably be on a hexagonal grid. These units shall be of appropriate and identical size "to capture relatively homogenous segments of a heterogeneous landscape" (ibid.).

All the large scale monitoring projects mentioned implement gapless grids which cover the whole area under study. Data representing certain features of a grid cell (as species richness or richness of landscape structure) are derived from one or several sampling locations inside the cell. Often data are accumulated or summarised. We propose a different strategy of data recording in hexagonal grids. Sampling takes place on regularly spaced units of the grid (Fig. A2.2). Spatial patterns of beta-diversity are explained through the calculation of (dis)similarity and distance measures between sampled grid cells.

Hexagonal plots - billions of bees cannot be wrong

We have already discussed advantages in the application of equidistant grids. But what is the appropriate shape of the sampling unit? We propose to use hexagonal plots. The first reason is consistency. It is neither possible nor expedient to conduct complete sampling in larger areas but if modelling is intended it might be useful if the grid is a complete one even though data recording is only done on evenly spaced sample plots (see Fig. A2.2). Furthermore it provides for iterative gap filling. If interesting patterns are found after the analysis of the primary data set, additional data can be recorded and used to understand these in more detail (Fig. A2.2).

There have been various attempts to find a proper plot-shape for vegetation analysis. Mueller-Dombois & Ellenberg (1974) proposed a nested quadrat to incoporate questions of scaling into the analysis. Shmida (1984) redeveloped the basic idea and proposed a nested design with different plot sizes and shapes inside a large rectangular plot (Whittaker-Plot). Later Stohlgren et al. (1995) introduced a Modified-Whittaker plot to correct some "design-flaws" after they experimented with a long-thin rectangular plot stimulated by Bormann's work (Bormann 1953). Bormann early showed that a long-thin rectangular plot contains more species than a square or circle plot of the same area especially if the vegetation is rather heterogeneous. The Modified-Whittaker plot is now a standard method (e.g. Campbell et

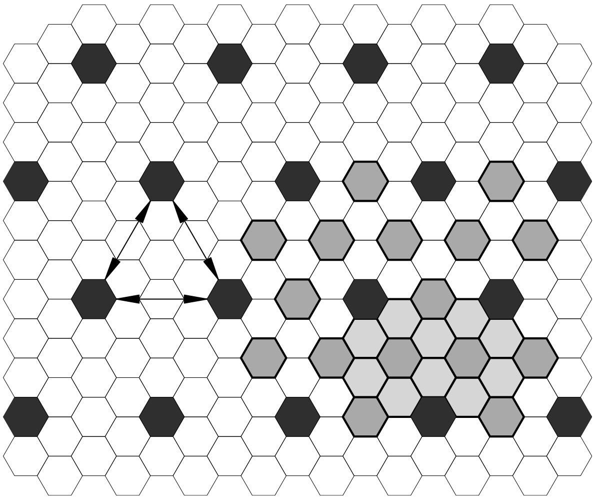

Figure A2.2 The grid provides for the possibility of iterative filling. This can be useful if a comprehensive description of a landscape is intended. The double-sided arrows symbolise the first step of calculation of similarities between adjacent cells of the primary grid (black cells). In areas of low similarity (or high dissimilarity) it is possible to record data on secondary grid cells (gray) and then again on tertiary grid cells (light gray).

al. 2002; Shackleton 2000; Barnett 2003) to assess mean species cover or to analyse plant diversity patterns at multiple spatial scales. It is appropriate if the variation in vegetation is studied but it seems to be "obviously inadequate for evaluating areal aspects of scale" (Podani et al. 1993). If a larger area is surveyed to reveal spatial patterns it is not suitable because in this case the sampling location itself should be rather homogeneous. Preferably the plot shape should be isodiametric to minimise vegetational heterogeneity captured by a single plot (ibid.).

Hexagonal plots show a smaller perimeter area ratio than square or rectangular plots. In this regard circular plots would be ideal. But it is hard to mark them out in the field unless working in open ecosystems like grasslands where compasses could be used or on very small plots. Schmidtlein (2003) used overlapping circular plots arranged in a triangular grid system for data recording but during calculation they turned to hexagons (because of the overlapping). So why not use hexagonal plots from the beginning as they are consistent with the hexagonal grid and have some more benefits: the lines which are used to mark out the plots in the field easily serve as a tool to assess quantitative data on structure.

The six equilateral triangles which build the hexagonal plot can also be used to record frequencies and it is very easy to set it up in the field with ropes and sticks (Jurasinski & Beierkuhnlein 2006). Beginning with a first triangle with one corner at the centre of the sampling unit and the reverse side facing North, the following segments can be set one after the other simply by adding two further ropes. The regular subdivision of a circle would be a far more complicated task as there would be no corners to relate to. Regularly shaped polygons with more than six corners show an ever decreasing perimeter area ratio, however, they are not consistent with the hexagonal grid. Furthermore, the effort for marking them in the field is increasing.

Discussion

Applying the hexagonal grid in the field

When systematic sampling is intended, a grid has to be developed dependent on the research or monitoring question. It can be constructed inside a GIS program package and projected over a region of interest. Up to now it was often a technical issue that squared or rectangular grids were used. With traditional methods it is easier to mark out a square grid in landscape. With modern DGPS (Differential Geographical Positioning System) techniques it is easy to navigate to the center points of the grid cells which are intended to be studied. Correction services via WAAS (Wide Area Augmentation System, available in the US) or EGNOS (European Geostationary Navigation Overlay Service in Europe) available today provide sufficient accuracy for navigation and already quite basic GPS devices are able to handle them. In less developed regions a more expensive DGPS set up with a base station and a rover can be used. With the implementation of the GALILEO system from 2008 a further increase regarding the accuracy of positioning is expected.

Spacing of sampling units (extent)

The specification of an "appropriate" mesh size or distance between neighbouring visited cells is a complicated task because it can extremely influence the results. This issue usually denoted as the zoning effect is well known to vegetation ecology (Greig-Smith 1983; Barkman 1989; Fortin et al. 1989). The computed similarity values will change with the distance (Nekola & White 1999) so the described pattern will change as well.

One possibility to handle this problem is the implementation of a spatially nested design where sampling takes place on different scale levels. Especially in species poor areas this might be useful. There it is likely that the scale on which changes emerge differs along relatively small distances. With this approach different plot sizes are used and the ratios to the distances can be the same on all scale levels. If the recorded cells belong to a complete grid array the distances between sampled cells follow from the amount of cells not sampled in between and their size. But how many of these should be left out? Pilot studies using cyclic sampling in transects might be a possible way to specify a suitable mesh size. E.g. when the distance between two neigbouring cells is given by x, 10 plots can be arranged along a linear transect such that 5 pairs of combination with the distance of x, 2x, 3x and 4x are resulting. With the species data gathered from these plots similarity indices can be calculated for all possible pairs of plots and then plotted against the geographical distance to examine the distance decay rate (Nekola & White 1999; Steinitz et al. 2006; Jurasinski & Beierkuhnlein submitted). From a given distance between plots the means of the similarity indices might no longer increase. This can then be used as the distance between recorded cells in the matrix.

This kind of pre-study possibly bears a general problem. If the variation in vegetation of the investigated area is non-isotropic one or two transects might lead to inappropriate conclusions regarding the distance between sampled cells. The gradients covered with this transects determine the decision for the "apposite" distance between plots for the whole data set. So more than one transect should be applied in different directions. Anyhow, it is important to keep the necessary labour in mind. As the grid is made up of a continuous array of hexagonal cells, it is obvious that with a change in cell size, the distance between visited cells (plots) would be affected as well. If this kind of pre-study is too labour intense or not operational, an alternative possibility may be the implementation of different distance levels. Recorded plots out of the grid can be set up with different spacing so that neighbours on each level share the same distance (Jurasinski & Beierkuhnlein 2006). This enables the assessment of the influence of spatial configuration and distance on the found patterns.

Size of sampling units

Not only the distance of the sampling units and the outer shape (arrangement) of the grid itself have to be adapted. Appropriate plot (cell) and mesh sizes have to be determined for each study dependent on the landscape/ecosystem under investigation and on the research question. The major problem in this regard is that the grain (size of the units of investigation (Wiens & Milne 1989; Allen & Hoekstra 1992) always effects the calculated similarities (Reed et al. 1993). This is known as the support or scaling effect in the geostatistical literature (Nekola & White 1999). With decreasing size of the observation unit the variation of a measured variable among those units is increasing (modifiable area unit problem - MAUP, see Openshaw & Taylor 1979).

Inside rather homogeneous systems it seems to be appropriate to use minimal area determination methods as known from vegetation ecology (increasing plot size subsequently and recording new species until the species area curve levels off). For hexagonal plots we propose to increase the area starting from the centre in steps of 1m radius. This means that the area is not exactly doubled as it is often done in similar approaches (Mueller-Dombois & Ellenberg 1974; Dierschke 1994; van der Maarel 2005). It is much easier to apply the area increase in that way because the ropes can be marked in 1m segments. Anyway, due to the nature of the hexagon it is almost a doubling in area from each step to the other. This leads to a type I curve after Scheiner (2004) with strictly nested plots. Each data point is based on a single measurement for a given size. Enlargement should be stopped when the number of species gained falls under a certain threshold. The procedure should be repeated several times on randomly located plots to obtain an adequate estimation for the appropriate plot size. We propose a conservative selection of plot size. Pre-study results should always be backed up by textbook knowledge.

If the investigation area is rather heterogeneous things might be more complicated. Investigation areas might exhibit heterogeneous vegetation mosaics as they are to find in Mediterranean ecosystems. In such situations, the largest minimal area has to be used, because plot size should be the same throughout one study. If different regions shall be compared with the proposed methodology it might as well be necessary to use the same plot sizes across investigation areas. Determination of adequate plot sizes is even more challenging in temporally variable conditions as found e.g. in semi-arid or Mediterranean systems. Imagine a study comparing vegetation patterns between dry and wet season in a semi-arid ecosystem. Again sampling units should be equally sized to obtain comparable data. So the plot size has to be set based on minimal area determination in wet season. This means that there can be very few species in a plot in dry season compared to wet season. This in turn might cause mathematical problems with the available similarity measures. Plotless sampling techniques could be a solution in situations like these (Mueller-Dombois & Ellenberg 1974; Kent & Coker 1994). In every case, when designing a systematic sampling we propose to start with the determination of the plot size. Even when plotless sampling is intended it is necessary to determine the cell size for the grid. If this is set, one can think about the mesh size (distances between sampled cells) because it depends on cell size.

Patterns emerge dependent on the scale of observation (Gustafson 1998). Through the setting of the sampling design it is predetermined which patterns are found. That is why it is crucial to accurately define the scope and the intention of studies trying to reveal and explain spatio-temporal patterns in nature. Preliminary investigations can be a possibility to determine the "best" plot size and distance between visited grid cells. However, the size of a plot and the distance to its neighbours are not necessarily linked. This might be a problem which can not be solved with pre-studies. With a hypothesis in mind regarding the potential factors influencing the expected patterns it should be possible to determine a cell and mesh size beforehand. We propose a spatially and dependent on variability in time also a temporally nested design to investigate the ecological factors shaping spatial patterns in nature comprehensively (Jurasinski & Beierkuhnlein 2006).

Applications and emerging issues

Regular sampling, especially when based on hexagonal grids, can be a valuable tool for a variety of applications ranging from long term conservation monitoring - where e.g. changes in species or vegetation distribution with time could be traced - to fundamental research regarding the relationship of vegetation patterns and underlying ecological and environmental factors (e.g. Jurasinski & Beierkuhnlein 2006). Especially for long-term monitoring purposes (Willis et al. 2005) where spatially and temporally explicit methods are needed, grid based methods can be of benefit. These offer profound assessment with relatively effortless sampling,

Research and data recording in vegetation ecology should be spatially and temporally explicit. Even when no spatial analysis is intended, this might provide for the incorporation of data in later meta-analyses. The hexagonal grid provides an efficient way to obtain such data. Furthermore it allows to track temporal changes in spatial patterns through periodically repeated sampling. The changes in spatial patterns can be assessed statistically (Jurasinski & Beierkuhnlein 2006). Thus, hexagonal grids provide an efficient methodology for the investigation and monitoring of spatio-temporal patterns on various scales.

The argument that non-square grids are harder to handle due to lacking methodology for analysis is simply not true. Recent studies implement hexagonal grids for modelling (e.g. Birch 2002; Céréghino et al. 2005; Jager et al. 2005). Software packages, such as FRAGSTATS 3.3 or packages of the R statistical system as gstat or sp, are freely available. These allow the implementation and analysis of data on hexagonal grids. Ricotta et al. (1997) proposed a way to calculate fractal dimension for non-square grids.

However, there are still open questions: How to determine the best plot size and a proper distance between sampling units for a certain question and ecosystem? Plant and community structure as well as previous field experience and preliminary investigations should govern our choices. A nested approach - with smaller sub-units inside sampling units and different distance levels - is an alternative way (Jurasinski & Beierkuhnlein 2006). It allows for the detection of the scale on which patterns emerge related to the variables in question.

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Appendix 3 Measuring multi-plot similarity with presence-absence data. *Ecology* (in preparation)

*Jurasinski, Gerald (gerald.jurasinski@uni-bayreuth.de); Retzer, Vroni (vroni.retzer@uni-bayreuth.de)

Address (both authors):
Biogeography, School of Biology, Chemistry and Earth Sciences, University of Bayreuth,
95440 Bayreuth, Germany

Abstract

Pattern diversity is an important level of spatial diversity. It can be assessed by calculating the similarity of one focal plot to its neighbors. Four approaches to the determination of similarity among multiple plots have been previously suggested in the literature: 1) mean similarity coefficient, 2) the standard deviation of the similarity coefficient, 3) additive and 4) multiplicative partitioning. These, however, suffer from serious drawbacks. Because they do not take species identity into account, different species pattern may result in the same value of the coefficient. This makes the explanation of the pattern difficult. Furthermore, additive and multiplicative partitioning exhibit strong edge effects which restrict applicability. Thus, we propose a new multi-plot similarity measure to neighbors (sim_{MPn}) which considers species identity. In tests with real and simulated data multi-plot similarity to neighbors performs best in the detection of gradients and hotspot. As investigations of pattern diversity rise in importance, multi-plot similarity may provide a valuable tool to investigate spatial pattern.

Keywords

beta diversity, pattern diversity, spatial pattern, conservation monitoring, gradient, hotspot detection

Introduction

Measuring and describing the distribution and diversity of organisms has long been a fundamental task for ecologists. A first framework for the description of diversity has been introduced into the ecological community by the work of Whittaker (1960; 1972a). His ideas have been subject to intensive debate and have been discussed, revised and expanded since (e.g. Routledge 1977; Wilson & Shmida 1984; Lande 1996; Vellend 2001). He introduced two diversity levels which until today are widely used: inventory diversity on one plot (commonly species richness or evenness, also known as alpha-diversity), and differentiation diversity between two plots (calculated as any resemblance measure, also known as beta-diversity). A third somewhat neglected level is the similarity of multiple plots: pattern similarity. According to Scheiner (1992) "pattern diversity is a measure of the relative arrangement of subunits within an ecological unit, such as communities in a landscape" (see also Pielou 1966; Turner et al. 1989). Comparisons of multiple neighboring plots seem a suitable method to investigate pattern diversity.

From 2-plot similarity to the similarity between multiple plots

For a comprehensive understanding and proper management of the biodiversity of an area all three levels are of importance. To evaluate the biodiversity on any plot, information is needed on its species richness and its similarity in species composition in relation to neighboring plots as well as on its uniqueness (or commonness) within the whole data set. Measures of inventory diversity (sampled or estimated species richness, see e.g. Colwell & Coddington 1994; Chao 2005) and resemblance coefficients (see reviews in e.g. Janson & Vegelius 1981; Wilson & Shmida 1984; Shi 1993; Koleff et al. 2003a) between two plots are well developed. However, commonly used similarity measures calculate the similarity between pairs of plots. This is a problem e.g. in conservation management, as the calculated values cannot be assigned to a certain plot, but rather to an area in between, which often has not even been sampled. This is especially problematic in diagonal comparisons of rectangular grids where two values exist. Additionally these coefficients calculate similarity between two plots. This makes them less suitable as in most applied sampling designs a given site (or plot) is surrounded by several neighbors, not just one.

Thus, a measure is needed, which describes the similarity of a sampled plot in relation to others (e.g. its neighbors) and thus directly allows an assessment of the uniqueness of the species composition of the focal plot in comparison to its neighbors. By doing so it indirectly integrates also information on species abundance.

Typical examples where multi-plot similarity is needed

Typical examples which call for the application of multi-plot resemblance measures are hotspot identification (e.g. Mittermeier et al. 1998; Myers et al. 2000) and gradient/boundary detection (e.g. Williams 1996; Heijnis et al. 1999; Harper et al. 2005). Questions for conservation management often involve some kind of hotspot identification. E.g. which area should be given priority for nature conservation? Typically, different potential areas have been selected in advance. To find the one with the most unique species composition all potential areas have to be compared to plots from the "normal" landscape. The area which differs most from the "norm" is given priority as it adds most to overall species diversity.

Another typical task in nature conservation is the design and improvement of agri-environment schemes in relation to gradients in land use intensity (e.g. Smart et al. 2006). To evaluate the contribution of single points along the gradient to overall diversity, these plots have to be compared to several neighboring plots. However, patterns in real landscapes usually do not follow single gradients. Therefore patterns which deviate from random have to be interpreted using appropriate environmental or land use variables.

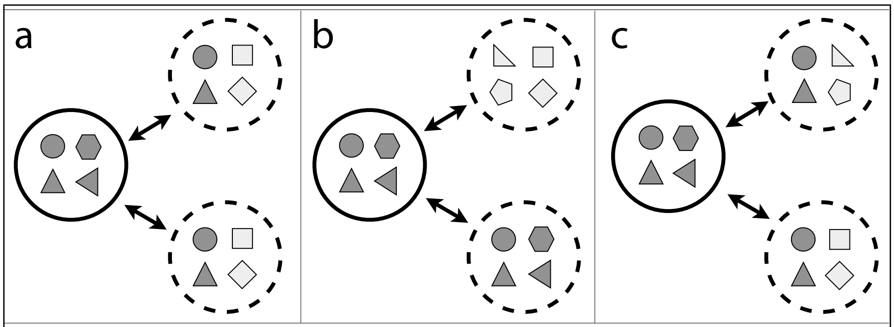
Results from the analysis can themselves be subject to further point pattern analysis regarding the distribution of pattern diversity in the landscape. The results can be directly used to improve nature conservation measures, for example by enhancing landscape connectivity for isolated hotspots in the landscape to improve seed dispersal and genetic exchange and thus stabilize populations.

Existing approaches to calculate similarity between multiple plots

Similarity between multiple plots has been calculated in different ways in the literature: 1) as the average (dis-)similarity between a focal plot and its neighbors, 2) as mean (dis-) similarity index and deviation from that mean, and 3) by additive partitioning of species richness. 4) Following the same logic as the latter, multiplicative partitioning could be used as well (see e.g. Williams 1996; Lennon et al. 2001).

Out of these, the simple averaging of similarities calculated between a focal plot and its neighbors, has been most frequently applied (e.g. Williams 1996; Gaston et al. 2001; Lennon et al. 2001). Scheiner (1992) proposed using mean similarity of a focal plot to all others as part of a measure for pattern diversity. Lennon et al. (2001) also used average Sørensen similarity and additionally introduced several other measures of multi-plot similarity (see also the review of Koleff et al. 2003a).

Multivariate dispersion – the average dissimilarity from individual observation units to their group centroid in multivariate space – is another expression of mean similarity to all other plots. It was recently proposed by Anderson et al. (2006) to measure differentiation (beta) diversity. However, all these approaches disregard species identities. Therefore, the same average values can derive from different patterns in species composition (Figure A3.1). Therefore its application for boundary detection or reserve selection is questionable.



sim_{mean} =	0.50	0.50	0.50
sim_{sd} =	0.00	0.71	0.00
sim_{add} =	0.66	0.50	0.50

Figure A3.1. Three different species patterns illustrating difficulties in the calculation of similarities between multiple plots. Species richness on each plot is constantly four while total species richness varies from six in **a)** to eight in **b)** & **c)**. For easier interpretation species occurring on the focal plot are in darker grey. The lower table gives the values of multi-plot similarity focal plot (solid circle) using the mean Sørensen similarity (sim_{mean}), its standard deviation (sim_{sd}) and additive partitioning (sim_{add}). Mean Sørensen similarity cannot detect any differences between the situations, the standard deviation describes the unequal distribution of shared species in **b)**, while additive partitioning detects changes in total species richness only.

Additionally the average similarity measures do not incorporate the variation of the values used to calculate the mean. Thus, several authors propose to include the variance of the pair-wise similarities (dispersion in the sense of Scheiner (1992), or part of a heterogeneity measure by Jurasinski & Beierkuhnlein accepted, see Figure A3.2). Coming from remote sensing, Mumby (2001) and Harborne (2006) calculate the mean Bray-Curtis dissimilarity and its variance from the plots of a moving window. However, even when the variation in mean similarities is included, it still disregards species identities: The same value of the similarity coefficient and its standard deviation can be derived from two very different situations (compare a & c in Figure A3.1).

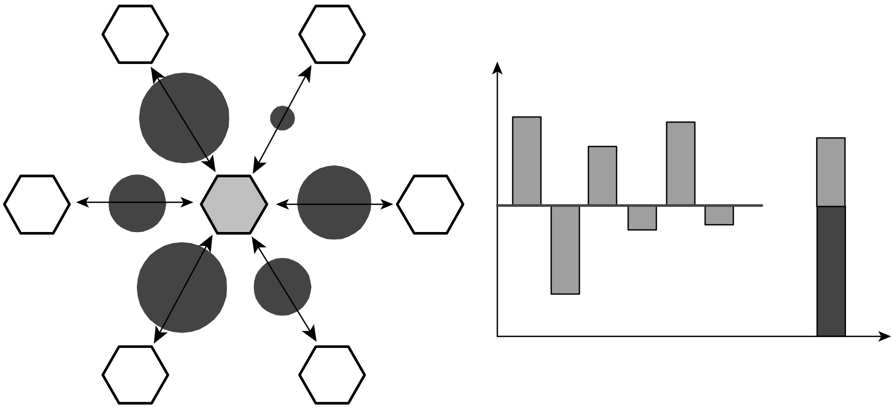


Figure A3.2. Representation of a measure for the similarity between a focal plot and its neighbors (as proposed by Jurasinski & Kreyling, accepted). a) The size of the black dots represents the similarity between the focal plot (grey hexagon) and the neighboring plots (white hexagons). b) To incorporate the spread of the similarities, the deviation of each single similarity value from the mean is taken into account (the grey line represents the mean similarity and light grey bars represent the deviation). The stacked bar represents the aggregated measure, with standard deviation of the deviations from the mean in light grey, and mean of mean similarity values in black (*sim_{mean}*).

Another concept for calculating similarity between multiple plots is additive partitioning (e.g. Lande 1996; Veech et al. 2002). In contrast to mean similarity it incorporates total species richness (see Figure A3.1). It is inspired by Whittaker's (1960) original definition of 'beta-diversity' as the average amount of diversity not found in a single random sample. Similarly, Whittaker's (1960) multiplicative partitioning of 'beta-diversity' as the relation of the diversity of a single plot to the aggregated diversity of multiple plots (usually the whole data set) can be applied to neighboring plots and thus used as a multi-plot similarity measure.

Required features for a robust measure of pattern diversity

From the introduction above it is obvious that a measure of pattern diversity should possess the following three properties:

1. It compares the similarity of a focal plot to several other plots, e.g. its surrounding neighbors taking species identity into account.

2. It yields a single value as result which can be directly attributed to the investigated focal plot.
3. Its values should range between 0 and 1 for the sake of standardization and ease of interpretation.

From the multi-plot similarity measures found in the literature and introduced above, none meets all these properties. Thus, we propose a new multi-plot similarity measure. We call it simply the coefficient of multi-plot similarity. The others discussed above are only here labeled with this term thus there are no name conflicts. The performance of this new measure regarding the detection of typical pattern (random, gradient and hotspot) is tested against that of the existing measures using a real and simulated data sets.

Material and methods

Data

For evaluating the performance of the different multi-plot similarity measures introduced above, a real data set from a Tundra ecosystem is used. As the "true" pattern in such data sets is unknown, new methodology is most commonly tested using artificial data sets with known properties (e.g. Kiflawi & Spencer 2004; Legendre et al. 2005). Here, we use the properties of the real data set and artificially re-arrange the position of the species on the sites to simulate different gradients (see Box A3.1 for an overview of the data sets implemented and the coefficients applied).

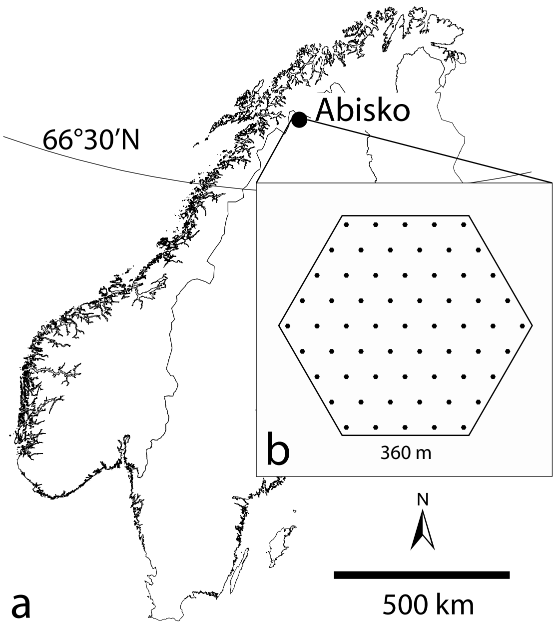


Figure A3.3. a) Location of Abisko in Northern Sweden (Map adapted from Rettenmaier 2004). **b)** Sampling grid established in the summer of 2004. Dots represent plots which were sampled for plant species. The grid consists of 61 plots with 5m radius. The plot centers share a distance of 90m. Size and distance to neighbors was determined during a pre-study in the field.

Real data

The data set is derived from a case study in a Tundra ecosystem near Abisko in Northern Sweden (Figure A3.3, see also Rettenmaier 2004). Precipitation in the Abisko valley is comparably low (304 mm/a), mean annual temperature is ~0.5°C. The dominant vegetation consists of a mosaic of dwarf shrubs and small fragments of birch forests mixed with small heath areas. Vegetation data was recorded in the summer of 2004 as abundance data on 61 plots of 5 m radius arranged in an equidistant hexagonal grid (see Figure A3.3). The distance between plot centres is 90 m. Size and distance to neighbors was determined by a pre-study. For the purpose of testing the new coefficient we transformed the species abundances to presence/absence data.

Artificial data - gradients and hotspots

To create the artificial data sets an R function (R Development Core Team 2005) has been implemented which reorganizes an input matrix according to the desired gradients in species composition (All functions discussed in this contribution are part of the package *simba* which can be derived from CRAN - http://cran.r-project.com/). The general characteristics of the artificial species matrix, such as: species richness, number of plots, and the species-abundance distribution, are taken from the input data (in our case the real Abisko data set). For a detailed explanation of the creation of the artificial data sets see Appendix I.

Box A3.1. Overview of the implemented data sets and the tested coefficients (see text for details).

datasets

- real data (Abisko, Northern Sweden)
- artificial data
  - random distribution
  - vertical gradient
  - diagonal gradient
  - hotspot in the centre
  - super artificial gradient (species are displacing each other regularly from North to South)

coefficients

- multi-plot similarity to neighbors
- multi-plot similarity to all other plots
- mean similarity between focal plot and its neighbors
- standard deviation of the similarities between a focal plot and its neighbors
- additive partitioning applied to the neighborhood of each plot (moving window)
- multiplicative partitioning applied to the neighborhood of each plot (moving window)

Three different virtual gradients are constructed and used to create the artificial data sets (see Figure A3.4): ‘vertical gradient’, ‘diagonal gradient’, and ‘hotspot centre’. Additionally two further artificial data sets which mark the extremes of species distribution are created: a totally random species distribution and a super artificial gradient. In the super artificial gradient the species displace each other in a regular manner from North to South with no variation from East to West and a regular turnover of 50 % of the species between each row (each plot has 32 species, see Table A3.1).

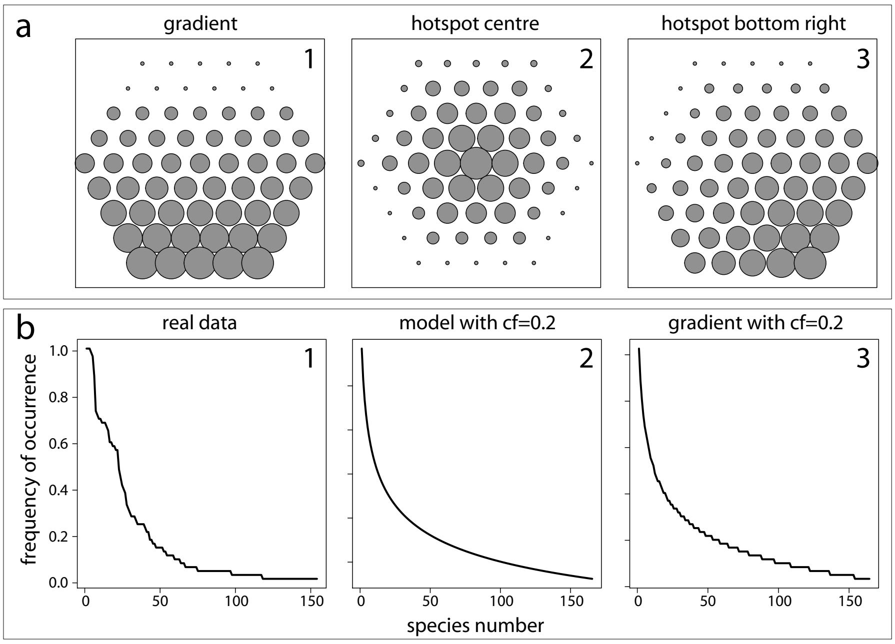


Figure A3.4. a) Visualisation of the gradients applied to the artificial data sets. Dot size represents the gradient but has no quantitative meaning. It just indicates in which direction the gradient is running. Along the gradient species composition changes (for details see text). **b)** Species frequency distribution curves for **1)** the real data from the abisko study, **2)** the model according to Formula 6, **3)** the vertical gradient (however, it is the same for all artificial datasets).

Table A3.1. Model matrix for the super artificial gradient. '1' represents 16 species, a row represents all plots in a row of the sampling grid, first row=accumulated species number, first column = accumulated plot number.

		accumulated species number									
row-number	accumulated plot number	16	32	48	64	80	96	112	128	144	160
1	5	1	1	0	0	0	0	0	0	0	0
2	11	0	1	1	0	0	0	0	0	0	0
3	18	0	0	1	1	0	0	0	0	0	0
4	26	0	0	0	1	1	0	0	0	0	0
5	35	0	0	0	0	1	1	0	0	0	0
6	43	0	0	0	0	0	1	1	0	0	0
7	50	0	0	0	0	0	0	1	1	0	0
8	56	0	0	0	0	0	0	0	1	1	0
9	61	0	0	0	0	0	0	0	0	1	1

Calculations of multi-plot similarity

sim_{MPn} and sim_{MPa} – the new multi-plot similarity measures

The basic idea of the new multi-plot similarity measures is to include species identity into the computation. The calculation is based on the occurrences of species on the compared plots, and thus is similar to a spatial extension of the well known binary similarity measures such as Jaccard (1901) or Sørensen (1948): The frequency of occurrence on the compared plots is summed up for all species. This value is normalized by the number of plots and the total number of species on compared plots (Formula A3.1, with n = number of plots compared (may vary due to edge effects), i = frequency of a certain species on the n plots to compare, s_i = number of species with frequency i on all n plots, SR_n = total species richness on the n plots).

$$sim_{MP} = \frac{\sum_{i=1}^{n} f_i}{n \times SR_n} \qquad \text{(A3.1)}$$

Furthermore, the index can be used to compare the focal plot either to all other plots in the data set (sim_{MPa}) or to certain neighboring plots only (sim_{MPn}): sim_{MPa} calculates a multi-plot similarity in comparison to the whole data set. sim_{MPn} compares a focal plot to all neighbors within a specified radius. Optionally, 'neighbors' can be defined within a ring around the focal plot by giving two radiuses. This can be used to evaluate the decrease of similarity with geographical separation (distance decay) from each plot.

Other diversity measures adaptable to multi-plot comparisons

All four coefficients adaptable to multiple-plot comparisons introduced above are implemented: The *average similarity* calculated from the similarities between a focal plot and its neighbors (sim_{mean} Formula A3.2, see e.g. Williams 1996; Lennon et al. 2001; Koleff et al. 2003b) and the *variation of these similarities* expressed as the standard deviation (sim_{sd}, Formula A3.3, Jurasinski & Beierkuhnlein submitted-a). Furthermore a simple coefficient of *additive partitioning* which takes species richness as the measure of inventory diversity (sim_{add}, Formula A3.4, see e.g. Lande 1996; Veech et al. 2002; Gering et al. 2003) and the coefficient of *multiplicative partitioning* in the full change notion of Whittaker (1972; sim_{mul}, Formula A3.5, see e.g. Kiflawi & Spencer 2004, Williams 1996). To our knowledge additive partitioning has not been used in this context yet. However, as it can easily be calculated not only for the whole data set but also for defined neighboring plots it is included in the comparison. Each of these coefficients is applied to each of the data sets (Box A3.1).

$$sim_{mean} = \frac{1}{n}\sum_{i=1}^{n} sim_i \qquad \text{(A3.2)}$$

$$sim_{sd} = \sqrt{\frac{1}{n-1}\sum_{i=1}^{n}\left(sim_i - \overline{sim}\right)^2} \qquad \text{(A3.3)}$$

$$sim_{add} = SR_n - \overline{SR}_n \qquad \text{(A3.4)}$$

$$sim_{mul} = \frac{SR_n}{\overline{SR}} \qquad \text{(A3.5)}$$

Testing the significance of multi-plot comparisons

The significance of the results is assessed with a permutation procedure. The null hypothesis is a random species distribution. After the calculation of the multi-plot similarity values, the species matrix is randomly rearranged in such a way that the frequency of each species is preserved but the species occurrences are randomly shuffled among the plots. Species co-occurrences in the sense of Miklós & Podani (2004, see also Gotelli & Entsminger 2003) are not taken into account. Significant values indicate that the respective similarity, calculated for a specific plot, is significantly different from random expectations. Significance is tested on both tails depending on the original multi-plot similarity value: If this is below average of the random distribution, the lower tail is tested, if it is above average, the upper tail is tested.

As neither the gradients in the real data nor in the random data are known we also relate the results to the species richness on the plots to evaluate to which extent the values depend on species richness on the focal plot.

Evaluating the performance of the measures

The performance of the six coefficients regarding the detection of the patterns in the six different data sets (Box A3.1) is assessed in two ways. The visual representation of the pattern is discussed in relation to the underlying known gradient and to the pattern derived from calculating standard pair-wise Sørensen similarity between neighboring plots. Sørensen is used because it is relatively widespread and has been proven reliable and robust with ecological data (e.g. Wolda 1981; Hubalek 1982; Shi 1993). Secondly, a more formal test was applied by calculating a Mantel statistic between the multi-plot similarity value of each plot and its position on the gradient. A good coefficient will have a high correlation with the position as this is what we seek to describe. In the gradient cases the species composition changes in two directions along the gradient. Therefore, the results are related to the absolute deviation of the geographic position from the centre of the gradient in these cases.

The significance of the correlation is obtained through a permutation procedure (Legendre & Legendre 1998). This is necessary because the values of the coefficients are not truly independent from each other as they are calculated in a moving window approach. This means, that all focal plots are also neighbors to others and their species composition determines the value of the coefficient for another focal plot.

Results

Visual interpretation

The results of applying the six different coefficients to the different data sets can visually be compared by scaling them all within the same range (Figure A3.5). The coefficient of multi-plot similarity to neighbors (sim_{MPn}) detects all gradients and the hotspot rather well, but fails in detecting the super artificial gradient. In contrast, multi-plot similarity to all (sim_{MPa}) performs worse for the normal (vertical) gradient (Figure A3.5.17). However, it is the only one which can visualize the super artificial gradient, in which species replace each other in a regular manner. Average similarity (sim_{mean}) behaves rather similar to the multi-plot similarity to neighbors (sim_{MPn}), although the latter seems to be more responsive to small changes (compare Figure A3.5.16 to A3.5.18 and A3.5.30 to A3.5.32). The pattern exhibited by the coefficient of standard deviation of the similarity values (sim_{sd}) does not reveal any of the gradients nor the hotspot. The patterns described by sim_{sd} are fundamentally different from those which all other coefficients detect. The multiplicative partitioning (sim_{mul}) and the additive partitioning coefficient (sim_{add}) show considerable edge effects. Thus, interpretation is restricted to the inner plots only. Both seem to detect the gradient, but multiplicative partitioning (sim_{mul}) performs better in detecting the diagonal gradient and the hotspot.

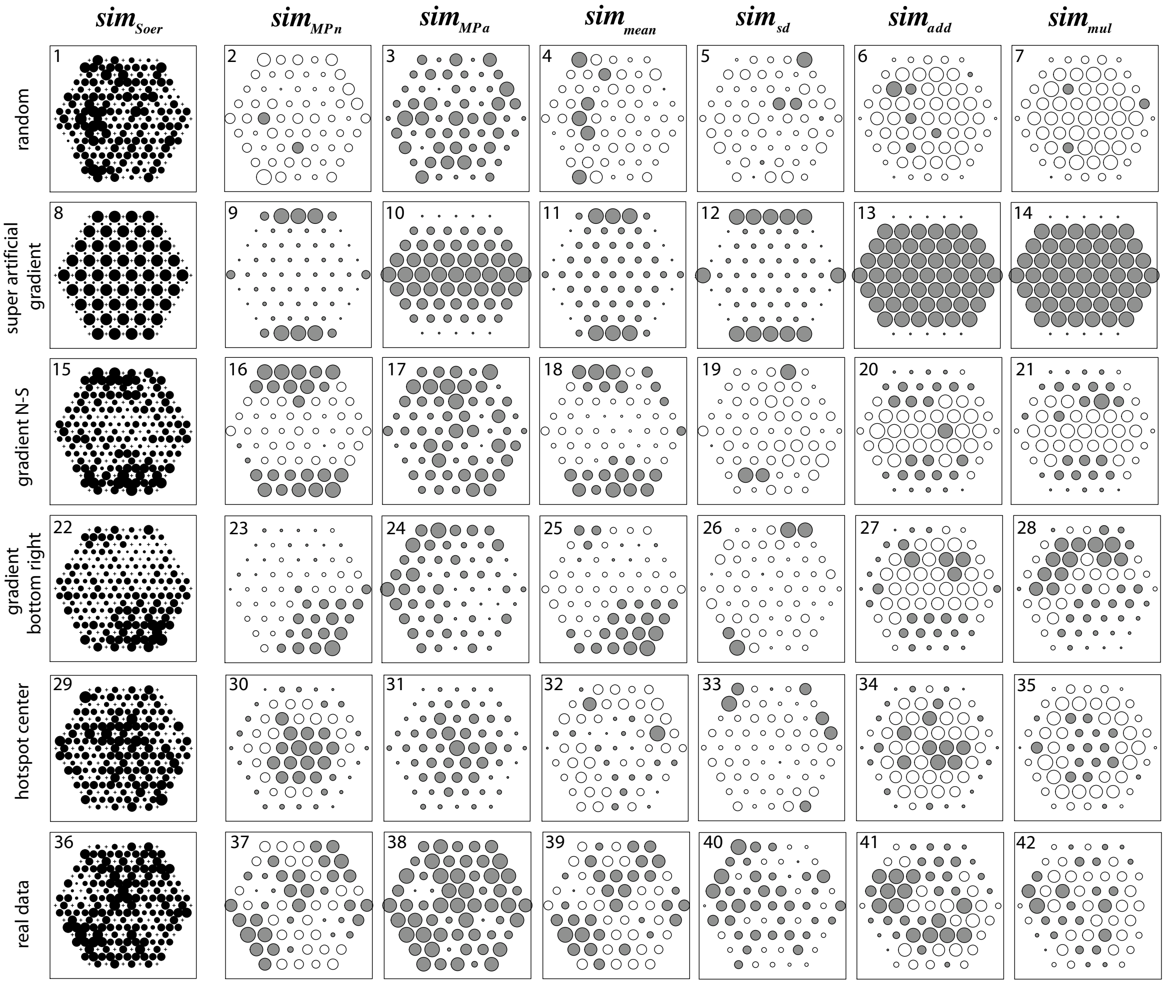


Figure A3.5. Similarity patterns resulting from the application of the tested indices to the six data sets. Each row represents the pattern for one data set. **1-7)** random distribution, **8-14)** super artificial gradient, **15-21)** vertical gradient, **22-28)** diagonal gradient, **29-35)** hotspot center, **36-42)** real data (Abisko, Northern Sweden). Bigger dots express higher similarity. Please note, that each subfigure is individually scaled between its minimum and maximum values. For comparison, the Sørensen similarity coefficient between neighboring plots are shown in the first column (crosses represent plot positions). Subsequent columns show the similarity of each plot compared to its neighbors calculated with the indicated coefficient. (column names). All indices are calculated with a moving window approach. If the distance to a neighbour in the equidistant grid is x, a neighbourhod consists of a plot and all other plots a distance x apart. Therefore plots on the edges have less neighbours. Gray dots display significant values (tested with a permuation procedure against random expectations). Note that in the case of hotspot center dissimilarities are displayed (because this is much mor interesting when hotspots are to be detected.

Correlation between coefficients

The Pearson product moment correlation between the different coefficients confirms the visual impressions (Table A3.2). For the vertical gradient, sim_{MPn}, sim_{mean}, sim_{add}, and sim_{mul} ı show a high correlation, while sim_{MPa}, and sim_{sd} are different (lower triangle). For the real data set, sim_{MPn}, sim_{MPa}, and sim_{mean}, as well as sim_{add} and sim_{mul} are highly correlated. Again, sim_{sd} and sim_{MPa} differ from all others, although sim_{MPa} is correlated with sim_{MPn}.

Detection of hotspot and gradients

Regarding the correlation to the position on the gradient, multi-plot similarity to neighbors (sim_{MPn}) performs best as well for both simulated semi-natural gradients as for the hotspot data set (see Table A3.3). Additive similarity (sim_{add}) performs second best for the vertical gradient, although this is not obvious in Figure A3.5. Multi-plot similarity to all (sim_{MPa}) performs second best for the hotspot and the diagonal gradient. However, the correlation with the diagonal gradient is negative. This indicates that similarity from a focal plot to all others is higher in the middle of the gradient. Furthermore, the coefficient of multi-plot similarity to all plots (sim_{MPa}) has the highest correlation with species richness on the plots for all data sets (Table A3.3). Again the correlation for this coefficient are generally negative. However, it is positive for the hotspot data. This is due to the fact that these are displayed and handled as dissimilarities because a hotspot qualifies itself by being different from the matrix. This means, that correlation to similarities is negative in this case as well. Thus the pattern is very general: the fewer species on a plot, the higher its value of sim_{MPa}. Apart from this coefficent, correlations of index values and species richness do not show such a clear pattern. The values of multi-plot similarity to neighbors (sim_{MPn}) are significantly correlated with species richness for all data sets. However, the relation is sometimes positive, and sometimes negative depending on data set. All coefficients are significantly related to species richness in the hotspot and the super artificial gradient data sets. Generally, species richness and the values of sim_{mean}, sim_{sd}, sim_{add}, sim_{mul} are related in a non-uniform way.

Table A3.2. Correlation (Pearson product moment) between the coefficients of similarity between multiple-plots. The upper triangles gives the correlations for the real data set, the lower triangle the ones for the vertical gradient. Significance was not tested.

	sim_{MPn}	sim_{MPa}	sim_{mean}	sim_{sd}	sim_{add}	sim_{mul}
sim_{MPn}	—	0,843	0,826	-0,057	0,557	0,454
sim_{MPa}	0,608	—	0,609	-0,253	0,173	0,160
sim_{mean}	0,842	0,232	—	0,132	0,419	0,363
sim_{sd}	-0,040	-0,026	0,045	—	0,272	0,328
sim_{add}	0,809	0,194	0,745	0,081	—	0,894
sim_{mul}	0,713	0,140	0,703	0,155	0,957	—

Performance of the different coefficients

Regarding the detection of the semi-natural gradients and the hotspot (visual interpretation and correlation), sim_{MPn} performs comparably well. The multi-plot similarity to all (sim_{MPa}) has a serious weakness in the detection of the vertical gradient, but grasps the super artificial gradient best. However, significance testing is problematic. Due to the comparison to all other plots in the data set the variance within a random data set is so low, that in comparison all others become significant. Mean Sørensen similarity (sim_{mean}) detects the gradients well, but fails to describe the hotspot. This describes exactly the problem of not taking species identity in account. The coefficient of sim_{sd} performs worst of all, and is not suitable as a multi-plot similarity measure. Due to the great edge effects sim_{mul} and sim_{add} are of very limited practical use: A large fraction of sampling effort cannot be used because only the pattern in the inner area can be interpreted (see last two columns in Figure A3.5). Furthermore, the high correlation with the hotspot (Table 3) more likely is due to these edge artefacts (smaller values at the outer plots) than to the real ability to detect the hotspot (compare Figure A3.5.34 and A3.5.35). Thus, taking all criteria into account, multi-plot similarity to neighbors (sim_{MPn}) is an appropriate tool for the detection of gradients and hotspot in diversity in small and medium scale studies.

Table A3.3. Mantel correlation between coefficients of multi-plot similarity and test variables. Because the values of the coefficients of the plots are partially interdependent, significance was tested with a permutation procedure (Mantel test). Bold values mark the highest and grey values mark the second highest correlation for the respective data set.

	coefficients expressing similarity between multiple plots					
data-set	sim_{MPn}	sim_{MPa}	sim_{mean}	sim_{sd}	sim_{add}	sim_{mul}
a) Correlation to the position on the gradient[1]						
gradient North/South	0,824***	0,364**	0,738***	0,082	-0,755***	-0,656***
gradient bottom right	0.878***	-0.635***	0.553***	-0.235*	0.103	-0.410**
hotspot center	0.940***	0.901***	-0.255*	-0.362**	0.878***	0.394**
b) Correlation to inventory diversity (measured as species richness) on the plots						
gradient North/South	-0,516***	-0,893***	-0,061	-0,152	0,134	0,089
gradient bottom right	0,851***	-0,882***	0,418***	-0,265*	0,204	-0,266*
hotspot center	0.918***	0.976***	-0.331**	-0.308**	0.771***	0.360**
real data	-0,721***	-0,862***	-0,328**	-0,292*	0,161	0,180
random distribution	-0,424***	-0,734***	0,458**	-0,183	-0,101	-0,051
super artificial gradient	0,527***	-0,972***	0,392***	0,469***	-0,690***	-0,690***

[1]) Only the data-sets with a known gradient can be evaluated like this.

Discussion

The detection of gradients and hotspots is an important task in nature conservation – e.g. for reserve planning and design. Thus, researchers have called for a stronger consideration of differentiation diversity in conservation (Wiersma & Urban 2005). Multi-plot similarity in general can provide a valuable tool for such applications. The coefficient of multi-plot similarity to neighbors (sim_{MPn}) performs better than other indices which have been implemented for gradient detection so far - the average diversity from a focal plot to its neighbors, and the multiplicative partitioning (Whittaker's *beta,* e.g. Williams 1996; Lennon et al. 2001; Koleff & Gaston 2002). Koleff et al. (2001) used an average dissimilarity measure (like sim_{mean}) to investigate the transition between different species compositions (which can be seen as gradient detection as well). Although sim_{mean} performs quite well in gradient detection, it is ouperformed by sim_{MPn} for all tested data sets.

One general problem of measures of similarity to multiple plots may be the detection of boundaries. As long as the calculation is based on all surrounding plots, it cannot differentiate directional change from alternating pattern. However, alternative boundary detection methods, e.g. from Fortin et al. (Fortin & Drapeau 1995; Fortin et al. 1996; Fortin 1997; Fortin 1999) are not directional as well. As 'real' boundaries usually are not that sharp anyway (Zonneveld 1974; van der Maarel 1976), this problem may remain purely academic.

Koleff et al. (2001) question the idea of choosing explicitly transitional areas for conservation purposes, as these do not protect the core habitats and thus strongholds of species, but rather their peripheral populations most vulnerable to random extinctions. Hence the overall dissimilarity of a site or plot to all other considered sites might be a stronger indicator for conservational value. This could be measured using $sim_{MPa,}$ which performs comparably well in detecting the hotspot (but not in gradient detection). This comes as no surprise as the dissimilarity to all other plots should be highest on the hotspot.

Problems arising with similarities between multiple plots: distance decay and MAUP

Due to the method of calculation all the coefficients tested here fulfil the requirements proposed in the introduction and compare the similarity of a focal plot to several other plots and yield a single value which can be directly attributed to the investigated focal plot. However, measures of similarity to all plots in the data set are generally problematic as they are subject to the phenomenon of distance decay - the similarity of units decreases with the distance between them (Tobler 1970; Nekola & White 1999). The distance of a focal plot to all others in a data set varies, dependent on its own position in space. Thus, each value of multi-plot similarity to all (sim_{MPa}) assigned to a specific plot contains an unknown proportion due to distance decay which varies from plot to plot. This might hinder the interpretation of any pattern detected. The coefficient of sim_{MPa} shares this problem with all measures which incorporate all plots in the data set, regardless of their distance (see e.g. Scheiner's (1992) affinity). Correspondingly, Vellend (2001), who proposes to measure heterogeneity in species composition among plots by calculating the mean (dis)similarity between pairs of plots, acknowledges that the spatial arrangement of plots is ignored.

Another difficulty related to distance decay becomes apparent in non-equidistant grids. Typically, data from rectangular grids has been used to calculate mean similarity between a focal plot to its eight surrounding neighbors (e.g. Williams 1996; Koleff & Gaston 2001; Koleff et al. 2003b). This approach disregards the different distances which occur in rectangular grids: The diagonal distances differ from the horizontal and vertical distances by a factor of $\sqrt{2}$. This difference in distance is not accounted for when the eight surrounding plots in a square array are treated equally. The only means to avoid this problem are equidistant sampling grids (Jurasinski & Beierkuhnlein 2006; Jurasinski & Beierkuhnlein submitted-b).

Additionally, some of the applied coefficients are heavily exposed to the modifiable area unit problem (MAUP, Openshaw & Taylor 1979): Due to the long-known species-area-relationship more species have to be expected on a larger area (e.g. Arrhenius 1921; Gleason 1922), thus comparing the focal plot to a larger area is problematic. This is mainly a problem of the coefficients based on additive and multiplicative partitioning. However, this is exactly what these indices are designed for: The investigation of the distribution of inventory (alpha) diversity across scales (Jurasinski et al. submitted). Indirectly the multi-plot similarities (sim_{MPn} and sim_{MPa}) are also affected by MAUP although they do not use species richness but frequencies. Lennon et al. (2001) sought to solve this problem by aggregating the species data for all neighbors and calculating the similarity between the focal plot and one 'virtual plot' containing all species from the neighboring plots. Koleff et al. (2003a) show, that the results deviate substantially from the average similarity value between the focal unit and its neighborhood. Therefore, this procedure is not advisable, because this calculation again is affected by the MAUP, although the coefficient of average similarity (sim_{mean}) and its standard deviation (sim_{sd}) are otherwise not exposed to the problem.

Special characteristics of some coefficients

The calculation of multi-plot similarity to all (sim_{MPa}) can be regarded an 'ordination on the spot'. As in ordination, the plots are described by their dissimilarity to all other samples. The species and sample dissimilarity spaces are defined by the floristic composition of the data set, and are thus floristic spaces (Gauch & Whittaker 1972; Økland 1986). However, the floristic composition in the data set and the relation of the composition of any focal plot to the composition of the others determine the value of sim_{MPa}. Thus it enables the detection of sites which considerably differ from the rest. Furthermore it exhibits the best (and always negative) correlation with species richness on the plots. This is based on likelihood. When there are many species on the focal plot, there is a higher chance that some of them do not occur on other plots, thus sim_{MPa} tends to be lower and vice versa. This approach is comparable to the coefficient of multivariate dispersion recently proposed by Anderson (2006) which is defined as "the average distance (or dissimilarity) from an individual sample to the group centroid" of a (dis) similarity matrix.

The variation in the mean similarities for a focal plot (sim_{sd}) has a radically different characteristic compared to all other coefficients tested (Table 2). Obviously it is not suited to measure turnover or detect gradients. As Legendre et al. (2005) state, it is not a measure of differentiation (beta) diversity which is clearly apparent in Figure 5 as well. However, it can be used as a measure of spatial heterogeneity, that is, the variability of compositional similarity in space (Jurasinski & Kreyling accepted).

Conclusion

The calculation of similarity values for a focal plot to express its similarity to neighbors is not new in ecology, but yet sparsely applied. All approaches implemented so far suffer from one or several problems (species area relation, disregarding species identity, distance decay, gradient detection ability). The newly introduced coefficient of multi-plot similarity to neighbors (sim_{MPn}) performs best of the tested coefficients. With increasing availability of spatial data such coefficients can be applied to numerous ecological questions. Possible applications lay in conservation planning or reserve design, but also in ecological research when species composition is to be related to drivers such as land use or climate.

Acknowledgements

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Appendix I – Artificial data set creation

First, an empty species matrix with the specified number of plots and species is constructed. These parameters are either derived from a real species matrix recorded in the field or can be specified as required. Then the gradient vector is applied to the empty matrix in such a way that the probability of occurrence along the gradient increases from 0 to 1 for half of the species and decreases for the other half.

This probability gradient matrix is randomly transferred into a binary gradient matrix: This is a random presence-absence manifestation according to the probabilities laid down in the probability gradient matrix. Thus, a plot with a 0.4 probability of occurrence of a certain species on average will receive four times out of ten a '1' and six times a '0'. The binary gradient matrix marks the positions at which species can potentially occur in order to form the defined gradient. About 50 % of all possible occurrences are now marked with '1' as potential occurrences of species and such describe the artificial gradient.

In the next step, a 'realistic' species frequency distribution has to be applied to the binary gradient matrix. The shape of the species frequency distribution is controlled by the parameter *cf* (Formula 6, with S_i= *i*th species and S_0 = frequency of *i*th species) which is set to a default value of 0.2 resembling a power-law distribution (see Figure A3.4b for representations of the curve with 161 species and *cf* = 0.2 compared to the natural curve of the Abisko data). Now presence of each species is randomly sampled from its probable occurrences laid down in the binary gradient matrix as often as it occurs in the data set (defined by its frequency).

$$S_O = \frac{1}{S_i^{cf}} \tag{6}$$

Additionally ubiquitous species which occur on more than 50 % of the plots are randomly re-arranged in the final species matrix and thus enter a erratic element which does not follow the gradient.

This procedure of creating artificial data sets is covered within the supplied R package *simba*. It can either be used to create artificial data sets “from scratch” or to re-arrange real data sets. It very closely mimics the frequency distribution of the species in the real set, total species richness and average species richness per plot. It does not preserve species co-occurrence pattern (compare Miklós & Podani 2004).

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Appendix 4 Spatial patterns of biodiversity - assessing vegetation using hexagonal grids. *Proceedings of the Royal Irish Academy - Biology and Environment* (2005) 106B: 401-411

*Jurasinski, Gerald (gerald.jurasinski@uni-bayreuth.de); Beierkuhnlein Carl (carl.beierkuhnlein@uni-bayreuth.de)

Address (all authors):
Biogeography, School of Biology, Chemistry and Earth Sciences, University of Bayreuth, 95440 Bayreuth, Germany

Abstract

We still lack quantitative and comprehensive methods to assess spatio-temporal changes in biodiversity of landscapes. Even more, we need methods to determine the amounts of change especially in the light of the current acceleration in the loss of biodiversity.

We have developed a widely applicable method to reveal spatio-temporal changes in vegetation patterns and relate them to ecosystem processes. We use a systematic grid of hexagonal plots in a spatially nested design (three spatial scales and levels) to examine these patterns. The hexagonal grid, as well as the hexagonal plot, provides several advantages compared to other methods. Most important in the context of evaluating patterns is the equidistant nature of the grid. This facilitates data analysis and circumvents statistical and logical problems (compared to squared or circular plots). Correlation is very strong (r=0.88**) between structural data assessed with the Line-Intercept-Method and that gathered from field sketches. This indicates that the lines used to mark out the plots provide an easy and feasible method to assess quantitative data on structure and disturbance. We show that frequency data does not perform better than presence-absence data regarding correlation with other variables. We conclude that the hexagonal grid provides an efficient method to assess patterns of biodiversity.

Keywords

beta-diversity, systematic sampling, equidistant grid, similarity measure, line-intercept method, Morocco.

Introduction

Land-use and land-use changes are amongst the main drivers of biodiversity loss (e.g. Austrheim et al. 1999; Crist et al. 2000; Sala et al. 2000; Allan et al. 2002). However, changes are often difficult to measure; individuals of a species may still be found flowering although the population has been in decline for decades and has only survived with a few over-aged specimens on a small remnant area. Furthermore, populations often change their geographic occurrence or their density in a given region. There are hardly any reliable methods to assess and track such changes.

In general, recent literature on the influence of global change on biodiversity focuses either on the human-environmental-system (very large scale and meta data analysis, e.g. in Ayres and Lombardero 2000; Hannah et al. 2002; de Vries et al. 2003) or on specific organisms or even organic responses to climate change (very small scale and mostly experimental, e.g. Constable et al. 1999; Bermejo et al. 2002; Hättenschwiler & Körner 2003; Körner 2003). Information at a medium scale (landscape, ecosystem, habitat) looking at shifts in community composition is scarce (e.g. Gottfried et al. 1998). Hence, we need spatially and temporarily explicit and widely applicable methods giving comparable results to widen our understanding of these processes as well as to monitor changes in biodiversity on a medium scale to predict long term responses of ecosystems to environmental change.

Even though a comprehensive concept of biodiversity encompasses more than just species diversity a lot of research is still based on species richness (alpha-diversity) as a measure of diversity (e.g. Tilman & Elhaddi 1992; Schulze & Mooney 1993; Krishnamani et al. 2004). Even the large body of literature which deals with the implications of biodiversity for ecosystem function (e.g. Grime 1998; Bednekoff 2001; Hart et al. 2001) focuses largely on alpha-diversity. The same holds true for literature on emerging patterns of vegetation (Richerson & Lum 1980; Addicott et al. 1987; Olsvig-Whittaker 1988; Cracraft 1992; Araújo 1999; Lister et al. 2000). There are only a few studies which actually apply parts of a comprehensive concept of biodiversity (including similarity/dissimilarity and functional diversity) in ecological field studies (e.g. van der Maarel 1976; Pitkänen 1998; De'ath 1999; Kluth & Bruelheide 2004). The concentration just on species numbers may, *inter alia,* indicate a lack of methodological applications of an extended biodiversity concept.

Our aim is to develop a spatially explicit, widely applicable method to assess phytodiversity encompassing species richness, spatial and temporal heterogeneity, and functional diversity and to relate it to environmental conditions (including site conditions and disturbance regime). There is an urgent need for standardised and comparable data in order to detect changes of biodiversity. Such methods are required to be representative as well as pragmatic due to the simple fact that there is insufficient time to obtain complete data sets relating to temporal trends. If biodiversity is lost rapidly at the landscape level, frequent re-investigations have to be done in order to detect and analyse such changes. Thus, our objective was to provide a method that allows for the tracking of changes in biodiversity at the landscape scale. In this communication we focus on the methodological aspects of our work. We will answer the following questions on the basis of field data recorded in a recent study in North-Eastern Morocco: 1) Is the hexagonal plot suitable for an easy and efficient assessment of structural variables? 2) Is there any benefit in assessing frequency values (compared to presence absence data).

Materials and Methods

Site description

The investigation area is situated at 34°N and 3°W at the edge of the North-Eastern Moroccan high plateau (Plateau du Rekkam) about 100 km from both the Algerian border and the Mediterranean Sea. It lies at an altitude of between 1550 and 1670 m a.s.l. The Gaada de Debdou, which marks the brim of the Plateau du Rekkam, is situated in an exceptional orographic position. It receives about 500 mm of precipitation a year, which is far more than the Plateau itself (about 200 mm a year). This allows evergreen forests to grow. On the edge of the plateau these forests consist mainly of *Quercus rotundifolia* L. (stone oak). On the slopes *Pinus halepensis* Mill. (Aleppo pine) and *Tetraclinis articulata* (Vahl) Masters (gum juniper) are the main species. On the plateau, where most of the sampling was done, only *Juniperus oxycedrus* L. *ssp. oxycedrus* (prickly juniper) occurs with the stone oak.

The principal anthropogenic influence is grazing with sheep and goats by semi-nomadic families. Because of the favourable climatic conditions the herds can graze over a long period even when food becomes scarce in regions further east on the plateau (Dahara) or in the western plains (Moulouya-Valley). Consequently, the nomads remain longer at the Gaada than elsewhere in the region as long as conditions are favourable for grazing.

Sampling Design

We implemented a spatially nested hexagonal sampling grid which provides several advantages compared to other methods. Systematic sampling means that sampling locations are objectively chosen, thus minimising the influence of subjective decisions (Traxler 1998) which might be a problem with preferential and even random sampling (Colbach et al. 2000). Compared to systematic sampling, random sampling was often found to be less efficient (e.g. Austin 1981; Kipfmueller & Baker 1998; Singer et al. 2002;

Higgins & Ruokolainen 2004). Additionally systematic sampling is the best choice when looking for spatial patterns (Cole et al. 2001).

In the hexagonal grid all adjacent plots are the same distance from each other and there is no overlap when comparing neighbouring sampling units (see Fig. A4.1). These are important prerequisites when using similarity indices to calculate spatial patterns. Moreover, we decided to use hexagonal plots for reasons of consistency and to minimise perimeter:area ratio. Circles would be ideal in this regard but they need more effort and are more complicated to set up in the field when working in woody vegetation.

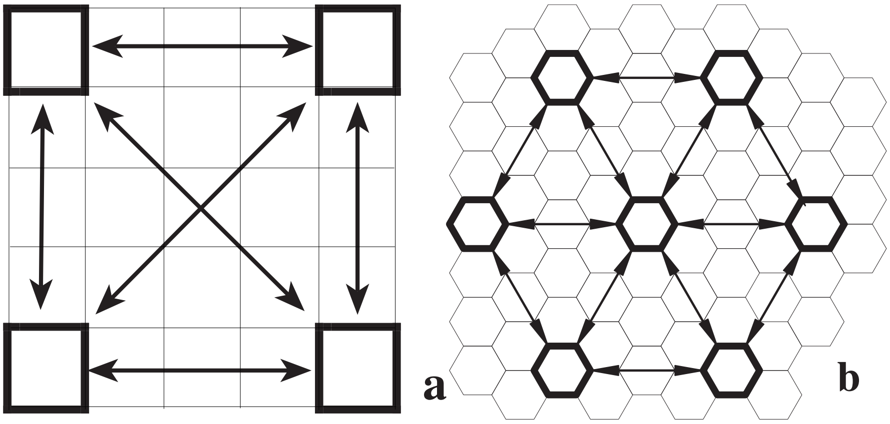

Figure A4.1. a) In a square grid the adjacent plots are not equidistant. Furthermore similarities calculated between different plots occur in one place (crossing diagonals). To calculate a mean of those is not acceptable. **b)** In a hexagonal (or triangular) grid all adjacent neighbours are equidistant. All calculated similarity (or dissimilarity) values are unique.

The proposed hexagonal sampling grid consists of three nested scale levels. With data recorded at different levels we can detect the scale at which disturbance-driven patterns emerge in vegetation. The hierarchical, spatially nested design is shown in Fig A4.2. The size of the grid is the same at all levels and consists of 19 equidistant sample cells. To investigate the influence of distance on spatial patterns of plant diversity the top-level is replicated at three distance levels. Some of the plots belong to more than one level, thus providing an efficient method to evaluate the influence of grain and extent on spatial patterns of biodiversity (see Nekola & White 1999 for a comprehensive review on the importance of scale in ecological analyses). It also facilitates the investigation of the different drivers which determine the patterns at the various scales.

The Sample-Plot is the main level of investigation. Data from the Sample-Plots are scaled up to provide information on the Plot. It is not possible to sample all sampling locations because this would result in 15523 sampling points. Therefore, only parts of the grid have been sampled completely at all levels, (i.e. all Sample-Plots in a Plot and all Sub-Plots in a

Sample-Plot) to enable the analysis of spatial patterns at these scales, whilst elsewhere randomly chosen plots inside the bigger units have been sampled.

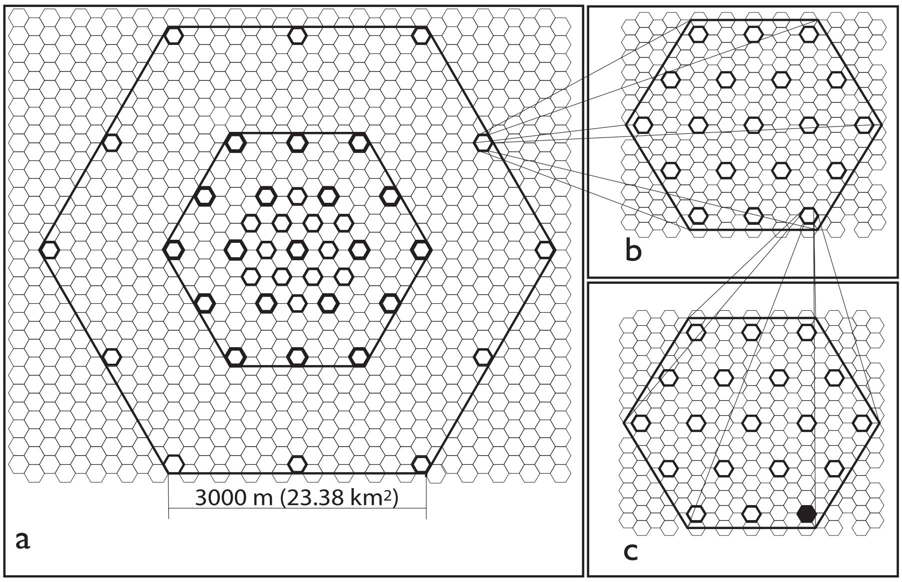

Figure A4.2. Nested sampling design. Inside the investigation area (**a**, side length 3000m, area 23.38 km^2) plots are arranged in a regular hexagonal grid (and replicated at 3 distance-levels). Inside the plots (**b**, side length 120m, area 3.74 ha) Sample-Plots are located and therein sub-plots **(c)**. The Sample-Plots (c) have a side length of 8m (area 166 m^2). One side of the sub-plot measures 0.6m, area is about 0.94 m^2). One of the Sub-Plots is filled black.

Spatial patterns of beta-diversity of the vegetation are calculated through the computing of similarity measures (such as Sørensen-Index (Sørensen 1948) or Jaccard-Index (Jaccard 1912)) and distance measures (e.g. Bray-Curtis-Distance (Bray and Curtis 1957), Squared Euclidean distance) depending on data properties. For the characterisation and evaluation of spatial patterns values between neighbouring cells have been computed. For information regarding the general spatial structure of the area investigated (e.g. via semi-variograms or correlograms) the values between all the recorded sample-plots were calculated.

Data recording

At the Sample-Locations, data on vegetation, site conditions, structure and disturbance were recorded to different extents, depending on the scale-level. Here we will focus on data used to answer methodological questions. These were recorded at Sample-Plot scale. Navigation to the Sample-Plots was done using GPS-Devices (Leica GS20 for exact marking of the Sample-Plots; a Garmin gpsmap 76a was used later when revisiting sites). The centre of the Sample-Plot was marked initially with a magnet to facilitate repetitions at exactly the same place. Starting with a North facing triangle the Sample-Plot is marked out in the field using 12 ropes of 8 m length so that all the Sample-Plots are oriented to the North.

To begin, a comprehensive description of the Sample-Plot was made. The severity of disturbance was categorised based on hoof marks, faeces of goats and sheep, grazing signs and the distance to tracks and tents (using GIS). Aspect, slope, elevation and relief were recorded to characterise the sites. The soil was classified in the field using the German Soil Classification System (Bodenkundliche Kartieranleitung 4, Anon 1996) and a soil sample was taken for later analysis of pH, C/N ratio, and conductivity in the laboratory of the University in Bayreuth. The depth of the A horizon, soil type, stone and gravel content, presence of roots and humus, bulk density and topsoil texture were also recorded.

The presence of higher plant species was recorded, unknown species being collected for further determination in Bayreuth. For efficiency and in order to simplify the process, species abundance was not recorded. This means less but more reliable information because the estimation of abundance might be vulnerable to subjective errors (Tüxen 1972; Leps 1992). More exact approaches, such as the point quadrat method, are too time-consuming, especially for species with low abundance (Goodall 1952; Everson et al. 1990) which make up the majority of the species in our samples.

Assessing Structures

To evaluate the possibility of assessing quantitative data on vegetation structure using the line-intercept-method (e.g. Mueller-Dombois & Ellenberg 1974), detailed sketches of the Sample-Plots, including the shape and cover of bushes and trees, the location of fire-sites, rocks and several other features were made in 125 Sample-Plots during the 2003 field-season. The quality and precision of the sketches is very high because they were drawn on a copied template (scale 1:100) of the hexagonal plot, which formed part of the field checklist. Furthermore, the ropes provided a means for a projection of recorded features on points along the line, thus increasing the accuracy of the sketches.

The proportions of bare soil and stones as well as the cover of trees, bushes and *Asphodelus microcarpus* DC. were recorded using the line intercept method. *Asphodelus* was recorded because of its importance as a structural element of the field layer. It is one of the few species in the study area which can be found with cover-values (after Braun-Blanquet, 1964) other than "+" or "r". It is a perennial member of the *Asphodelaceae* with straight, succulent leaves and considerable clonal growth. Due to its growth habit it provides shade and strongly influences micro-climatic conditions for other plants. In general, animals avoid this plant, resulting in *Asphodelus* carpets. These do not form a closed canopy, thus allowing ephemerals and annuals to grow where they are protected from grazing, direct sunlight and drought.

The ropes which were used to mark out the plots are segmented (alternating red and white every 20 cm with additional marks at every meter and 2 meters) to facilitate recording. On each rope the proportion covered by a certain feature was assessed and recorded in a checklist (Figure A4.3). The cover-value for a certain feature on the Sample-Plot was later calculated automatically inside the database by summing the proportions on the 12 lines. For analysis regarding the quality of the line-intercept-method we only used the cover-values of the bushes and trees because these matched the sketched features. The sketching of the proportion of open soil, open stones and Asphodelus microcarpa would have been very time consuming and too elaborate to undertake.

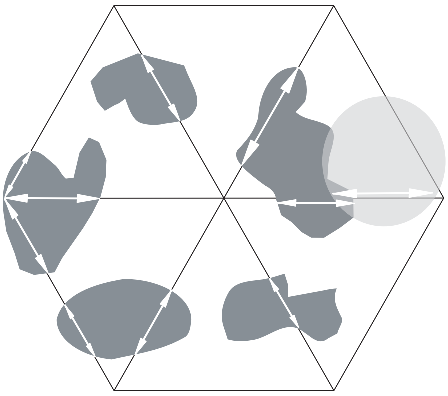

Figure A4.3. Using the marking ropes for assessing data on structure or species through the implementation of the line-intercept method: The ropes are segmented for more efficient working: general division is red/background every 20cm. Background changes every 2m plus 1m markers and a centre marker (not displayed).

Figure A4.4 shows the steps in the preparation of the sketches. These were scanned and geo-referenced in ArcMAP® (part of the ArcGIS® package from ESRI, which was also used for the following procedures). The elements recorded were digitised separately for each species and sample-plot. All features occurring fully or partly inside a plot were mapped. In the data-table belonging to the created shape-file (.shp) further information (vegetation layer, height, etc.) was assigned to the digitised features to enable later queries. The shape-files were then merged into a single file. Due to the implementation of a global identifier it is still possible to separate the shapes by their sample-plot-code, vegetation layer, height and species.

All parts of the shapes outside the hexagonal plot were cut off at the edges so that only those parts inside were included in further analysis. As we were interested in the cover of bushes and trees regardless of species identity we combined the species and ordered them in relation to their presence in the vegetation layers. Based on this, the polygons of a sample-plot were combined into one single shape, which allowed the calculation of a single value per sample-plot for the area covered by a certain feature (bush or tree).

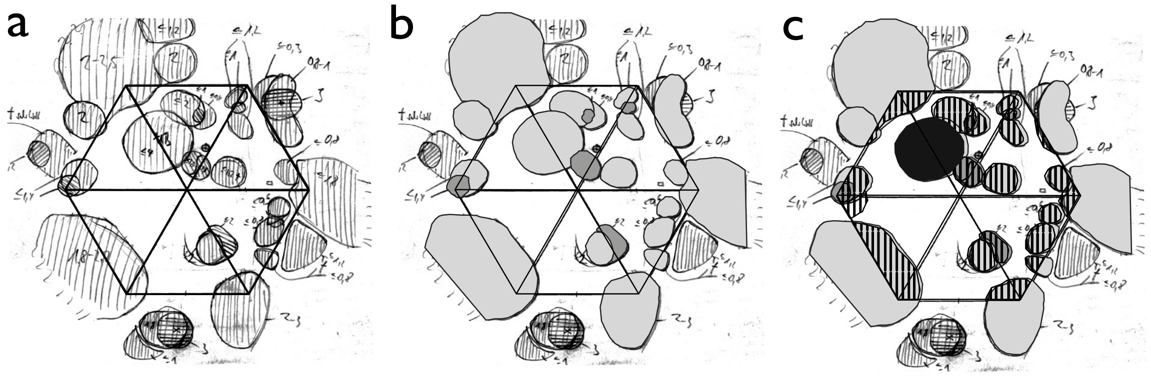

Figure A4.4. Sketch preparation. The sketches were scanned from paper **(a)**, then all features inside or intersecting the hexagonal plot were digitised (including species identity): **b)** the light grey symbolises Quercus rotundifolia, grey are Juniperus oxycedrus bushes. **c)** shows that the digitised features were then combined and ordered according to their layer (bush: black hash, tree: black fill) and cut off at the edges of the hexagon. (Change note: In the original publication the arranegment is vertical.)

Frequency data versus presence-absence data

During sampling in 2005 frequency data were obtained to examine whether this changed the response of the calculated similarity indices (or distance measures respectively) in relation to other variables. Data were recorded in 15 Sample-Plots belonging to 3 structural types so that every type is represented by 5 replicates. The structural types were defined on the basis of shrub and tree cover data from previous years' recordings and can be defined as:

- "steppe-like" (no bushes or trees)
- "scattered bushes" (bush-cover 2 - 30%, tree-cover ≤ 2%)
- "maquis-like" (>30% of bush cover, ≤7% of tree cover)
- "park-like" (>20% of tree-cover, ≤5% of bush cover)
- "forest-like" (tree-cover > 40% , bush-cover 5% - 35%)
- "mosaic" (bush-cover > 20%, tree-cover > 20%)
- the remainder, where none of the above conditions was met.

Only Sample-Plots from the structural types "steppe-like", "maquis-like" and "bush-like" were sampled because significant differences were anticipated between them. The Sample-Plots were chosen randomly so that at least one of the 5 in every structural type was sampled in both of the previous years' of study and 2 each of the others were sampled in 2003 and in 2004 respectively. This allowed temporal changes to be investigated.

To obtain frequencies, the 6 triangles forming the hexagonal plot were sampled separately so that the occurrence of a species in all of the triangles would be represented in a frequency value of 6. Species-data were stored in the database as they were recorded. For further analysis data were aggregated into a species list containing the names of every species found in a Sample-Plot plus their frequency, which was calculated automatically from the data. With the software-application PC-Ord® (McCune and Mefford 1999) several distance-measures (Bray-Curtis, Relative Sørensen, Jaccard-distance, Chi2-distance) were calculated. A very similar species list containing the names of the species recorded in Sample-Plots but without frequency information was used to obtain similarities (Sørensen, Jaccard, Whittaker and several others). See Koleff et al. (2003) for a comprehensive review of similarity indices.

All the existing similarity measures use the same variables. To be independent of the similarity measures offered in existing Software (e.g. PC-Ord®, SPSS®) a perl-script was used to apply a search algorithm which identifies the pairs of Sample-Plots to be compared. It searches a file containing the coordinates and names of the Sample-Plots. With the information of each possible pair of Sample-Plots, another file, containing the species-list in database format, is searched for all the species recorded in these Sample-Plots. The values of the variables a, b, c, and d which are used in similarity indices are determined on a text-based comparison (see formulae 1 and 2 for examples). These variables represent:

(a) species found in both of the Sample-Plots (shared species)
(b) species found only in one of the compared Sample-Plots
(c) species found in the other of the two compared Sample-Plots
(d) species found only in the rest of the data set.

Through a simple count algorithm the numbers of species in each variable for each Sample-Plot pair are calculated and written to a file containing all the information needed to calculate similarity indices. It is imported into a database file where many of the existing similarity indices are stored as formulae. As the data are imported all the similarities for all given pairs and formulas are calculated.

The calculated similarity indices were then related to other variables (such as vegetation structure or disturbance). The correlation cannot be calculated directly with variables recorded in the plot because the similarities represent the relationship of attributes (presence of plant species) in pairs of plots. Therefore, the plots were compared (using distance measures because of the quantitative nature of the data) with other variables (e.g. pH, C/N, conductivity, other site conditions, structure, and disturbance). The distance values obtained were then evaluated regarding their correlation to the distances and similarities based on species data. Several distance measures and similarity indices have been applied to the data, using standard formulae (Jaccard 1912, Sørensen 1948, Bray & Curtis 1957).

Results

Assessing Structures

The cover values derived from the line-intercept-method and from the sketches were compared and correlated. The results show that there is very good correlation (Pearson). Figure A4.5 shows the scatter-plots of the correlation for bush and tree cover values respectively. The cover values based on line-intercept and the sketches are highly significantly correlated. The correlation of the bush-cover-values is slightly better (R^2 = 0.78, r = 0.88***, *** indicates significant at the $p < 0{,}001$ level) than the correlation of the tree-covervalues (R^2 = 0.70, r = 0.84***). This could be due to the crown projection which may have been imprecise especially in the case of taller trees. In addition we calculated the Bray-Curtis distances between the values. This allows for the combined evaluation of the proximity of the values for bush and tree cover with the two different methods. All the calculated values were combined into the box-plot in Figure A4.6. The distances are mostly very small (see the Whiskers position) as are the median and standard deviations (thick black line and box), indicating that the values for the structural variables obtained with the two different methods are very close to each other.

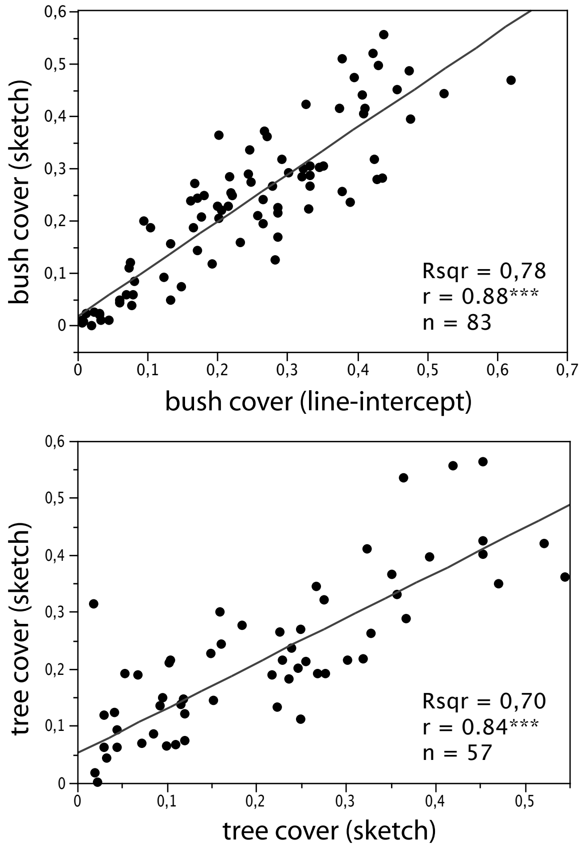

Figure A4.5. Correlation between the values derived from the assessment of structures via the line-intercept-method and the sketches based on bush and tree cover values respectively. r is the Pearson correlation coefficient, the line is the regression line. n is less for tree cover values because not all plots incorporated in the analysis actually had trees.

Frequency data versus presence-absence data

The calculated similarities (Sørensen, based on presence-absence data) and distances (Bray-Curtis, based on frequency-data) show a very close relation if plotted against each other (Fig. A4.7 a, r = -0.92***, R^2 = 0.85), indicating that presence-absence data suggest a similar vegetation structure to frequency data. The relationship is negative because of the nature of the measures - one measuring dissimilarity (or distance) and the other measuring similarity.

Regarding their relation to other variables, they both show the strongest correlation with the dissimilarity of structures. This was anticipated from other work (not described here), where we found that the similarity of vegetation based on presence-absence data showed a stronger correlation with dissimilarity of structure than with the dissimilarity of other factors, such as disturbance, soil parameters, aspect, or slope. The Bray-Curtis distances ($R^2 = 0.35$, $r = 0.59^{***}$) perform moderately better in this regard than the Sørensen similarities ($R^2 = 0.26$, $r = -0.51^{***}$, see Fig. A4.7 b and 3.12 c), suggesting a slightly better relationship with frequency data compared to presence-absence data.

Overall, these analyses suggest that recording presence-absence results in only a slight reduction in useful information compared to the more time consuming measurements of frequency.

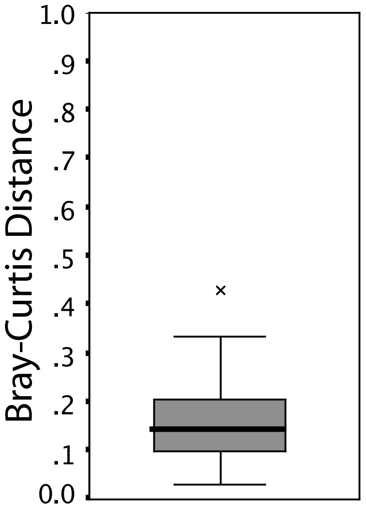

Figure A4.6. Distances (dissimilarity) between the values for the cover of trees and bushes combined derived with line- intercept method and from the sketches (n =57). The thick line represents the median, the box represents the interquartile range. Whiskers are extremes. The 'x' is an outlier.

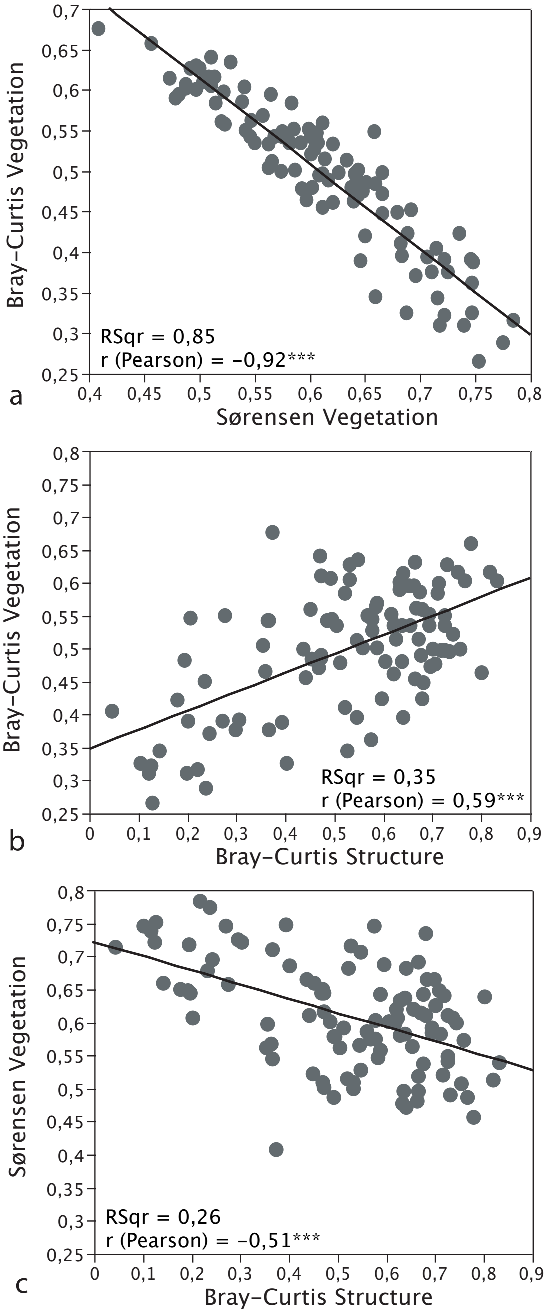

Figure A4.7. Frequency versus presence-absence data. **a)** The distance values (Bray-Curtis) plotted against the similarity values (Sørensen) reveals close relation between these different methods. **b)** Bray-Curtis distance on structural variables plotted against Bray-Curtis distance based on frequency species data. **c)** the Bray-Curtis distances based on structural variables plotted against Sørensen similarity based on presence-absence species data.

Discussion

Assessing structures

The comparison of the structural variables recorded with the line-intercept-method and with the sketches reveals a very close relationship between the respective values. This is true regardless of the technique used to compare the two methods. This indicates that the recording of structural features in the hexagonal plot with the line-intercept-method is a very reliable and efficient method to quantitatively characterise vegetation structure. It can be completed in just 20% of the time needed for the sketches (all working steps summarised) which makes it a realistic and labour-saving alternative. It also provides possibilities elsewhere. In a recent study in a Tundra-ecosystem, where micro-relief has an important ecological function (e.g. Matveyeva 1988; Walker 1995; Callaghan et al. 2001), Rettenmaier (2004) showed that it is also possible to assess surface roughness using a slightly adapted hexagonal plot sampling methodology. The ratio between the length of a rope following all the surface bumps and hollows to the direct distance was successfully used to quantify surface roughness. In this case the methodology also successfully assessed the proportions of bare fine substrate, open stones, vegetation-covered stones, small ponds and boggy depressions.

As the ropes cross the plot through the centre and at the perimeter, the structural variables are assessed systematically and exactly. They are valid at the sampling location on which they were recorded even though there might be some auto-correlation because of the geographical proximity of the lines (which may be considered as short transects). The sketches which were made during the first field season provide a more exact basis for structural data but require much more work both in the field and in the lab. As we wanted to provide a methodology which minimises effort whilst giving sufficiently accurate data on biodiversity and environment, the line intercept approach on the hexagonal plot seems to be a very efficient and easily applied method.

Frequency versus presence-absence data

We have shown that the results obtained on the basis of frequency data and presence-absence data respectively differ only slightly regarding the correlation between similarity (or dissimilarity) of vegetation and distance-values based on other environmental variables. But additional information is obtained if quantitative data on species are used, and we have to admit that the 6-triangle method produces very coarse frequency values. It is very likely that even more information could be obtained through a finer resolution of frequency values, although this would increase the effort required. We also found that for the methodology presented here the additional information obtained using frequency values at a finer resolution does not reflect the increase in effort required for data recording (Beierkuhnlein 1999; Neßhöver 1999; Retzer 1999), which is much greater compared to the assessment of presence-absence data.

Similar arguments apply in regard to cover values. Since one of our major objectives is the development of a comprehensive and reproducible method to assess spatial patterns of biodiversity, we avoided using cover values because they are often found to be highly variable. This is because they depend on the recorder, time of day, vegetation height and other factors (Dierschke 1994, Mueller-Dombois & Ellenberg 1974). Even though subjective methods might be as precise as objective methods under certain circumstances (Floyd & Anderson 1987; Dethier et al. 1993; Kent & Coker 1994; Brakenhielm & Qinghong 1995) we think that it is more appropriate to use very simple methods, especially when implementing long term monitoring. If a lot of sampling must be done in as short a time as possible - as is often the case with systematic sampling grids - it is better to use presence-absence data instead, particularly if they compare well with other, much more elaborate and time-consuming approaches.

Conclusions

The systematic sampling on a hexagonal grid is a good way to reveal patterns of biodiversity and to relate them to other environmental variables. Here we presented results showing that hexagonal plots provide several advantages. However, it is most important to state that the patterns that emerge are dependent on the scale of observation. By deciding on the sampling design we, as scientists, predetermine which patterns are found. Consequently, it is crucial to accurately define the scope and the purpose of the studies trying to reveal and explain spatio-temporal patterns in nature. Preliminary investigations can be used to determine the “right” plot and grid shape, but problems persist because the size of a plot and the distance to its neighbours is not necessarily linked, although both determine the described patterns. We propose a spatially and temporally nested design to investigate the ecological factors shaping spatial patterns in nature. The hexagonal grid approach has the potential to serve as a tool for a rapid, reliable and comprehensive assessment of biodiversity.

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Appendix 5 Distance decay and non-stationarity in a semi-arid Mediterranean Ecosystem. *Journal of Vegetation Science* (submitted)

*Jurasinski, Gerald (gerald.jurasinski@uni-bayreuth.de); Beierkuhnlein Carl (carl.beierkuhnlein@uni-bayreuth.de)

Address (all authors):
Biogeography, School of Biology, Chemistry and Earth Sciences, University of Bayreuth, 95440 Bayreuth, Germany

Abstract

Question: Is there considerable distance decay of compositional similarity on a meso scale in a dry Mediterranean ecosystem? How does it affect the correlation to predictor variables? Are the patterns driven by disturbance?

Location: A Mediterranean Holm Oak (*Quercus rotundifolia* L.) forest in transition to semi-arid steppe-like vegetation on the Northeastern Moroccan High Plateau.

Methods: Compositional similarity and environmental distances between plots are calculated based on species data and a comprehensive environmental data set recorded on a nested equidistant grid. Subsets of the data covering different geographic extents are defined and Mantel tests, Mantel correlograms and related permutation procedures are employed to assess the relative importance of geographical separation and the dissimilarity of environmental variables for compositional similarity.

Results: Compositional similarity decreases very fast but not continuously with distance compared to other studies. The model which best decribes the relationship changes with scale - for subsets of the data log-transformed geographical distances give better fits. The correlation to environmental variables also depends on scale and can be seen as less influenced by spatial auto-correlation at around 2000m between plots.

Conclusions: Disturbance is a major driver of vegetation patterns in the investigated ecosystem. However, as correlations between predictor variables and compositional similarity changes with the gradient covered and therefore with geographical separation between sampling units, one scale studies regarding vegetation patterns and their drivers should be evaluated with care. Hierarchically nested sampling can handle this problem.

Nomenclature

(Valdés et al. 2002)

Keywords

compositional similarity, similarity measures, spatial pattern, heterogeneity, spatial autocorrelation, disturbance, semi-arid, North-Eastern Morocco, Mediterranean

Introduction

Within the constraints of environmental conditions patterns in vegetation are driven by processes such as dispersal and disturbance (Watt 1947; see Van der Maarel (1996) for a review). However, the spatial configurations of processes and conditions do not necessarily match. Therefore it is indispensable to incorporate space as a variable into ecological investigations (Legendre 1993; Dale et al. 2002; Fotheringham et al. 2002). Otherwise findings and models might be misleading (Wagner & Fortin 2005). Here, we examine the relative importance of geographical versus environmental distance for patterns of compositional similarity and its change with scale.

Patterns in vegetation can be expressed through the variation in species composition between plots, which has been termed 'beta-diversity' by Whittaker (1960; 1972). The general importance of beta-diversity has been emphasised in recent years (e.g. Srivastava 2002; Gering et al. 2003; Sax & Gaines 2003; Olden et al. 2006). However, even though Legendre (2005) postulates that "beta diversity is a key concept for understanding the functioning of ecosystems, for the conservation of biodiversity, and for ecosystem management", implementation is still scarce compared to measures of species richness, alpha-diversity and its derivates (but see e.g. Pitkänen 2000; Condit et al. 2002; Kluth & Bruelheide 2004). As 'beta-diversity' has multiple meanings (e.g. Lande 1996; Qian et al. 2005) we prefer to use 'compositional similarity' or 'differentiation diversity' instead. Regardless of the term used, it generally decreases with distance between plots. This phenomenon is called 'distance decay' of similarity (Tobler 1970) and can be seen as a characteristic of all geographic systems. Nekola & White (1999) investigated species compositional similarity between fir and spruce stands across North America (see also Qian et al. 1998; Qian et al. 2005) and concluded that distance decay of similarity might be useful as a descriptor of diversity distribution as well as for the study of factors influencing the spatial structures of communities. The few comparative studies investigating distance decay for more than one group of organisms show that it heavily depends on organismal groups as well as on the region under study (Ferrier et al. 1999; Oliver et al. 2004).

Although it is far from being well covered, the spatial change in species composition has received some more attention in recent years. The phenomenon was utilised to evaluate the validity of the dispersal theory (Hubbell 2001) against niche concepts in the Tropics: Condit et al. (2002), Duivenvoorden et al. (2002), Ruokolainen et al. (2002), and Chust et al. (2006a) investigated distance decay in terra firme forests in Panama, Ecuador, and Peru, whereas Duivenvoorden et al. (1995), Ruokolainen et al. (1997), and Tuomisto et al. (2003) concentrated on rain forests in the Amazon basin. Most of these studies deal with comparably large scales. Their results regarding the relative importance of spatial separation and environmental dissimilarity on compositional similarity vary. Only recently one study investigated these relations on a much smaller scale, covering about 5.7 km^2 of tropical lowland forest in Costa Rica (Jones et al. 2006).

Non-tropical ecosystems are not so well covered, but recently studies were published discussing the drivers of vegetational patterns in temperate forests in the context of dispersal and spatial dependence (Svenning & Skov 2002; Gilbert & Lechowicz 2004). Kluth & Bruelheide (2004) analysed diversity in a nested hierarchy of scales in therophyte communities in Germany and Italy also covering some aspects of distance decay. Steinitz et al. (2006) investigated dispersal and patterns of similarity in Mediterranean ecosystems throughout Israel and very recently Chust et al. (2006b) published a meso-scale study on the influence of habitat fragmentation on species composition (including issues of distance decay) in Mediterranean ecosystems. Here, we also focus on a Mediterranean ecosystem and investigate the relative importance of environmental factors and spatial configuration on compositional similarity in a meso-scale study in North-eastern Morocco. The system is a Holm Oak forest (*Quercus rotundifolia* L.) in patchy transition to steppe-like vegetation. The explicit consideration of disturbances is novel to the analysis of compositional similarity. This is surprising regarding the importance of disturbances as a process generating pattern especially in Mediterranean ecosystems (Naveh & Whittaker 1979; Lavorel 1999; Osem et al. 2002). In the presented study, disturbances are understood as temporarily limited events, which affect particular organisms or communities - changing spatial patterns, temporal dynamics, physical environment or the flow of information (Pickett & White 1985; White & Jentsch 2001).

The relevance of disturbances as an ecological factor has been a subject of intense and ongoing debate (e.g. Pickett et al. 1989; Milton et al. 1997). Also the response of ecosystems to disturbances and the characteristics of disturbance regimes (e.g. Turner et al. 1993; Johnson et al. 1996; White et al. 1999; Fukami et al. 2001) have been discussed. However, the impact of disturbances on spatial patterns in vegetation has been widely neglected. Only few studies incorporate disturbances as one factor shaping spatial patterns (e.g. Bobiec 1998; Pitkänen 2000) but they do not consider spatial dependence of the relationship between disturbances and species composition. Here, we investigate the distance decay of compositional similarity whilst accounting for the change of the relationship between compositional similarity and its drivers with geographical distance between plots.

Steinitz et al. (2006) note that it is not well studied to which extent patterns of distance decay depend on the position along environmental gradients. Accordingly Jones et al. (2006) emphasise that explanatory power of variables might increase with the length of the gradient covered. Based on this we hypothesise:

(1) Similarity in plant species composition decreases continuously with distance. Due to the small scale of the study (largest geographical distance covered is 6 km) the rate of distance decay will be relatively low compared to large scale studies.

(2) The correlation between compositional similarity of vegetation and the dissimilarity of predictor variables (disturbance, vegetation structure, abiotic environmental conditions) is changing with geographical distance between plots. We expect the correlation to increase with spatial scale/distance between sampling units because the sampled environmental gradient is likely to increase as well.

(3) Disturbance is the main driver of vegetation patterns in the regarded transitional ecosystem. We especially consider disturbances because Mediterranean ecosystems have a long-lasting disturbance history and stress tolerators are clearly favoured compared to competitors (Pignatti 1978; Naveh & Whittaker 1979).

Materials and Methods

Investigation area

The investigation area is situated at 34°N and 3°W at the escarpment (Gaada de Debdou) of the Northeastern Moroccan high plateau (Plateau du Rekkam) about 100 km South of the Mediterranean Sea. Altitude ranges between 1130 and 1670m a.s.l. The Gaada receives far more precipitation (ca 500 mm a year) than the Plateau itself (ca 200mm a year) and allows evergreen forests with *Quercus rotundifolia* L. (Holm Oak) to grow on the edge of the plateau. On the slopes the Oaks are accompanied by *Pinus halepensis* Mill. (Aleppo Pine) and *Tetraclinis articulata* (Vahl) Masters (Gum Juniper). On the plateau where most of the sampling was done only *Juniperus oxycedrus* L. *ssp. oxycedrus* (Prickly Juniper) occurs with the Holm Oak.

The anthropogenic influence is manifested primarily through semi-nomadic grazing with sheep and goats. Because of the favorable climatic conditions the herds can graze over a long period even when in regions further east on the plateau (Dahara) or in the western plains (Moulouya-Valley) food becomes sparse. So there are tendencies to continuous settlement, and the nomads leave their tents longer at the Gaada than elsewhere in the region (Steinmann 1998) which causes relatively high grazing pressure. However due to accessibility and preferences regarding tent sites disturbance intensity and severity is not uniform throughout the investigation area.

Sampling design

We implemented a spatially nested equidistant sampling grid (Jurasinski & Beierkuhnlein 2006). Adjacent plots share the same distances and there is no overlap when comparing all neighbouring sampling units. These are important prerequisites when applying similarity measures to identify spatial patterns (ibid.). Moreover we decided to use hexagonal plots for the reasons of consistency and minimised perimeter area ratio. Circular plots would be ideal in this regard but they are more complicated to be set up in the field when working in woody vegetation.

The hierarchical, spatially nested sampling grid is shown in Figure A5.1. The configuration of the grid is the same on all scales and consists of 19 equidistant hexagonal units. To evaluate the influence of distance on spatial patterns of plant diversity the top-level (large plots) is replicated at three distance levels (see Fig. A5.1). Data was recorded in 2004. In each of the 43 large plots 2 to 4 plots were chosen randomly for sampling. This resulted in 143 sampled plots. Due to the hierarchically nested arrangement plot density decreases from centre to margin of the investigation area (see Figure A5.1).

Data recording

Maps of the region were scanned and geo-referenced in advance to field work. Based on a pre-investigation visit and test recordings in 2002 the grid was developed and placed on the map. Navigation to the plots was done using GPS-Devices (Leica GS20 and Garmin gpsmap 76a). The plots were marked out using 12 ropes of 8 m length. The presence of higher plant species was documented, unknown species were collected for further determination. Furthermore data on site conditions, disturbance, and vegetation structure were recorded.

Slope aspect, slope inclination, height a.s.l., and relief position were recorded to characterise the sites. The soil was classified in the field using the German Soil Classification Guide (Bodenkundliche Kartieranleitung 4, (Anon. 1996)). The depth of the A horizon, soil type, stone and gravel content, presence of roots and humus, bulk density, and topsoil texture have been documented. A soil sample was taken and pre-processed (air drying, sieving) for later analysis of pH, CN ratio, and conductivity. 10g of soil were mixed with 2.5 parts 0.01M H_20-dest and shaked overnight. The next day pH was measured with a QpH 70 meter (VWR International), conductivity with a LF 197-S meter (WTW). To obtain CN ratio the mass percentages of C and N were detected with a CHN-Analyser (Carlo-Erba) after the samples have been crushed with a ball mill (Retsch MM200).

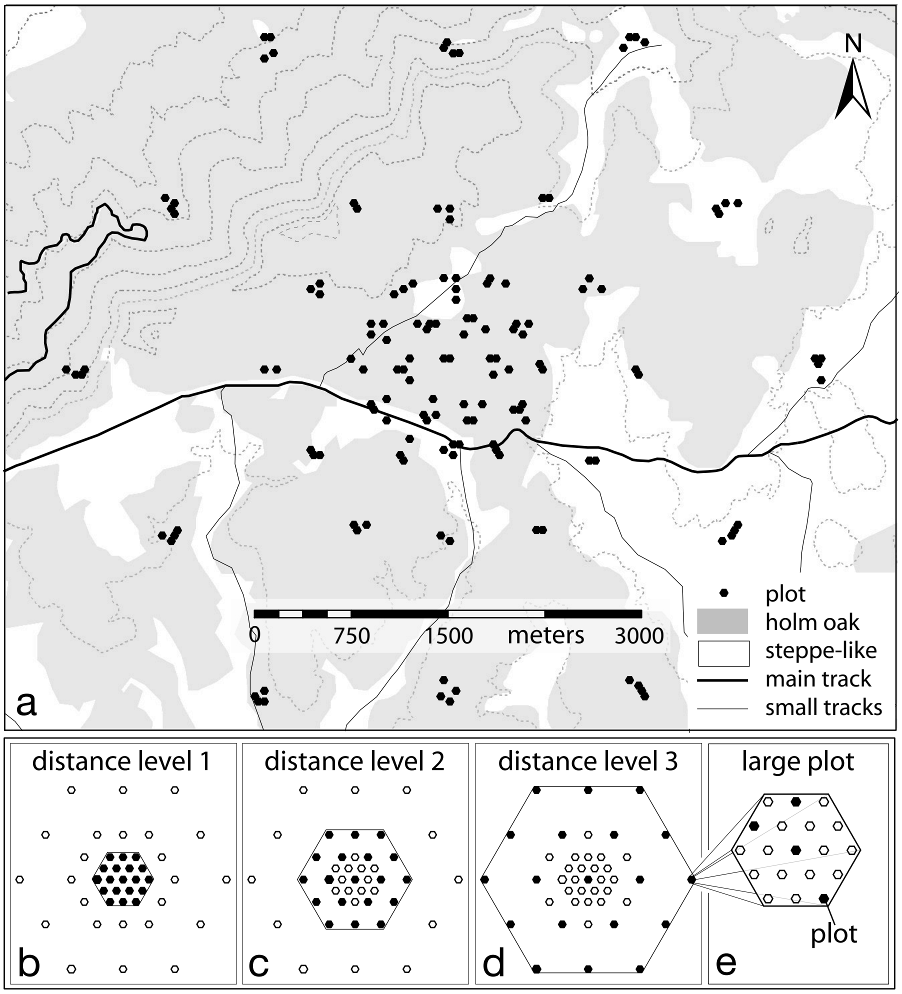

Figure A5.1. a) Exact geographical positions of the sampled *plots* on the map. **b-d)** Based on the arrangements of the 43 *large plots* it is possible to define regular grids of 19 *large plots* on three distance levels on which the spacing between neighbouring *large plots* is as follows: **b)** dl1 - 360m, **c)** dl2 - 720m, **d)** dl3 - 1440m. **e)** Each *large plot* contains a regular grid of 19 *plots*. They have a side length of 8m (166 m^2). Sampling was conducted on 2 to 4 randomly drawn *plots* of each *large plot*.

Disturbance was characterised based on hoof marks, faeces of goats and sheep, grazing signs and the distance to tracks and tents. The latter was achieved through calculation inside the GIS. Data on vegetation structure were recorded using the line-intercept method on the marking ropes. The proportions of bare soil, stones, the cover of trees, bushes and *Asphodelus microcarpus* Salzm. & Viv. have been recorded. The latter was included because of its importance as a structural element of the field layer. Due to its growth habit it provides shade and strongly influences micro-climatic conditions for other plants. In general, animals avoid this plant, resulting in *Asphodelus* carpets, allowing ephemerals and annuals to grow where they are protected from grazing, direct sunlight and drought.

Three plots had to be omitted from further analysis. These were situated in one large plot in the eastern part of the investigation area. Due to heavy rains in winter a temporary lake emerged in 2004. The excluded plots either lay inside the water or were almost totally without vegetation because the water just had retrieved before data recording. Their similarity to all other plots was close to zero independent of the geographical or environmental distances between them. Including these plots in the analysis had a negligible effect on the results. These exclusions lead to a total number (N) of 140 plots from which data were used in the analysis. As $n = N^*(N-1) / 2$ this results in a number of 9730 plot pairs for further analysis.

Data analysis

Compositional similarity and distances

We use 'beta-diversity' as a descriptor of spatial patterns of biodiversity. It is a measure of differentiation between units or the turnover in species composition along a gradient (Whittaker 1972). For alternative definitions see (Whittaker 1960; Lande 1996; Vellend 2001). It can be calculated with resemblance measures. Sørensen similarity (Sørensen 1948) is used to calculate compositional similarity of the field layer throughout the presented study. Sørensen similarity does satisfy the criteria of linearity, homogeneity (if all values are multiplied by the same factor the value is not changing), symmetry (independence from calculation direction (after Janson, 1981)) and scaling between 0 and 1 (Koleff et al. 2003). It is well established and extensively used especially in vegetation ecology (e.g. Condit et al. 2002; Kluth & Bruelheide 2004). This guarantees comparability with other studies.

Geographic distances between plots were obtained through the calculation of Euclidean distances between the x- and y-coordinates. Euclidean distances based on environmental factors, structural features and disturbance classification were calculated with the function *dist* of the R package base (R Development Core Team 2005). They were not calculated on the environmental data altogether but separately for single variables and groups of variables (see Figure A5.2 for details). This provided for the separate evaluation of the correlation between similarity of vegetation and proximity of other parameters and parameter groups.

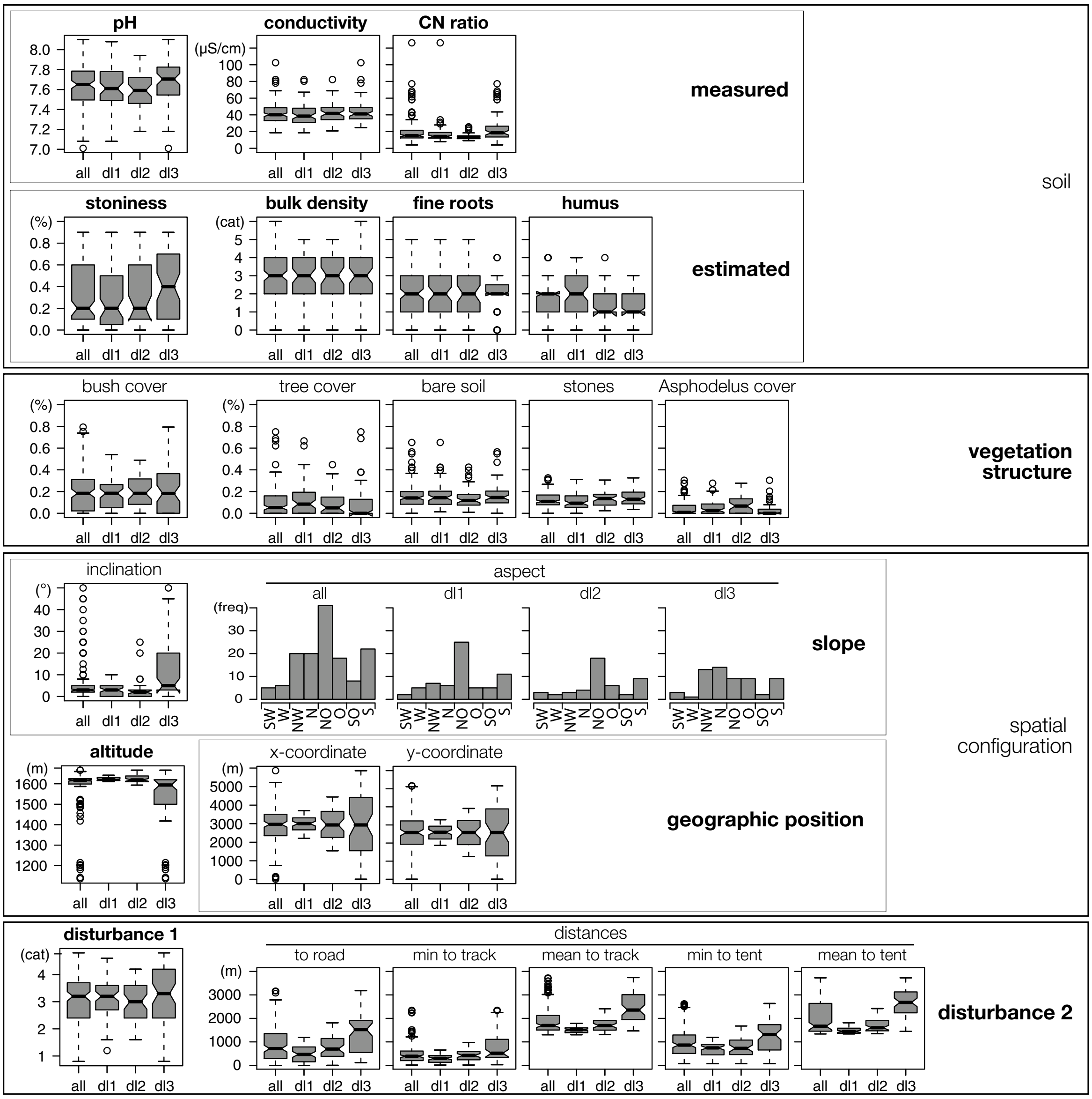

Figure A5.2. Each small graphic depicts the ranges of the indicated predictor variables on all plots (*all*) and on the three distance levels (*dl1-3*) as boxplots. Exception: the aspect values are given as histogram for each subset. Variables belonging together are surrounded by an outline and a descriptive name for their combination is given. Variables and combined variables for which dissimilarity between plots (Euclidean distance, great-circle distance on the unit sphere) has been calculated are written in **bold**.

Example: Dissimilarity has been calculated based on the disturbance classification alone (**disturbance 1**) and based on the disturbance classification and the distances to tracks and tents together (**disturbance 2**)

Slope aspect and slope inclination may have a significant effect on species richness (Badano et al. 2005) and species composition especially in semi-arid vegetation (Sternberg & Shoshany 2001). To obtain a distance measure integrating aspect and inclination we use the model of a unit sphere and calculate great-circle distances between virtual locations

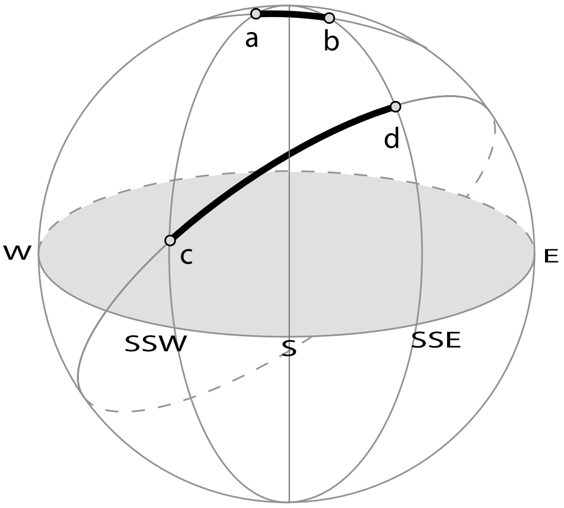

Figure A5.3. Calculating the great-circle distance on a *unit sphere* as a measure of similarity regarding slope aspect and inclination. Longitude reflects aspect as derived from the directional reference made in the field. The equator of the sphere is thought as the *compass circle* and the Prime Meridian of the virtual unit sphere is the great circle through North and South of the compass. As in geographic terms longitude counts positive in Eastern and negative in Western direction. Latitude reflects 90°-inclination (measured in the field with a Thommen inclinometer). With ϕ = latitude = 90°-inclination and Lambda = longitude = aspect the great-circle distance between A and B can be calculated with formula 1. Apparently there are no values on the South Hemisphere and the maximum distance is π.

Example: *b* and *d*, as well as *a* and *c* share the same aspect. However, due to low and very similar inclination *a* and *b* are much closer than *c* and *d*, which exhibit higher and very different inclination.

(Figure A5.3). This allows for the generation of continuous rather than class variables as e.g. found in Kjällgren (1998). For each plot a virtual location on the sphere is defined using the values for aspect as longitude and 90°-inclination as latitude (we measured inclination in the field with a simple Thommen inclinometer). Therefore the virtual points are located in the pole region as long as inclination is low which leads to small (virtual) distances between them. The idea behind is that solar radiation, wind or other factors highly depending on aspect and inclination (Wilkinson & Humphreys 2006) are not considerably different on plots with varying aspects as long as inclination is low. As we use a unit sphere the maximum distance between two inclination/aspect pairs is perimeter/2 of the sphere which is by definition π. To scale the possible distances between 0 and 1 the results of Formula 3.1 are divided by π. Thus, a great-circle distance of 1 is rather scarce in the real world, however, two vertical rock walls with opposite aspect would share it.

$$\zeta = \arccos(\sin(\phi_A)\cdot\sin(\phi_B)+\cos(\phi_A)\cdot\cos(\phi_B)\cdot\cos(\lambda_B-\lambda_A)) \qquad (3.1)$$

Statistical analysis

All statistical analyses were performed using functions of the packages *base*, *stats*, and *vegan* of the R statistics system (R Development Core Team 2005) as well as own functions for R. They are released under the name *simba* on CRAN (Comprehensive R Archive Network: http://cran.r-project.org/). For better reading we refer to the functions in the form 'function[package]' in the following.

Distance decay

Distance decay or spatial auto-correlation of quantitative univariate variables is usually calculated using semi-variograms (Legendre & Legendre 1998). For multivariate data Mantel correlograms can be applied (Sokal & Rohlf 1981; Legendre & Legendre 1998). A simple possibility for vegetational data is to regress similarity of units regarding species composition against their geographical separation (Nekola & White 1999; Steinitz et al. 2006). To test for the influence of distance levels on patterns of compositional similarity data was divided into 3 subsets (Figure A5.1). The similarity values of the 3 distance levels are compared with an ANOVA-like function (mrpp[vegan], see Oksanen et al. 2007) and tested for significant differences using a permutation procedure (diffmean[simba]). Normal tests and ANOVA might fail here because the similarities are not independent from each other.

After testing for significant differences between the three distance levels, the differences in mean similarity have been tested with a permutation procedure (diffmean[simba]). The difference in mean similarity between two sets is calculated. The two sets are joined together and two random sets the same size as the original sets are selected and their difference in mean is calculated. Then the sampling units and their associated pairwise distances are permuted, and the difference in mean is recalculated based on the permuted data. The last steps are repeated N times. N defaults to 1000 which provides a possible significance-level of $p<0.001$ as significance is tested against the distribution of the permuted values.

To answer the question if distance decay is increasing with distance level even on these small scales, the slopes of the distance decay relationship have been calculated for the three subsets and compared. A permutation procedure following Nekola & White (1999) has been implemented as an R function (diffslope[simba]) to test for significance (see Appendix). In accordance with Nekola & White (1999) geographical distance and compositional similarity both have been log-transformed and regression was done on all possible combinations of transformed and non-transformed values to examine the best fit. In the following we refer to the different models using 'response~predictor', so that the model with untransformed similarity against log-transformed distance would be termed the norm~log model.

Correlation and Correlograms

The entries of distance/similarity matrices are not independent. Thus, significance can not be assessed directly. Therefore, a Mantel-like permutation procedure was implemented to examine the relation between compositional similarity and the dissimilarity of predictor variables (vegetation structure, disturbance, soil and other abiotic parameters). This allows to obtain statistical inference for the correlation of distance/similarity matrices. Further analysis was only done for predictor variables for which the distances between plots exhibited considerable and significant correlation with compositional similarity.

Legendre et al. (2005) recently pointed out that Mantel tests can be used to study the variation in beta-diversity among sites but are less suited for analysing spatial variation of community composition among sites. The first is in focus of the present paper. In the following we often refer to the dissimilarity of the predictor variables by the name of the variable alone, however, we always mean the first. We also test for the influence of space itself with the calculation of Mantel correlation between compositional similarity and geographical separation. Therefore we wrote an R function (pcol[simba]) which can handle distance matrices as well as vectors and provides a two tailed test of significance.

The function allows for the automated computation of data-points for Multivariate Mantel Correlograms (Legendre & Legendre 1998). These display the correlation of a multivariate dissimilarity matrix with the geographical distance between sampling units and are useful to investigate spatial auto-correlation in the multivariate data. They are achieved by calculating Mantel correlations between a dissimilarity matrix and matrices of the same size containing a binary coding. The pairs of sampling units which fall into a distance class are connected with 1 whereas all other pairs have 0. This is done for every distance class. For this task we transferred the similarity values to dissimilarities by subtracting them from 1 to make them comparable to the dissimilarity values for the other parameters. To investigate the influence of geographical distance on the correlation between dissimilarity matrices we used an adapted approach where each point in a Mantel correlogram represents the correlation between two dissimilarity matrices for a given distance class. For each point Mantel correlation is computed between matrices only containing the dissimilarities calculated between pairs of plots which fall into the very distance class. The function pcol[simba] automates these tasks.

The distance classes are not to be mixed up with the distance levels mentioned earlier. The geographic distances between two compared plots in our data set span a range between about 50 m for the closest possible pairs to approximately 5930 m for the remotest pairs. To achieve a displayable correlogram the geographic distance is classified and all pairs which share a distance within the range of a class fall into it. The smaller the class widths the better auto-correlation or correlation with distance can be resolved but the smaller is as well the number of pairs which make up a class. We experimented with different class widths from 200m to 500m and ended up with 400m as a good compromise between resolution and number of pairs (n) inside the classes as then n is relatively constant among distance classes. However, due to the nature of the problem n always decreases with increasing distance. Thus, in all distance decay and correlogram plots the last 3 to 5 displayed boxes should not be trusted. Artefacts are then more important than real data for the displayed pattern as comparably very few pairs of plots make up the values. Legendre (1998) suggests for correlograms not to take the coefficients for the larger distance values into account "because they are based on a small number of samples and only include the pairs of points bordering the series or surface". This holds for the presented distance decay plots as well, where beyond the 4000 m class data is not reliable (marked by a vertical line in the figures). Alternatively classification could be done by dividing the total number of plot pairs by the number of desired classes. This keeps n constant but leads to very different class widths which we wanted to avoid as the change of correlation with distance is under study.

Results

Plot data

On 143 plots (total area surveyed adds to 2.38 ha) 358 species have been recorded from which 11 where woody species growing mainly as trees. Most of these only occur on the slopes of the Gaada with the exceptions of *Quercus rotundifolia* L. and *Juncus oxycederus ssp. oxycedrus* L. which make up the shrub and tree layers on the plateau. Mean alpha diversity amounts to approximately 84 species per plot. Maximal number of species per plot was 112, minimal species number was 39.

Distance decay of compositional similarity

Compositional similarity (Sørensen) between all plots spans a fairly large range of the possible values between 0 and 1 (from 0.07 to 0.80). The overall mean similarity is 0.51 ±0.14. There are no significant differences neither in mean nor in variance between distance levels 1 and 2 regarding compositional similarity between all possible pairs of plots (Figure A5.4). However, distance level 3 is significantly different from the two others regarding mean similarity (lower) as well as the variance (higher) of the similarity values.

Compositional similarity decreases considerably with distance (Figure A5.4 a) if all pairs of plots are considered. For better recognition of the spread of the similarity values they are plotted as boxplots with boxes comprising all similarity values for a given distance class (Figure A5.4). The distance classes have - as the classes of the correlograms - a width of 400m. Hence - due to the hierarchically nested design - the first distance class comprises all intra-large-plot similarities. Figure A5.4 a exhibits a relatively large step in decrease of compositional similarity beyond the 2000m distance class. From the following distance class on similarity decreases less fast which is reflected in the regression plot as well (Figure A5.4 b).

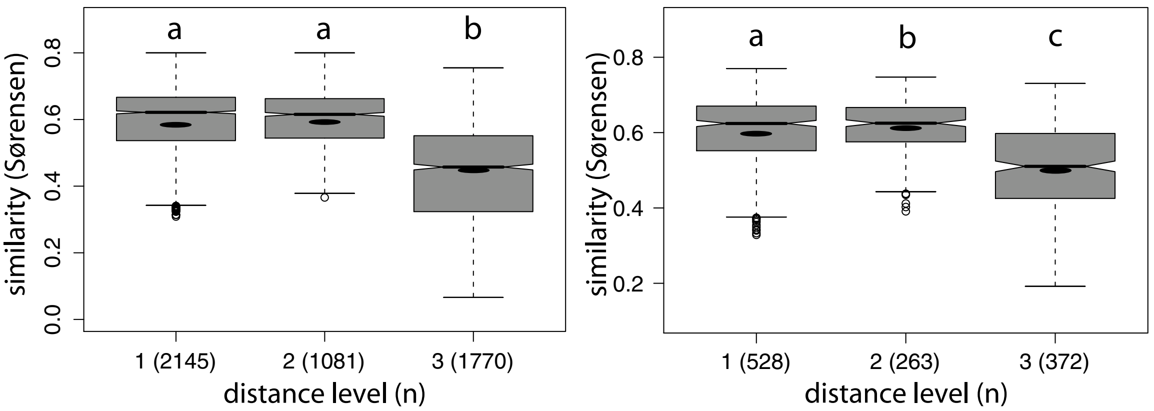

Figure A5.4. Compositional similarity (Sørensen) on distance levels (dl). Differences are tested with a permutation procedure (see text), **a)** All pairs of plots. Means and variances differ significantly between dl 3 and dl2/dl1 ($\Delta Soer_{1\text{-}2} = -0.005^{ns}$ ($F = 1.95^{ns}$), $\Delta Soer_{1\text{-}3} = -0.1596^{***}$ ($F = 1593^{***}$), $\Delta Soer_{2\text{-}3} = -0.1644^{***}$ ($F = 1086^{***}$)) **b)** Pairs of plots of neighbouring large plots. Means and variances differ significantly between distance levels. ($\Delta Soer_{1\text{-}2} = -0.017^{***}$ ($F = 6.35^{***}$), $\Delta Soer_{1\text{-}3} = -0.099^{***}$ ($F = 189^{***}$), $\Delta Soer_{2\text{-}3} = -0.115^{***}$ ($F = 192^{***}$))

In the presented data set distance decay is best described by the relationship between geographical distance and compositional similarity (norm~norm model, not log-transformed) when all possible pairs of plots are taken into account. The differences in distance decay rates for the three distance levels are rather small (Table A5.1, Figure A5.5 c). Only the slopes of the distance decay relationships of distance levels 2 and 3 are significantly different. The compositional similarity decreases slowest on distance level 2, whereas the distance decay rates for distance levels 1 and 3 are higher and their difference is negligible. However, it is apparent from Figure A5.5 c that the intercept values differ between distance levels and interestingly it is highest for distance level 2.

Table A5.1. Slopes of the distance decay relationship (headers and rownames) and differences in slope between them (entries) for the 3 distance levels. Slopes are given in decrease per kilometre. Significance was tested with a permuation procedure (see text).

	DL 2 (-0.033)	**DL 3** (-0.044)
DL 1 (-0.041)	-0.0077 ns	0.0034 ns
DL 2 (-0.033)	—	0.011***

Compositional similarity and environmental distances on distance levels

Mantel correlation between compositional similarity (Sørensen) and the Euclidean distances of predictor variables (with the exception of inclination/aspect for which great-circle distances were computed) has been calculated for the whole data set as well as for the distance levels separately (Table A5.2). Correlation coefficients vary heavily with distance level and only few variables (e.g. vegetation structure, CN ratio) exhibit relatively constant correlation throughout. Correlation is negative because a similarity matrix (compositional similarity) was related to distance matrices. The strongest correlation for the whole data set exhibit altitude, slope, structure, disturbance and geographical separation. However, their relative importance and values differ considerably between distance levels. Especially slope, altitude and disturbance are much less important on distance levels 1 and 2. This holds also for the influence of geographical distance between plots: with increasing distance between plots the Mantel correlation coefficients are increasing as well.

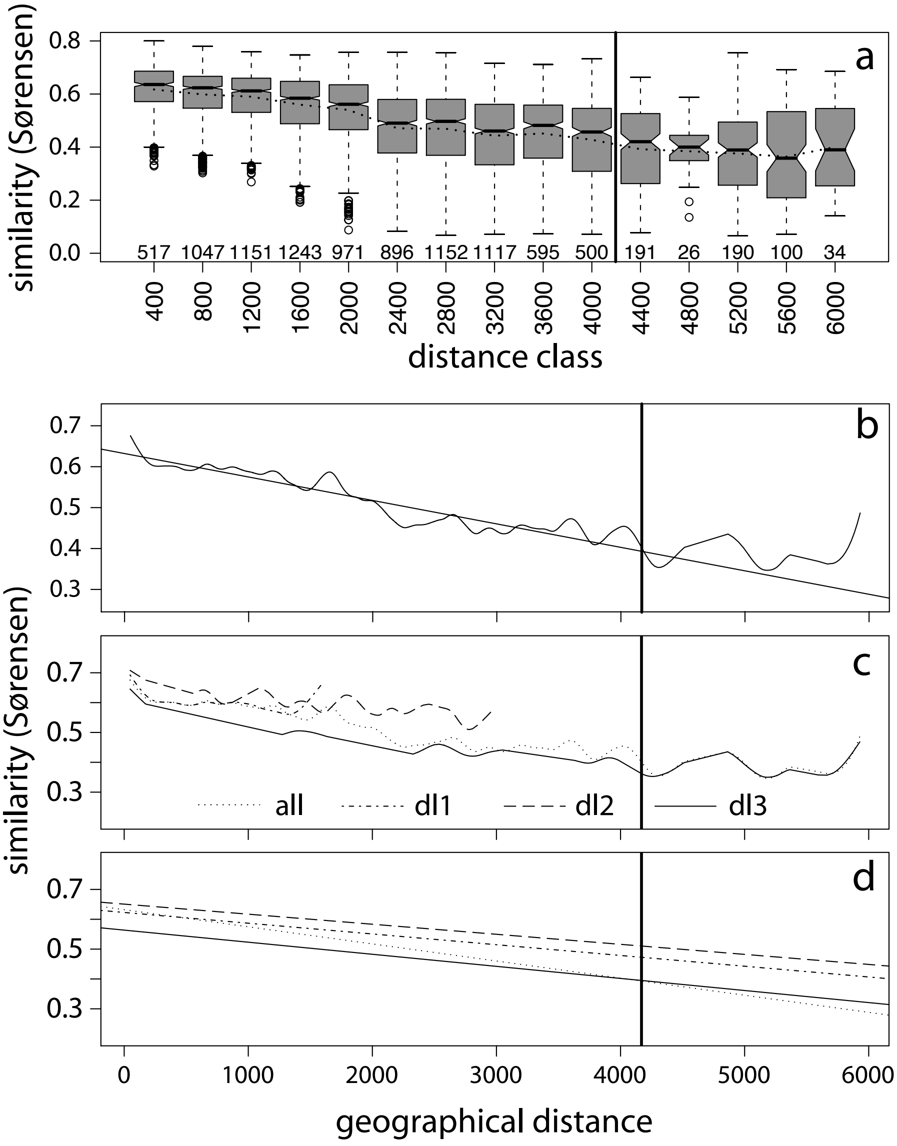

Figure A5.5. Unidirectional distance decay plots. Values right of the vertical line should not be interpreted (see text) **a)** Box-plots showing develop-ment of similarity with distance classes of 400m width. **b)** Line-plots displaying linear and spline regression lines of distance decay. The spline was fit with smooth.spline [stats] and defaults. Slope of the linear regression is 0.058 (per km) **c)** Spline and **d)** line regression plots for the distance levels compared to the whole data set. For differences in slope see Table A5.1. For statistics regarding the linear regressions see Table A5.3.

The dissimilarities of soil parameters show weak to almost no correlation with compositional similarity on all distance levels and behave arbitrary regarding positive or negative correlation. One exception is CN ratio with correlation coefficients between -0.21 and -0.35. Apparently CN ratio also accounts for most of the correlation of the compound variable soil measured. That's why CN ratio is the only soil parameter regarded in the following. To determine the parameters to be used in further analysis, the means of all correlation values for one parameter are calculated and compared against the mean of these means (-0.26). This lead to the selection of the distance matrices of the predictor variables altitude, slope, structure, disturbance, and CN ratio for further analysis (the order reflects the magnitude of mean correlation values).

Table A5.2. Mantel correlations between compositional similarity (Sørensen) and the dissimilarity of predictor variables (Euclidean distance and great circle distance on the unit sphere1)) for the whole data set (*All*), and for the three distance levels (*DL1, DL2, DL3*). The number of pairs included is given in parenthesis. Significance levels: *** = p < 0.001, ** = p < 0.01, * = p < 0.05, without asteriscs = ns.

predictor variables	Mantel correlation of dissimilarity of predictor variables with compositional similarity				
	All (9730)	DL1 (2145)	DL2 (1081)	DL3 (1770)	DL3[3] (372)
CN ratio	-0.354***	-0.213***	-0.211***	-0.316***	-0.428***
pH	-0.141***	-0.019	0.018	-0.146***	-0.118*
conductivity	-0.094***	0.044*	0.083**	-0.134***	-0.074
stoniness	-0.066***	-0.033	-0.011	0.0	-0.047
humus	-0.026*	-0.103***	0.038	-0.031	0.007
fine roots	0.018	0.032	-0.130***	-0.010	0.029
bulk density	0.026**	-0.050*	-0.038	0.018	0.104*
soil measured	-0.333***	-0.153***	0.044	-0.346***	-0.378***
soil estimated	0.012	-0.059**	-0.101***	0.001	-0.088*
structure	-0.588***	-0.428***	-0.308***	-0.678***	-0.526***
slope[1]	-0.653***	-0.067**	-0.222***	-0.580***	-0.592***
altitude	-0.737***	-0.125***	-0.264***	-0.746***	-0.632***
disturbance1[2]	-0.326***	-0.229***	-0.053*	-0.407***	-0.268***
disturbance2[2]	-0.617***	-0.233***	-0.297***	-0.523***	-0.372***
distance	-0.474***	-0.125***	-0.275***	-0.386***	-0.008

1) dissimilarity regarding *slope* inclination and aspect was calculated with a unit sphere model (see text)

2) *disturbance1* represents the dissimilarities based on disturbance classification assessed in the field, *disturbance2* bases in addition on the distances to tents, tracks and roads

3) only pairs of plots of neighbouring large plots are taken into account

Spatial auto-correlation patterns

To evaluate spatial auto-correlation of the chosen predictor variables spatial Mantel correlograms are computed (Figure A5.6 a). All of the predictor variables, as well as the response (compositional similarity) exhibit similar patterns of correlation with space. Until a distance of about 2000 m between plots they show significant negative spatial auto-correlation. All predictor variables but CN ratio start with negative values between -0.1 and -0.3. After 2000 m there is a short and clear increase in correlation followed by values between 0 and 0.2 for most variables. Disturbance exhibits the widest range of values (-0.33 to 0.26) and the largest increase at 2000 m. The majority of the single correlation values is significant after Bonferroni correction (with initial alpha = 0.05, Figure A5.6 a).

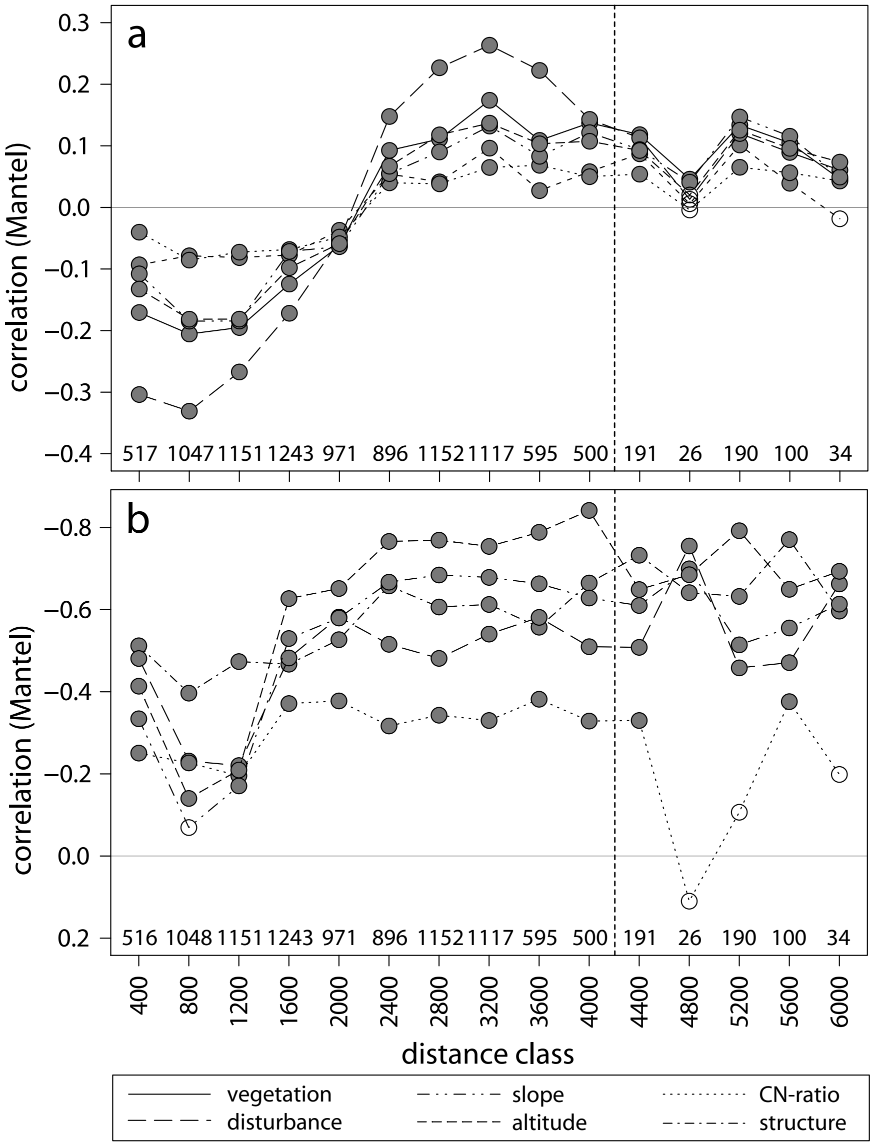

Figure A5.6. Mantel correlograms (true distance classes, changing n). Significance was obtained through permutation (filled circles: significant after Bonferroni correction with initial alpha = 0.05). Beyond the vertical, dashed line the correlograms should not be interpreted. **a)** Spatial auto-correlation for different variables. The distance matrices of the variables (see legend) are correlated to a geographical distance matrix which is different for each distance class in it's coding. Pairs which fall into the very distance class are coded 1. The rest of the pairings is coded 0. **b)** Correlation between compositional similarity (Sørensen) and distance values of explaining variables (Euclidean distance or great-circle distance) varies among variables and changes considerably with distance classes.

Compositional similarity and environmental distances in space

The correlation between compositional similarity of vegetation and environmental predictors (expressed by their dissimilarity) changes apparently with geographical separation between the plots (Figure A5.6 b). The relation between vegetation structure and species composition is relatively strong also for small distances between plots (dash-dotted line in Figure A5.6 b) and increases slightly with increasing geographical separation. The correlograms for the other variables show more or less the same trend. A sudden decrease from the first distance class to the second is followed by a sudden increase from the 1200 m to the 1600 m class. From there most relationships exhibit not much change although most of them increase slightly until noise is becoming increasingly important (beyond the 4000 m class). The dissimilarities of slope and altitude have the highest amplitude of correlation values whereas CN ratio has the lowest. The latter is generally less correlated with compositional similarity as it had to be expected from the correlation on distance levels.

Discussion

Plot data

It is well known that Mediterranean ecosystems are highly diverse, exhibit high total and local species richness and are spatially heterogeneous (e.g. Lavorel 1999; see Hobbs (1995) for a review regarding the legacy of literature on Mediterranean ecosystems). This is confirmed by our results where we find high species richness compared to the total area of sampling (358 species on 2,38 ha). A species accumulation curve calculated from the data shows a very fast increase in species richness with increasing number of sampled plots (Figure A5.7): 90% of the species richness would also be sampled on average if only 62 plots (1,03 ha) had been sampled.

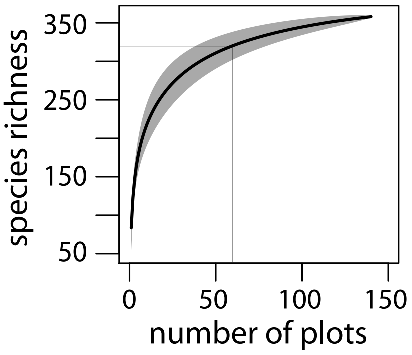

Figure A5.7. Species accumulation curve. On average 90% of the species richness could have been sampled on 62 plots, which is less than half the total area sampled.

Compositional similarity

If all plot pairs are taken into account (9730 data-points) we find a fairly wide range of similarity values which is comparable to studies from the tropics (e.g. Condit et al. 2002; Jones et al. 2006). However, it is surprisingly large with regard to the overall scale of the study (which is small in comparison to other studies, e.g. Condit et al. 2002; Kluth & Bruelheide 2004) although compositional similarities are by far not comparable to values found in Mexican tropical dry forests (Balvanera et al. 2002) where very low similarity was found for relatively short distances up to 90 m.

Distance decay of compositional similarity

For the comparisons of similarities between distance levels all possible pairs of each distance level have been considered. But there may be substantial distance decay inside one level. We controlled for that using only the similarities calculated between plots of neighbouring large plots, thus keeping the geographic distances between plots in a small range. The results are very similar: There is only a slight difference between distance level 1 an 2 but distance level 3 is apparently different from both (Figure A5.4 b, all means are significantly different). It seems, that the relatively high dissimilarity values are caused by plot pairs sharing relatively large distances. Although the plots of distance levels 1 share distances between 165 m and 1585 m whereas the geographic distances between plots of distance level 2 range between 555 m and 2975 m respectively, mean similarity does change only very slightly (and in an unexpected direction). Thus, distance decay might take effect only beyond a certain distance (The plots on distance level 3 share distances between 1275 and 5930 m). These results are contradictory to the findings regarding the patterns of distance decay and might be caused by the longer gradients covered on distance level 3 (see Figure A5.1).

The boxplots as well as the regression plots (Figure A5.6) show that there is considerable decrease in similarity. This means, that there is distance decay on the plateau although the environment is relatively constant (Figure A5.1). Sheep and goats are known to contribute to diaspore transport to a considerable amount (e.g. Shmida & Ellner 1983; Fischer et al. 1996; Couvreur et al. 2004) and in the investigation area animal access is hardly restricted. Therefore reasons could lay - among others - in different accessibility, changes in microclimate, or in history. Surely the pastoralism which builds the main income for the nomads on the Plateau du Rekkam for centuries lead to a homogenisation of the vegetation - as found in related studies (e.g. Couvreur et al. 2004). However, the harsh environment and the adaptation to it produces a highly diverse (in terms of species richness and differentiation diversity) vegetation mosaic ruled by chance and opportunity.

Compared to other studies we found similarity to decrease very fast (from 0.016 to 0.079 per kilometre distance, Table A5.1) which clearly leads to the rejection of hypothesis 1 (low distance decay because of small scale). These rates are much higher than the rates found in studies in the tropics (e.g. Condit et al. 2002, 0.0019-0.00055) and far apart from those calculated for boreal forests (Qian et al. 1998; Nekola & White 1999, 0.00011-0.00067). Even in therophyte communities in Germany the rates are about one order of magnitude lower (Kluth & Bruelheide 2004, 0.0054) although the vegetation is - to some extent -

structurally similar. In the presented case the rates base on the relationship between untransformed distance and similarity whereas in the mentioned studies the rates base on a semi-log model where the similarities are log-transformed. If we log-transform the similarity values the slopes get even steeper.

After the unified neutral theory (Hubbell 2001) similarity should decline linearly with log-distance. This assumption has been backed up - at least partially - by some studies (e.g. Condit et al. 2002; Phillips et al. 2003; Steinitz et al. 2005; Jones et al. 2006) mainly in the tropics. Vormisto et al. (2004) found better relations of similarity with log-distance compared to untransformed distance in two regions in the western Amazon basin. In boreal forests the log~norm model gave the best fit (e.g. Qian et al. 1998; Nekola & White 1999; Qian et al. 2005) which is not a problem to Hubbel (2001) as he states that his theory applies to saturated ecosystems only. To control for the consistency of the relationship we performed a test on our data and subjected the different distance levels to all possible transformations (norm~log, log~norm, log~log, norm~norm, Table A5.3). Although linear regressions fit generally poor it is apparent that the power of the relationship changes with distance level. Depending on that, different models can have the best explanatory power. However, despite in the case where all possible pairs of plots are included the semi-log model with log-distance tends to give the strongest explanation (highest R^2 and best Mantel coefficient). With increasing distance level (i.e. the landscape structural gradient is increasing) the normal relationship gains in explanatory power relative to the other models.

In the light of the fact that even in our relatively small scale study we found such differences we conclude that one scale studies can give obscure results when assessing patterns of distance decay. The different patterns might be caused by the shifting importance of processes depending on spatial scale. On comparably large scales basic environmental preferences or large scale niches of the species drive their occurence (e.g. geological substrate, climate, hydrology). As these change comparably slow with distance the log~norm model gives the best explanations (e.g. Qian et al. 1998; Nekola & White 1999; Qian et al. 2005). On intermediate scales the most important drivers of species composition change to e.g. soil, disturbance, as well as meso- and micro-climate. They vary on a much smaller scale. Therefore, the norm~norm model is best suited to describe the relationship between compositional similarity and geographical separation. However, the question which is intermediate scale highly depends from the system under study. On small scales dispersal seems to be more important and the norm~log model gives the best relationship (Table A5.3, Jones et al. 2006). Therefore we find a relatively fast decrease in similarity for the very close plots followed by a long tail of slower decrease (Figures A5.5 and A5.6) which contradicts the first part of our first hypothesis (similarity decreases continuously with distance). The pattern can be found in all subsets and some of the above mentioned studies make similar observations:

Table A5.3. Parameters and fits for different regression models for subsets of the data. The first term of the rownames describes the transformation of the response (composi-tional similarity), the second term gives the transformation of the predictor (geographical distance). *norm* means no transformation, *log* means log-transformation. **a)** Adjusted R^2-values. **b)** Mantel correlation coefficients - all are signifcant on the $p < 0.001$ level. **c)** Distance decay rates (slopes of the linear model). For norm-distance given per km, for log-distance given per log-m.

	model	all	DL1	DL2	DL3
a	norm~norm	0.2246	0.0151	0.0750	0.1483
	log~norm	0.2043	0.0133	0.0711	0.1385
	log~log	0.1668	0.0176	0.0820	0.1176
	norm~log	0.1965	0.0207	0.0904	0.1488
b	norm~norm	-0.474	-0.1248	-0.2753	-0.3857
	log~norm	-0.452	-0.1171	-0.2682	-0.3728
	log~log	-0.409	-0.1345	-0.2877	-0.3436
	norm~log	-0.443	-0.1453	-0.302	-0.3864
c	norm~norm	-0.0573	-0.0360	-0.0336	-0.0405
	log~norm	-0.1379	-0.0627	-0.0576	-0.1113
	log~log	-0.1934	-0.0404	-0.0600	-0.1743
	norm~log	-0.0833	-0.0236	-0.0359	-0.0689

Jones et al. (2006) found “similarity to decline very rapidly over short distances”. From 100m on the decrease was much slower. But both the linear as well as the spline regression poorly fitted the data. Our results indicate that this might be caused by poor coverage of larger distances as our fits generally increase with distances covered regardless of model utilised (Table A5.3). Condit et al. (2002) also calculated a fast decrease on shorter distances for their three investigation areas (Peru, Ecuador, Panama) which only persisted over more than 50 km in Panama. However, the scale of their study is different to ours and where their rapid decline happens (from 3 to 5 km) our whole scale fits in. This illustrates the problem of finding really comparable distance decay rates for different ecosystems. If one would take only the data of the Condit-study (ibid.) into account which fits in our scale, their distance decay rate would presumably be much higher. The fast decrease in similarity for short distances (dependent on the respective system studied) seems to validate the theory of dispersal. The farther away two plots are the more likely is the influence of other variables and processes on species composition. This pattern leads us to suggest that also in other studies the best fitting model would change with scale if data would be divided in subsets.

Although most studies do not utilise spline regression fits, which makes it hard to tell if this is a general pattern, hints can be found elsewhere too: Garcillán & Ezcurra (2003) fitted Whittaker’s exponential model to mean similarities for 50 km wide distance classes in a large scale study in the Baja California Peninsula. At least in two of three cases the very first distance class has a considerable higher similarity than the preceding. Despite of the different measure utilised to examine similarity, Palmer (2005) also found faster decreases for small distances in a meso-scale study in Costa Rican lowland tropical forest. Similarly Phillips (2003) found that floristic similarity can be described by a log-function of distance in assemblages of Amazonian trees on larger scales (distances up to 100 km) which means that there is also faster decrease for shorter distances.

Compositional similarity and environmental distances on distance levels

We found correlation between environmental variables and species composition to change with distance level. Nevertheless there was very weak to no correlation of species composition with soil variables, be it single or aggregated. For most variables correlation was highest if the whole data set was analysed. The reason might lay in longer gradients covered, which makes it likely for correlation to increase: Duque et al. (2002) found better explanation of compositional similarity by environmental distance if all landscape units (uplands well-drained and lowlands) were taken into account compared to the case when only sites on upland well-drained soils were included. This means that correlation is likely to be higher when the environmental gradient sampled is longer. In Duque et al.'s study (ibid.) space had - in most cases - far more important influence on upland well-drained soils. But the upland well-drained sites in their study also shared a much wider range of geographical distances which might have lead to artefacts due to the longer geographical gradient sampled. Comparably Potts et al. (2002) report that for long environmental gradients floristic similarity is dominated by habitat effects (environmental variables) whilst for truncated environmental gradients (sampling only within environmentally similar subsets) effects of geographic distance become much more important.

Correspondingly short gradient length might be a reason for the weak correlation of dissimilarity of soil variables with compositional similarity in the presented case. Especially for pH the gradient is rather short and all values are in the neutral to slightly alkaline range (7.0 - 8.1, Figure A5.2). This does not hold for CN ratio. Provided the exclusion of outliers the values for CN ratio range between 4.02 to 77.27 which means that a considerably long gradient is covered. Accordingly the correlation between compositional similarity and the dissimilarity of CN ratio is much higher than for pH.

We hypothesised that disturbance is the main driver of species composition. However, it seems to be not the most important one although the relative importance is changing with data subset and distance level. The influence of the dissimilarity of vegetation structure on compositional similarity is relatively high and - in comparison to other variables as slope, altitude or disturbance - relatively stable throughout distance levels and data subsets. Vegetation structure is described mainly by the spatial configuration of the tree and bush layer, bare soil and stones on the plot which in turn means that its actual configuration is - to considerable extent - caused by past disturbance events (logging, grazing, etc.). Thus, the structural configuration can be understood as an integrating surrogate over past disturbance regimes and can be seen as a measure of disturbance as well. This supports our hypothesis, that spatial patterns of vegetation (field layer) are mainly driven by disturbance.

Another reason for the mediocre correlation between disturbance and species composition might be the disturbance assessment. This is generally weak as it relies - among other features as the count of faeces or hoof marks - on the condition of the vegetation itself. Better data is hard to assess as detailed land-use maps are and will not be available (due to the semi-nomadic pastoralism). Despite of some minor efforts to develop methods for reliable disturbance assessment under such conditions (Culmsee 2004) there is much work to do in this regard. Maybe progress in the spatial and temporal resolution of remote sensing data will provide possibilities to obtain reliable data on land-use and disturbance in remote regions. Another possibility are exclosures but these are not easy to establish in the region because such measures are not easily communicated.

The highest correlation of compositional similarity can be found with the dissimilarity of the landscape structural variables altitude and slope when all data is included (Table A5.2). Correlation here is drastically lower on distance levels 1 and 2 which supports our hypothesis 2 and the idea that long gradients of the predictors are necessary to get high correlation with the response variables. That's why it seems likely that correlation with space as such tends also to be higher the broader the range of distances covered.

Compositional similarity and environmental distances in space

Surprisingly all variables more or less share the same pattern of spatial auto-correlation (Figure A5.6 a). This could be based on an intrinsic geographical scale of the investigation area. The correlation between predictors and environmental variables might be most valid for plots sharing distances around 2000 m because then neither negative nor positive auto-correlation due to spatial configuration occurs (Fig. A5.6 a). For the correlation between the dissimilarity of predictor variables and compositional similarity the picture is different. After a more or less pronounced decrease for the first distance classes, correlation between predictors and response increases considerably from the 1200 m to the 1600 m distance class. Although the general pattern is the same for all variables (only the variable 'structure' does not follow that pattern), there are considerable differences between them (Fig. A5.6 b). Correspondingly, Chust et al. (2006b) observe changing correlation coefficients between compositional similarity (Jaccard) and landscape similarity with geographical distance (and not only with the length of gradients) in a recent study in the Mediterranean on similar scales. They find a strong increase for the very short distances (up to approx. 250 m) followed by another step of increase around 1000 m distance. This is followed by a long plateau with slow increase. When partialling out the geographical distance the best correlation between landscape and floristic composition is obtained directly after the fast increase at 220 m.

In the presented study, the drastic extension of the altitudinal and morphological gradient with increasing geographical distance between plots (whereas the gradient in structure does change very little, Figure A5.2) might be responsible for the observed pattern. In the majority of the field studies it is very likely that variables (predictors and responses alike) are sampled on gradients of different extent. Our results suggest that not only spatial auto-correlation in compositional similarity is an issue (Legendre 1993). The different relative gradient length of the variables might be even more important. If variables describing environment are aggregated it is not possible to account for this problem.

Most recent studies include Mantel tests on distance matrices without accounting for scale issues (e.g. Duivenvoorden et al. 2002; Svenning & Skov 2002; Steinitz et al. 2006). Often multiple regression analysis on distance matrices (Legendre 1994) is carried out in addition to avoid “a loss of information” as only the best combination of the variables is included into the analysis (Jones et al. 2006). This assumes stationarity of the relationships and does not account for change of correlation with scale. Wagner & Fortin (2005) proposed direct multiscale ordination to deal with this problem of spatial non-stationarity because a global parameter estimate of a correlation or regression coefficient is meaningless when the species–environment correlation changes with scale. The method relies on multivariate ordination methods as CCA and such. However, it does not account for differing gradient lengths of the environmental variables. Here we work directly on distance matrices and evaluate the different relationships in parallel. If relative gradient lengths differ considerably between variables it might be better to regard single variables or ecological meaningful combinations instead of a pooled “environment” variable. Another possibility for avoiding spatial dependencies in hypothesis testing was suggested by Gilbert & Lechowitz (2004) in selecting sites systematically in a manner that any correlation between environment and distance would be avoided. However, this does again not account for differing gradient lengths and might not be feasible in any case.

To consider spatial non-stationarity in direct applications on quantitative data, Fotheringham et al. (2002) suggested a geographically weighted regression approach. A recent application can be found in Foody (2004). With a meta-analysis on African bird species richness they show that non-stationarity is an issue. They conclude that non-stationarity may affect any study using spatial data. Based on our results we agree with their findings and would like to emphasise the need to further spread spatial awareness in the ecological research community.

Sampling Design

A possibility to avoid problems with spatial auto-correlation might be the sole inclusion of neighbouring plots sampled in equidistant systematic grids (Jurasinski & Beierkuhnlein 2006) which is somewhat similar to the approach of Gilbert & Lechowitz (2004). Distance between plots is then constant throughout the analysis and relations are likely to be based on the environmental variables alone. Here we used data from randomly chosen plots out of a nested array where the primary grid (large plots) is given in the form of equidistant grids on three distance levels. If we consider - based on the auto-correlation analysis - the distance of 1440 m between neighbouring large plots as appropriate and the minor differences in distance between the plots of these as negligible we can use the data of distance level 3 to test this assumption. The broad picture doesn't change compared to our former analysis (Table A5.2, last column): Altitude and slope still show the strongest correlation with species composition followed by disturbance, structure and CN ratio (in this order). Geographic distance does not show any relation - there is no spatial auto-correlation. Therefore the resulting relations most likely reflect the actual influence of the variables on compositional similarity. But how do we know, that we didn't sample on the "wrong grid"? It is an almost not solvable dilemma that the setting of the grid in terms of grain, extent, and location will strongly influence the results. Thus it may be inappropriate to conclude from one scale studies (meaning fixed in grain and extent) about the general nature of the relationship between species composition and environmental variables.

As already mentioned, there are less and less pairs of plots with growing geographic distances between plots in any given data set (Legendre & Legendre 1998). Because of our grid design with nested distance and scale levels the short distances are even more over-represented. However, as the number of included plot pairs in the distance decay and correlation plots (Figures A5.5 and A5.6) indicate, this poses not to much of a problem. But with our design we gained the possibility to combine neighbour based analyses with distance based analyses.

Conclusion

Correlation and relative importance of the dissimilarity of predictor variables to compositional similarity is scale-dependent. However, this is rather based on increasing gradients than on the covered scale itself. Through the inclusion of different scales and distances we could show that correlation between compositional similarity and the dissimilarities of predictor variables heavily depends on scale and distance and the relationships exhibit non-stationarity especially when for some of the variables the length of the gradient is increased. This in turn means that one scale studies regarding vegetation patterns (or species composition) should be critically evaluated as relations found on one scale might not be true for another.

Considerable distance decay can be found even on relatively small scales. However, similarity does not decrease continuously with distance - distance decay is a general phenomenon the rate is not. There is fast followed by slower decrease in all of our subsets and in similar studies (e.g. Condit et al. 2002; Jones et al. 2006). Also the model which describes the relationship best changes with distance which reflects the shifting importance of processes driving spatial pattern in vegetation. With increasing scale the focus shifts from the individual (dispersal) to the community (resource competition, small scale environmental variation) to the whole population (feasible habitat, large scale environmental variation). With the scale which is inherent to the important drivers the model which best describes the relationship changes from a semi-log model with log-transformed geographic distances to a non-transformed to a semi-log model with log-transformed similarity. However, if the imposed environmental constraints are very strict and driven by man (controlling several important variables) no considerable distance decay might be found (Buhk et al. submitted).

It could not clearly be shown that disturbance in terms of grazing and its intensity is the main driver of the vegetational patterns of the field layer in the investigated system. However, it might lead to a meso-scale homogenisation because of diaspore transportation and offering chances for recruitment (bare soil). This is supported by the fast decrease in similarity for very close distances. Wood-cutting, especially in concert with intense grazing, does form the vegetation structure in the investigation area. This means that the structural variables can be seen as integrating surrogates for the disturbance regime. However, there is still much research to be done regarding the efficient and reliable assessment of disturbances.

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Appendix 6 Beyond richness - Upward shift of alpine plants leads to homogenisation of mountain summits. *Journal of Vegetation Science* accepted

*Jurasinski, Gerald (gerald.jurasinski@uni-bayreuth.de); Kreyling, Jürgen (juergen.kreyling@ufz.de)

Address (corresponding author):
Biogeography, School of Biology, Chemistry and Earth Sciences, University of Bayreuth, 95440 Bayreuth, Germany

Abstract

Question: Does the upward shift of species and accompanied increase in species richness, induced by climate change, lead to homogenization of Alpine summit vegetation?

Location: Bernina region of the Swiss Alps

Methods: Based on a data set from previous literature we expand the analysis from species richness to beta-diversity and spatial heterogeneity. Species compositions of mountain summits are compared using a two-component heterogeneity concept including the mean and the variance of Sørensen similarities calculated between the summits. Non-metric multidimensional scaling is applied to explore developments of single summits in detail.

Results: Both heterogeneity components (mean dissimilarity and variance) decrease over time, indicating a trend towards more homogeneous vegetation among Alpine summits. However, the development on single summits is not strictly unidirectional.

Conclusions: The upward shift of plant species leads to homogenization of alpine summit regions. Thus, increasing alpha-diversity is accompanied by decreasing beta-diversity. Beta-diversity demands higher recognition by scientists as well as nature conservationists as it detects changes which cannot be described using species richness alone.

Keywords

beta-diversity, climate change, heterogeneity, similarity, non-metric multidimensional scaling, Alpine, Bernina, long-term monitoring

Abbreviations

NMDS = Non-metric multidimensional scaling, rmse = root mean square error

Introduction

Shifts in species distributions have been linked increasingly to climate change (e.g. Grabherr et al. 1994; Hughes 2000; Walther et al. 2001; Parmesan & Yohe 2003; Root et al. 2003). Experiments have proven a causal link between warming and species reactions: modified competitive power or changes in reproductive success lead to changes in species composition (Chapin et al. 1995; Harte & Shaw 1995; Arft et al. 1999). However, with such experiments neither broad scale nor long term range shifts can be detected. Long term data sets are needed to estimate and predict range shifts due to climate change (Grabherr et al. 2001).

Alpine regions show strong gradients in abiotic conditions and contain highly specialized biota (Grabherr 1997). Therefore they are especially suited for long term observational studies of range shifts related to climate change. High alpine plant species are thought to be temperature-limited and thus changes in their distributions can be directly interpreted as changes in temperature (Grabherr et al. 2001). Furthermore, alpine regions appear to be subject to more rapid response to climate warming than other regions (Beniston 2003). Numerous studies show that there is an upward shift of plant species (Hofer 1992; Grabherr et al. 1994; Walther et al. 2001; Kullman 2002; Parmesan & Yohe 2003; Walther et al. 2005). All these studies indicate an increase in species numbers without loss of species. However, Klanderud & Birks (2003) find reduced occurrence of less competitive species native to the highest altitudes in a long-term comparative study in Norway.

Up to now, most studies on climate change and diversity focused on species richness, but conservation and management decisions, as well as scientific investigations regarding the influence of global change on ecosystems, should be based on a comprehensive measurement of biodiversity (Millennium Ecosystem Assessment 2005). Beta-diversity or heterogeneity is an additional important factor in this regard (Vellend 2001; Su et al. 2004). It is a key concept for understanding ecosystem function, conservation of biodiversity, and ecosystem management (Legendre et al. 2005; Balvanera et al. 2002; Condit et al. 2002; Kluth & Bruelheide 2004). However, up to now none of the studies focusing on the impact of climate change incorporates the question of homogenization which is intensively debated in the research area of invasive species (e.g. McKinney 2004; Kühn & Klotz 2006; Olden et al. 2006; see special issue of Biological Conservation 127). In general, biodiversity can decrease for two reasons: First, species may go extinct. Second, beta-diversity might decrease as specialized species are replaced by ubiquitous species. The resulting homogenization can lead to a reduction of spatial biotic diversity (McKinney 2005).

At global to continental scales biotic heterogeneity is expected to increase with climate warming because of asymmetries in warming trends (Walther et al. 2002). However, homogenization due to invasions and range shifts might contradict this pattern. The pool of species which benefit from warming by expanding their ranges upward in a specific alpine region is largely the same for all summits of that region. That's why we hypothesize that the increase in species richness (alpha-diversity) on mountain summits - which is driven by climate change - is accompanied by homogenization, expressed as a decrease in differentiation (beta-diversity or heterogeneity) between summits. We use a long-term data set from the literature which covers three points in time to test this hypothesis.

Material and Methods

Data set

The data used for the presented analysis were assembled by Walther et al. (2005). They resurveyed mountain summits which had been studied prior to 1907 (Rübel 1912) and in 1985 (Hofer 1992). This analysis included ten summits of the Bernina Group in the Swiss Alps. Eight consist of siliceous rock, two consist of calcareous rock (Piz Alv and Piz Tschüffer, Table A6.1). In all three surveys, the uppermost 10m of each summit was searched in detail and the presence of vascular plant species was recorded. One exception was Piz Languard where 30m was searched (for details see Walther et al. 2005).

The calcareous summits differed substantially from the summits underlain by siliceous rock regarding their abiotic features, as well as their species inventory (Walther et al. 2005). As there were not enough replicates to overcome such a high initial noise, we omitted the calcareous summits from the analysis. For the same reason we excluded Piz Trovat, as the top of this summit is "completely composed of loose scree" (Hofer 1992). It showed the lowest species numbers at all sampling dates (8, 8, and 7 species respectively) and strong, trendless differences between the surveys. The main difference was that two species were absent in the second sampling but were found in the first and third sampling. Therefore we assumed that the highly dynamic substrate dominates the species composition of this summit and conceals all other trends.

We used the recorded presence data and applied the following procedures to describe and analyze heterogeneity of the data set based on dissimilarity between the summits.

Table A6.1. Description of investigated mountain summits. The last three (in italics) were not included in the analysis due to their differences in bedrock and morphology.

Summit	Altitude [m asl]	Rock	Morphology	UTM WGS84	
				easting	northing
Munt Pers	3207	gneiss	compact, little scree	3207’	793302
Las Sours	2979	gneiss	compact	2979	790891
Piz Languard	3262	gneiss	compact	3262	793294
P. Chatscheders	2986	gneiss	compact, little scree	2986	797950
Piz Minor	3049	gneiss, mica slate	compact, fine scree	3049	798946
Piz dals Lejs	3041	gneiss, mica slate	compact, fine scree	3041	799680
P. Lagalb	2959	gneiss	compact, blocks, fine scree	2959	798642
(Piz Trovat)	*3146*	*gneiss*	*coarse scree*	*3146*	*794660*
(Piz Tschüffer)	*3123*	*dolomite*	*compact, fine scree*	*3123*	*796814*
(Piz Alv)	*2975*	*dolomite*	*blocks, fine scree*	*2975*	*796744*

Assessing spatial heterogeneity

We use the dissimilarity between summits as a descriptor of spatial patterns of biodiversity or more specific as a measure of differentiation among landscape patches of similar habitat. Thus, it is a measure of beta-diversity (Whittaker 1972). Beta-diversity is described here as the dissimilarity in species composition between summits, measured by Sørensen dissimilarity, expressed as the complement of the Sørensen similarity coefficient (Sørensen 1948; for a broad discussion of binary similarity indices see Koleff et al. 2003). We use it to express heterogeneity in the data set.

Heterogeneity is presented here in two components. A mean dissimilarity component which can be compared to attempts by Williams (1996) or Lennon et al. (2001) was calculated as the mean of all dissimilarities between a focal mountain summit and all other summits in the data set (see Fig. A6.1).

To incorporate the variance of the dissimilarities calculated for a focal summit, we accounted for the deviation of each dissimilarity value from the mean. We call it the variance component. The higher it is for a given summit, the more variable (heterogeneous) the calculated dissimilarities are between this summit and the other summits in the data set. Furthermore, the variance of the variance components can be seen as a measure of spatial heterogeneity itself. Thus, decreasing variance indicates increasing homogeneity. For a proper representation of the spread around the mean we use the standard deviation of the dissimilarity values calculated for a focal summit. See Figure A6.1 for a graphical representation of the concept.

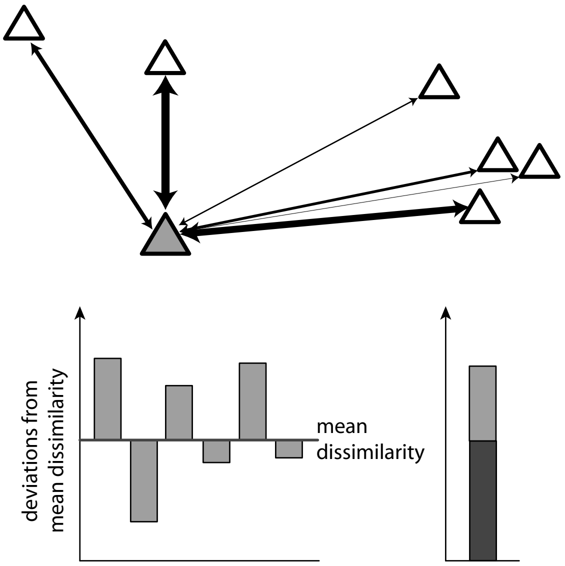

Figure A6.1. Heterogeneity concept. Arrangement approximates actual geographic position of the summits. Width of arrows represent the similarity between the focal summit (grey triangle) and the other summits (white triangles). To incorporate the spread or variability of the similarities, the deviation of each single similarity value from the mean is taken into account (the grey line represents the mean similarity and light grey bars represent the deviation). The stacked bar represents the aggregated measure, with standard deviation of the deviations from the mean in light grey, and mean of mean dissimilarity values in black. Sørensen similarity (β_{Sim}) is transformed to dissimilarity by calculating 1 - β_{Sim}.

As we investigated the changes of the similarity structure over time in a constant spatial configuration, we are not affected by the inherent problems of distance decay due to unevenly spaced objects (Tobler 1970; Legendre 1993; Nekola & White 1999). It is likely, that there is a variability in the similarity values which is based on spatial configuration, but it is not responsible for changes in time. Therefore we did not account for spatial auto-correlation in our analysis.

Comparison between groups

Data points of dissimilarity matrices are not independent. Furthermore, our sample size is rather small (for each sampling period, n equals the number of summits (7)). Therefore mean dissimilarity of the summits was compared between the different time steps using a permutation procedure. The mean dissimilarity values for all summits of each sampling date are compiled and the difference in mean between two sampling dates is calculated (*delta*). Then the values of these two sampling dates are put into a combined set from which two random sets of the same size as the original sets are drawn. The difference in mean between these random sets is calculated and stored (permuted *deltas*). Repeating the last step 1000 times provides a potential significance-level of $p<0.001$ by testing the original *delta* against the distribution of the permuted *deltas*. Because of the small sample size and as we are testing against 1000 permutations all differences in mean with $p \geq 0.01$ are understood to be not significant.

Non-metric multidimensional scaling (NMDS)

For illustration and interpretation of the heterogeneity analysis results, we applied a non-metric multidimensional scaling (Kruskal 1964) with the species data of all included summits and time steps. Here, NMDS was conducted according to the procedure recommended by Minchin (1987), which is based on the algorithm described by Kruskal (1964) and Mather (1976) with several random starts to find the best global solution. An important factor describing the quality of the solution is the stress. It is a measure of the mismatch between distance measures and the distance in ordination space. Stress values smaller than 20 generally lead to usable pictures and interpretations (Kruskal 1964; Clarke 1993). Again, the Sørensen coefficient was used to quantify the dissimilarity in species composition between summits. The NMDS was calculated with the function *metaMDS* in the package *vegan* (Oksanen et al. 2005) for the R statistics system (R Development Core Team 2005). It was conducted with the presence/absence data and *metaMDS* was used with defaults (two-dimensional solution, maximum number of random starts=50).

Results

The two components of heterogeneity

The mean dissimilarity components decrease over time (Fig. A6.2 a). The decrease is significant on the $p < 0.001$ level from 1907 to 1985 and from 1907 to 2003. However, it is not significant for the last time step (1985 to 2003, for details see Fig. A6.2 a). The values of the variance component are also dropping significantly from 1907 to 2003. Analogously to the mean dissimilarity component the decrease is less pronounced for the variance component between 1985 and 2003, but it is still significant ($p < 0.01$). However, from 1907 to 1985 there is no significant decrease in the variance component (see Fig. A6.2 a). From the boxplot in Figure A6.2 b a change in spread of the values is apparent. An increase from 1907 to 1985 is followed by a decrease from 1985 to 2003. The variance of these values is itself a measure of heterogeneity. To test whether the change in variance is significant we employed Levene‘s test for the unequality of variances. Although Figure A6.2 b depicts changing variances, they do not differ significantly between the three sampling dates (F-ratio = 3.56 with $p = 0.05$).

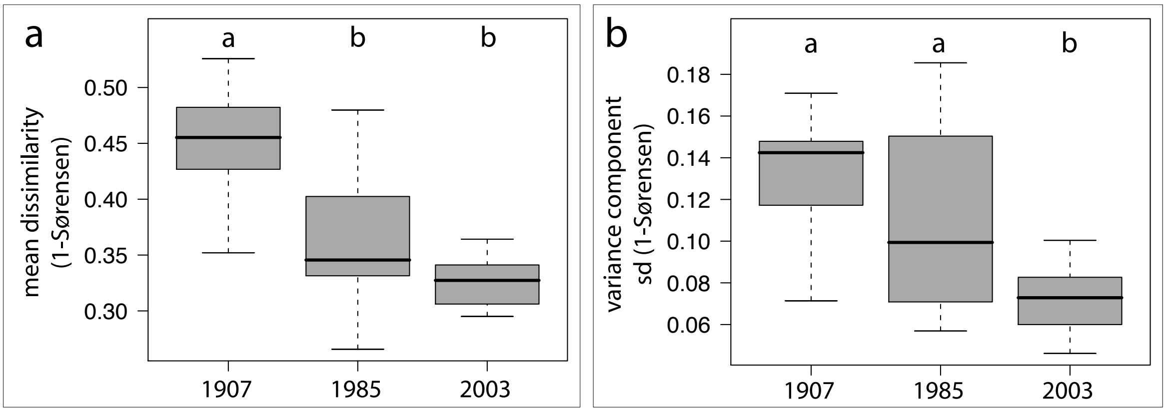

Figure A6.2. Development of heterogeneity through time: **a)** Mean dissimilarity component. The decrease is significant (tested with a permutation procedure) from 1907 to 1985 and from 1907 to 2003 ($p<0.001$ for both), though less pronounced, between 1985 and 2003 ($p=0.027$). **b)** Variance component. The decrease is significant from 1907 to 2003 ($p<0.001$) and from 1985 to 2003 ($p=0.008$). For 1907 to 1985 $p=0.134$. (Box legend: thick black line: median, lower box end: 1st quartile, upper box end: 3rd quartile, whiskers: extremes)

Summit specific developments

Increasing species richness is accompanied by decreasing dissimilarity among summits (Figure A6.3). Nevertheless, this general pattern of increasing homogeneity and decreasing spatial variability is not uniform for all summits. The development on Piz Lagalb and Munt Pers was not uni-directional and less obvious as seen in the barplots in Figure A6.3. The summit specific developments are best reflected in the NMDS plot shown in Figure A6.4 a which depicts the dissimilarity situation in the data sets. The final stress value of 10.77 is very low, and the low rmse implies that the probability is very high that the chosen solution is the global solution.

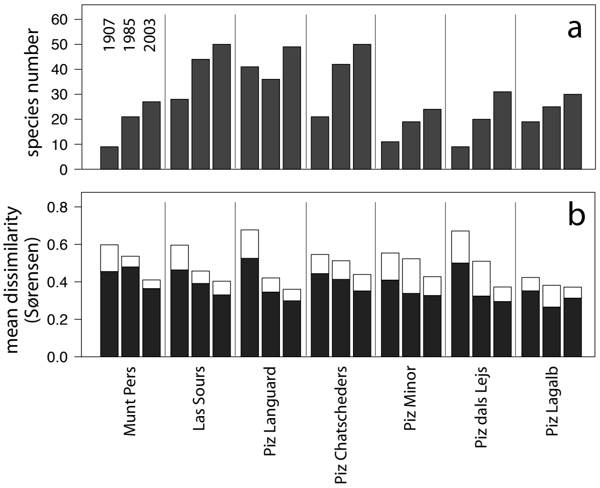

Figure A6.3. Development on single summits (for each from left to right: 1903-09, Rübel (1912); 1983/85, Hofer(1987); 2003, Walther(2005)). **a)** Species numbers generally increase (for details see Walther et al. 2005). **b)** Mean dissimilarity (black) generally decreases, development is not always uni-directional (see Piz Lagalb, Munt Pers); the variance component (white) generally decreases and development is again not always uni-directional (see Piz Lagalb and Piz Minor for deviations).

It is evident from Figure A6.4 that the different peaks do not evolve linearly and in the same direction. On the contrary a "back and forth" development can be seen in Piz Languard, whereas most of the other summits exhibit a somewhat "hooked" development. „Hooked" means that a displacement in one direction for time step 1 is roughly orthogonal to the direction for the second time step. Only Piz Minor and Piz dals Lejs develop largely unidirectional (broadly along axis 1). Munt Pers, Piz Chatscheders, Piz dals Lejs and Piz Minor show the strongest changes. The direction of change in species composition over time seems to be similar for Las Sours and Munt Pers whereas the development on Piz Chatscheders was different. Even though the direction of development is different for the summits, an evident trend can be seen: in Figure A6.4 c the positions of the summits at the three time steps are outlined (shortest boundary) showing that the summits are clumping closer together over time, indicating a homogenization of species composition. This holds even true for summits not belonging to the same massif although there are apparent differences between summits of different ridges. Especially when the development over time of the single summits is taken into account, three groups according to the different massifs can be relatively clearly distinguished in the NMDS plot (compare Figures A6.4 a and b). The most obvious is the dissimilarity of Munt Pers which is clearly separated from the other summits on axis 2. In real geographical space the large Bernina valley disconnects this summit (together with the summit of Piz Trovat which is on the same ridge) from the others. Piz Lagalb, Piz dals Lejs, and Piz Minor belong to another group distinguishable from the group of Las Sours, Piz Languard, and Piz Chatscheders mainly along NMDS axis 1. In reality these groups are separated by the da Fain valley.

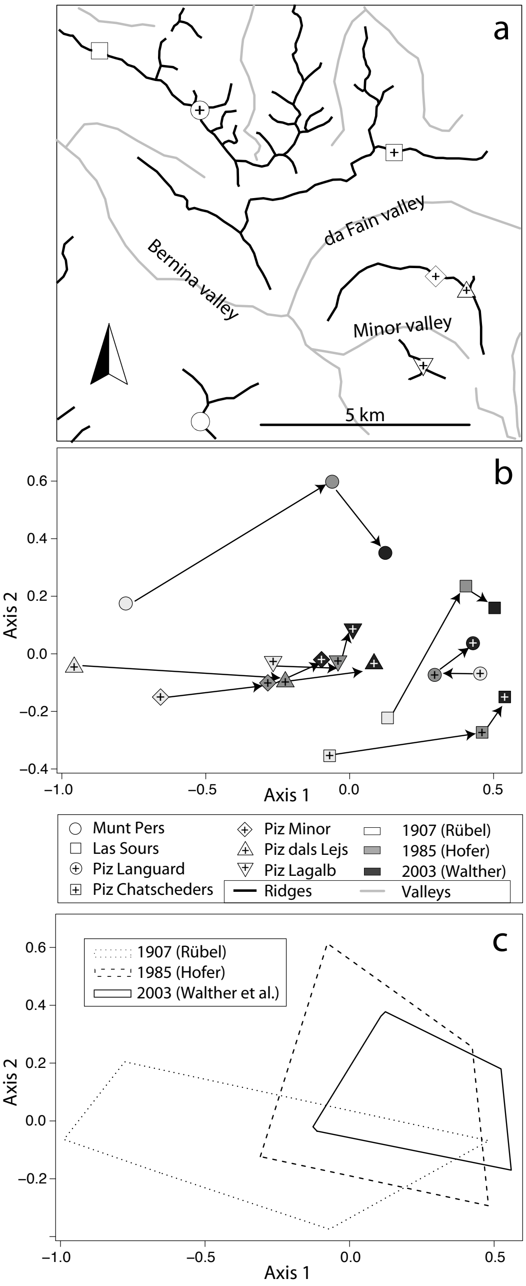

Figure A6.4. a) Map sketch of the investigation area showing ridges, valleys (see legend below b) and position of the summits. **b**) NMDS-ordination of species compositions of seven mountain peaks (symbols) at three time steps (grey scale). Shown is the output after 19 random starts (final stress=10.77, rmse=3.770 e-05, max residual=0.000103) as then a global solution was found (see text for details). **c**) Outlines of the positions of the summits in ordination space (shortest distance) show that homogenization is occurring.

Discussion

Homogenization

In the time period covered (1907-2003) mean dissimilarity of the investigated Alpine summits is decreasing, indicating ongoing homogenization. However, initial species composition, geographical position, and geographical context of individual summits have resulted in the general trend not being reflected equally on all summits. Another important issue might be the accessibility and popularity to humans as vectors - carrying and spreading diaspores - but we have no data on this. Nevertheless, we found an increase in the spread of the variance component for 1985 (although it was not significant). This might be due to the non-linear developments on the different summits. Piz dals Lejs and Piz Minor exhibited comparatively high variance components in 1985 (Fig. A6.3 b) leading to the large spread of the values. These were amongst the summits with most dramatic changes in species number and identity which started from a rather low level. The increase of the spread of the variance component in the 1980's might be due to delayed developments on other summits. Future investigations of the summits might help answer this question.

When the position of the summits in ordination space is compared to the position in geographical space, a clear congruence can be seen. This might have various reasons. A simple one could be that the summits share different geographical distances. Summits which are geographically closer are most likely to have more species in common than far away summits. This distance decay of similarity is a well known characteristic of geographical systems (Condit et al. 2002; Nekola & White 1999) and is often explained by the dispersal capacities of the species.

We did not account for spatial auto-correlation because the spatial configurations of the summits do not change over time. For that reason we are not able to tell which part of the variance is due to the spatial configuration alone. It is possible to partial out the space component (e.g. Borcard & Legendre 1992; Wagner 2005), but one needs to test against the variation caused by environmental variables which we do not have. To obtain an idea regarding the influence of geographical distance on compositional similarity we conducted a Mantel test (Legendre 1998). The results hint to a generally high importance of spatial configuration on the observed pattern although there is much change between the time steps (Mantel correlations between compositional similarity (Sørensen) and geographical distance between summits (Euclidean distance): 1907 = -0.64 ($p < 0.001$), 1985 = -0.33 (ns), 2003 = -0.82 ($p < 0.001$)).

Especially in mountain regions things are even more complicated as the pool of available species for colonisation might differ - at least partially - on different massifs due to barriers (e.g. deep mountain valleys or ridges) which certain species cannot overcome or which prolong the possible dispersal way. In Figure A6.4 a and b the combined effect of geographical distance and belonging to massifs or ridges is apparent although we cannot tell which is more important. However, we rather want to focus on another point: even summits on different massifs become more similar. In 1907 the grouping was much less apparent and the summits were more distinct in species composition than they are in 2003. Today the summits of the Minor group are not only much more similar to each other but also more similar to the summits of the Languard group (which also have more species in common now) from which they are separated by the da Fain valley. This clearly illustrates the ongoing homogenization. Such relations might also be the reason for the hooked developments of Piz Languard or Piz Minor because warming possibly changes dispersal ways. However these questions cannot be answered with the presented data and more research in this regard is desirable.

Meeting at the top

When plant species' ranges are shifting, it is to be expected that those traveling upwards will meet species already present. Walther et al. (2005) show that there are currently more species than there have been recorded before on the investigated summits. They also find that in general up to 2003 no species was lost from the summits. Although the pattern is not as evident as the upward shifting, our results show that there is a homogenization of Alpine summits. Alpine regions are very special concerning the spatial organisation of their biota and ecosystems. Because of the tremendous small-scale variation of environmental parameters, particularly at mountain tops, no peak is like another regarding its environmental conditions. An ongoing homogenization leads to a decrease in beta-diversity in Alpine summit regions even though alpha-diversity is increasing on the summits. Different aspects of biodiversity develop in different directions. If only one of the aspects is taken into account, wrong conclusions might be drawn. This special example could be taken as a model for ecosystems in general although it must be tested if our results can be replicated for other alpine regions as well.

Biodiversity is more than just species richness. Therefore the assessment and analysis of ecosystems has to include heterogeneity (which can be expressed by beta-diversity) and possibly functional diversity as well (Beierkuhnlein 2001). Otherwise unreliable conclusions might be drawn. Increasing alpha-diversity means increasing biodiversity and is thus positive from a conservationist view. However, as this might be accompanied by a decrease in beta-diversity it is not so simple. See Gering et al. (2003), Sax & Gaines (2003), Legendre et al. (2005), and Olden et al. (2006) for the importance of beta-diversity in science and conservation.

Data set

If all ten summits of the original dataset would be included in the analysis, the observed tendencies are generally the same, but less obvious and not significant (neither for the mean dissimilarity nor for the variance component). This implies that either the results are not valid generally or that the sample size of the original data set is too small relative to the noise level. The significant results for the reduced data set of similar abiotic conditions support the second conclusion and indicate that comparable environments which differed historically in species composition are currently becoming more similar. Nevertheless, the insignificant homogenization effect for the whole data set implies that the effect is still weaker than the variance in species composition due to abiotic differences. This is not surprising regarding the considerable differences in environmental conditions between siliceous and calcareous rocks. At large there is the same species pool of possible colonisers for all of the summits in the region. More information on environmental variables would be needed to clarify the reasons for the actual species composition but this is not the scope of this contribution.

Conclusions

Our results indicate that the upward shift of plant species might lead to a homogenization of alpine summit regions due to decreasing dissimilarity between summits. Thus, increasing alpha-diversity is accompanied by decreasing beta-diversity. This shows that species richness alone cannot be used as an indicator for the impact of changing climate on biodiversity. One option might be to study the reaction of single species to climate warming. However, the reactions will presumably be ambivalent and results may not be easily generalized. A possibility to incorporate single species reactions into analysis and thus widen our understanding regarding the impacts of climate change on mountain biota is demonstrated in the presented paper.

Studies not incorporating a comprehensive view on diversity - adding at least differentiation (beta-) diversity - should be evaluated with care. Our findings add to the recent debate about the importance of beta-diversity: beta-diversity demands greater recognition by scientists and nature conservationists as it detects changes which cannot be described by species richness (Balvanera et al. 2002; Condit et al. 2002; Legendre et al. 2002) and is able to widen our understanding of ecosystem processes (Legendre et al. 2005).

Even though the trend of homogenization can clearly be shown with this data set, it becomes apparent that the effect is much weaker for the time step between 1985 and 2003. The reason might be that 15 years is not a long time for mountain-summit species. We still do not know much about the life spans of plants smaller than trees or bushes, but available results suggest that these can be quite long (e.g. Steinger et al. 1996). This highlights the importance of long-term data sets for an understanding of the effects of global change. Without such data sets findings will often be weak and statistical evidence hard to obtain. Data on more summits would have been desirable in the presented study but long-term and large data sets are quite rare. As we can see by the problem of different bedrock, such long-term monitoring sites have to be chosen very carefully, with statistical requirements and ecological theory in mind for being useful to future analyses. To gain further insight in the homogenizing effect of climate change induced range shifts, more research with larger data sets should be done.

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Appendix 7 simba-Manual (simba - Similarity Analysis for Vegetation Ecology)

The simba Manual is compiled from the source code of the help files with R functionality provided by R CMD Rd2dvi. Therefore it does not match the design of the document but the design of R package manuals. Page numbering is also separate.

R documentation

of all in 'simba'

April 16, 2007

R topics documented:

`abis` *Vegetation and environmental data recorded in a Tundra ecosystem in Northern Sweden (Southeast of Abisko).*

Description

Vegetation and related data from field sites in a Tundra Ecosystem in Northern Sweden. `abis.spec` holds abundance information of 158 species on 61 sites.

Usage

```
data(abis)
```

Format

abis.env contains some environmental variables from the Abisko field sites. These are:

X	Numeric: The x-coordinates of the field sites (utm). The sites are arranged in a regular equidistant grid. Each site is a hexagon plot with 5m radius.
Y	Numeric: The y-coordinates of the geographic position of the field sites.
alt	Integer: Height a.s.l. of the field sites.
aspect	Exposition of the sites. In degree from 0 to 180/-180. Counts negative in westward direction and positive in eastward direction.
slope	Numeric: the inclination of the sites in degree
pH	Numeric: pH value of soil samples taken on the sites (mixed samples from three
n.spec	Integer: Number of species on the site.
shannon	Numeric: Shannon index calculated from the species data.
even	Numeric: Evenness calculated from the species data.
simps	Numeric: Simpson diversity index for the site.
ephwtrs1	Numeric: Cover of ephemeral waters
ephwtrs2	Numeric: Cover of dried out ephemeral waters?
roughn	Numeric: Roughness index for the site. Obtained through calculating the ratio between the length of the straight lines dissecting the hexagonal plot and the lengths of lines along this dissections but exactly following the surface.
stones.cov	Numeric: Proportion of area of site covered by rocks which are covered with vegetation.
stones.uncov	Numeric: Proportion of area of site with uncovered, bare rocks.
bare.soil	Numeric: Open soil (most often sandy substrates).
water	Numeric: Proportion of area covered by permanent water bodies.
bog	Numeric: Proportion of area covered with boggy depressions.
lemming	Numeric: Counts of Lemming feces.
elk	Numeric: Counts of Elk feces.
ren	Numeric: Counts of Ren feces.
ripa	Numeric: Counts of Ripa feces.
fox	Numeric: Counts of Fox feces.
grubbings	Numeric: Amount of mole grubbings.
tread	Numeric: Amount of hoof tread.
betula	Numeric: Cover of *Betula*.

CEC	Numeric: Cation Exchange Capacity measured from the mixed soil sample taken in the field.
base.satur	Numeric: Base saturation.
heath	Binary: Does the site belong to the vegetation type 'heath'?
shrubs	Binary: Does the site belong to the vegetation type 'shrubby vegetation'?
protect	Binary: Does the site belong to the vegetation type 'protected snow heath'?

Source

Jurasinski, G. and Retzer, V. (in. prep.) Measuring multi-plot similarity with presence-absence data.

Rettenmaier, N. 2004. Räumliche Muster der Biodiversität in der skandinavischen Tundra - Diploma thesis (unpublished), Department of Biogeography, University of Bayreuth, pp. 96.

Examples

```
data(abis)
```

`ads.ternaries` *Artificial data-set for studying the mathematical behavior of asymmetric similarity coefficients*

Description

Artificial data-set as utilized in Koleff et al. 2003, and Jurasinski 2007 to study the mathematical behavior of asymmetrical similarity indices. The corresponding values of all indices computable with `sim` are contained. See example!

Usage

```
data(ads.ternaries)
```

Format

ads.ternaries	`data.frame` with the three matching components of asymmetric binary similarity measures `(a, b, c)` with all possible combinations of these components derived from a virtual dataset with 100 variables (species). These are the first three columns. The preceding columns contain the values of the similarity coefficients computable with `sim` according to the three matching components. This information can be used to study the mathematical behavior of the indices. See example

Source

Jurasinski, G. (2007) Spatio-Temporal Patterns of Biodiversity and their Drivers - Method Development and a Case Study from Northeastern Morocco. PhD-Thesis, Department of Biogeography, University of Bayreuth

Koleff, P., Gaston, K. J. & Lennon, J. J. (2003) Measuring beta diversity for presence-absence data. *Journal of Animal Ecology* **72**: 367-382.

Examples

```
data(ads.ternaries)
library(plotrix)
##take any index you want to study, see the help for sim() for available
##asymmetric indices or the names of the data.frame:
names(ads.ternaries)

##make a tmp from the index you want to study (we perform a transformation
##to obtain values between 0 and 1). if you want another index,
##just change the name in the next line:
tmp <- ads.ternaries$mountford
tmp <- (tmp-min(tmp))/max(tmp)
triax.plot(ads.ternaries[,c(2,3,1)], main="mountford",
col.symbols=grey(seq(0.1,1,0.1))[floor((tmp*100)/5)+1], pch=16)

##don't wonder: mountford is strange, just try another one:
##this time with rainbow-colors
tmp <- ads.ternaries$soerensen
tmp <- (tmp-min(tmp))/max(tmp)
triax.plot(ads.ternaries[,c(2,3,1)], main="sørensen",
col.symbols=rainbow(10)[floor((tmp*100)/10)+1], pch=16)

##and an interesting shape: routledge in greyscale...
tmp <- ads.ternaries$routledge
tmp <- (tmp-min(tmp))/max(tmp)
triax.plot(ads.ternaries[,c(2,3,1)], main="routledge",
col.symbols=grey(seq(0.1,1,0.1))[floor((tmp*100)/5)+1], pch=16)
```

`aslopect` *Calculate similarity of plots based on slope aspect and inclination*

Description

Allows for the comparison of plots regarding the two variables slope aspect and slope inclination at once. To obtain a distance measure integrating aspect and inclination the model of a unit sphere is used and great-circle distances between virtual locations are calculated. For each plot a virtual location on the sphere is defined using the values for aspect as longitude and 90°-inclination as latitude. See `details` for more...

Usage

```
aslopect(asp, slo, names=rownames(asp), listout = FALSE)
```

Arguments

`asp`	Numeric vector with aspect values, given in degree. Expects values between 0° (North) and 180°/-180° (South). Eastward directions count positive, westward directions count negative.
`slo`	Numeric vector with slope inclination values. Expects values between 0°(flat) and 90° (vertical wall)
`names`	Plot names, defaults to the rownames of `asp`, but a separate vector can be specified. Its length has to match the length of `asp` and `slo`.

`listout`	Shall the results be given in list-format (`data.frame`). Defaults to FALSE which means that a matrix of class `dist` is returned

Details

To obtain a distance measure integrating aspect and inclination the model of a unit sphere is used and great-circle distances between virtual locations are calculated. For each plot a virtual location on the sphere is defined using the values for aspect as longitude and 90°-inclination as latitude. This means that as long as the inclination is low the virtual points are located in the pole region so that, regardless of aspect, plots with low inclination are rather close to each other regarding these qualities. The idea behind is, that solar radiation, wind or other factors highly depending on aspect and inclination are not really differing between plots with different aspect as long as the slope is low. The longitude values on the unit sphere are derived from the values of slope aspect. The equator of the sphere is thought as the compass circle. The Prime Meridian of the virtual sphere is the great circle through North and South of the compass. As in geographic terms longitude counts positive in Eastern and negative in Western direction. With ϕ = latitude = 90°-inclination and λ = longitude = aspect the great-circle distance between A and B can be calculated with the following formula.

$$sim = \zeta = \arccos\Big(\sin(\phi_A) \cdot \sin(\phi_B) + \cos(\phi_A) \cdot \cos(\phi_B) \cdot \cos(\lambda_B - \lambda_A)\Big)$$

Value

Returns a `dist` object or a `data.frame` (depending if listout = FALSE or TRUE). As a unit sphere is used, the maximum distance between two inclination/aspect pairs is perimeter/2 of the sphere which is by definition π. To scale the possible distances between 0 and 1 the results are divided by π. Thus, a great-circle distance of 1 is rather scarce in the real world, however, two vertical rock walls with opposite aspect would share it. If listout = TRUE a `data.frame` with the following variables returns.

`NBX`	one of the compared sampling units
`NBY`	the other part of the pair
`x`	The returned aslopect value

Author(s)

Gerald Jurasinski

See Also

Examples

```
data(abis)
## identify columns with slope and aspect data
names(abis.env)

## calculate aslopect
abis.aslop <- aslopect(abis.env[,4], abis.env[,5])
```

`bcoov` *Calculate Bray-Curtis distance for only one variable*

Description

Calculates Bray-Curtis distance for only one variable: How dissimilar are the units regarding for instance pH?

Usage

```
bcoov(x, names, listout = FALSE)
```

Arguments

`x`	numeric vector with quantitative data from sampling-units, standardization may be applied before
`names`	where should the names be taken from, must be a vector of the same length as `x` and should give the names of the sampling-units
`listout`	Shall the result given in list-format (`data.frame`)? Defaults to FALSE

Details

It is just a simple way to calculate similarity based on only one variable. In the future there might be a possibility to choose from some functions. However, you could also use the difference in the data-values instead (which is the Euclidean distance in one dimensional space).

Value

Returns a `dist` object or a `data.frame` (in the case of `listout` = TRUE) with

`NBX`	one of the compared sampling units
`NBY`	the other part of the pair
`x`	The returned distance value. It is named like the tested variable

Author(s)

Gerald Jurasinski

See Also

`vegdist`, `dist.quant`, `dsvdis`

Examples

```
data(abis)
names(abis.env) ##take a look at the data
##calculate the similarity (Bray-Curtis) between the plots
##regarding pH
pH.dist <- bcoov(abis.env$pH, names=rownames(abis.env))

## directly give it as a list (data.frame)
pH.dist.ls <- bcoov(abis.env$pH, names=rownames(abis.env)
```

```
, listout=TRUE)
```

`boxes` *An adaption of boxplot.n.*

Description

Uses `boxplot` to produce a boxplot, which is then annotated with the number of obbservations in each group. Does allow for more flexibility compared to `boxplot.n`. Default size of the text is bigger and per default the numbers are not plotted directly on the x-axis and their distance from the axis can be changed.

Usage

```
boxes(..., top = FALSE, shrink = 1, textcolor = NULL, yadj = NULL)
```

Arguments

`...`	Parameters passed to `boxplot`.
`top`	Should the numbers of observations be printed below or above the boxes? Defaults to below (top = FALSE).
`shrink`	Parameter to scale the size of the numbers of observations. Above 1 increases size, below 1 until 0 decreases size.
`textcolor`	Color of the text. Defaults to NULL which than uses the actual plotting colour of the graphics device.
`yadj`	Can be used to adjust the vertical plotting positions of the numbers of observations. Defaults to NULL - no adjustment.

Author(s)

Gerald Jurasinski

See Also

`boxplot`, `plot`, `boxplot.n`

Examples

```
data(abis)

## see environmental data (see documentation on data for details)
abis.env

## calculate the difference in similarities for the three major
## vegetation types
## therefore created a vector from the data expressing belonging
## to the vegetation types:
tcs.sub <- rep(0, 61)
tcs.sub[abis.env[,29]==1] <- 1
tcs.sub[abis.env[,30]==1] <- 2
```

```
tcs.sub[abis.env[,31]==1] <- 3

## calculate similarity (Jaccard) between all pairs of plots
abis.jacc <- sim(abis.spec, method="jaccard")

## make boxplots regarding the similarities for each vegetation
## type, including the number of pairs contained in each box.
boxes(as.matrix(abis.jacc)~tcs.sub, shrink=1.2)

## prettier
boxes(as.matrix(abis.jacc)~tcs.sub, notch=TRUE, col="grey50",
shrink=1.2, ylim=c(-0.1, 0.9))
```

`com.sim` *Compare mean similarity between subsets of data*

Description

Related to `mrpp`. Are the differences in mean similarity between data subsets significant? Function takes the whole data-set (species matrix) and a subsetting vector and computes a specified similarity between all sampling units (rows). Then subsets are compared regarding their mean similarity. Statistical inference is obtained through permutation.

Usage

```
com.sim(veg, subs, simil = "soerensen", binary = TRUE,
    permutations = 1000, alpha = 0.05, bonfc = TRUE, ...)
```

Arguments

`veg`	Species matrix with columns = sites, rows = species. Deliver presence/absence data or abundance data. However, `binary` has to be set accordingly.
`subs`	Vector containing the subset definition. Same entries are understood to indicate belonging to the same subset (can be characters, factors or numerics). For each subset similarities/distances are calculated. Then all subsets are compared regarding mean and variance of the similarities/distances.
`simil`	Sets the coefficient to be used for calculating similarities/distances. If `binary` = TRUE, see `sim`, otherwise see `vegdist` for possible choices.
`binary`	Changes the function used for the calculation of similarity/distance. If binary species data ist provided in `veg` keep the default (`binary` = TRUE). In this case `sim` is used to calculate the similarities. Set to FALSE when abundance or frequency data is provided. This calls `vegdist` to calculate the distances between sites in species similarity space.
`permutations`	Number of permutations performed to obtain the statistical inference. See Details.
`alpha`	Initial alpha level to test against. Defaults to 0.05.
`bonfc`	Shall Bonferroni correction be applied? Defaults to true.
`...`	Further arguments to functions.

Details

Entries of similarity/distance matrices are not independent. Therefore normal statistics might fail. One possibility is the application of permutation procedures. This means that the statistical distribution against which significance is tested is derived from the data.

Here it is implemented as follows: For each subset the similarities/distances between all sites (plots) are calculated with the specified coefficient. Then the resulting similarity/distance matrices are compared with `diffmean`. This is done for the comparison of each subset with each other subset. If specified (defaults to TRUE), Bonferroni correction is applied (to correct for multiple testing).

Depending on the number of subsets and the number of sites per subset it may take some seconds to be computed.

Value

Returns an object of class `cslist` containing the call to the function, the used method for similarity/distance calculation, a comparison matrix showing the connections between data-subsets (rows and columns connected with "*" are significantly different), the number of subsets involved, the number of permutations and a matrix giving information about the following components for each comparison between subsets:

`X`	Subset identifier for one of the compared subsets
`Y`	Subset identifier for the other compared subset
`mean.x`	Average distance/similarity for subset X.
`mean.y`	Average distance/similarity for subset Y.
`diff`	Difference in average distance/similarity for this comparison
`sig`	Significance of the difference in mean of the similarities.
`sigs`	Significance flag for the comparison ("*" means significant differences, "ns" means that the differences are not significant).
`F`	F-value for the Comparison.
`sigF`	Is F significant?
`sigsF`	Significance flag for F.

Author(s)

Gerald Jurasinski

See Also

`mrpp` for an anova like approach for comparing the differences of species data subsets.

Examples

```
data(abis)

## see environmental data (see documentation on data for details)
abis.env

## calculate the difference in similarities for the three major
## vegetation types
## therefore create a vector from the data expressing belonging
## to the vegetation types:
```

```
tcs.sub <- rep(0, 61)
tcs.sub[abis.env[,29]==1] <- 1
tcs.sub[abis.env[,30]==1] <- 2
tcs.sub[abis.env[,31]==1] <- 3

## calulate differences with Bray-Curtis as the distance measure
com.sim(abis.spec, tcs.sub, simil="bray", binary=FALSE)

## calculate differences with Soerensen as the similarity measure
com.sim(abis.spec, tcs.sub)
```

`dfcor` *Calculate permuted (Mantel) correlations between one and many variables*

Description

The function uses `permcor2` to calculate permuted correlation on vectors. One vector is compared to various vectors of the same length. Useful e.g. if one variable has to be tested against various variables.

Usage

```
dfcor(ox, y, method = "pearson", permutations = 1000, ...)
```

Arguments

`ox`	Numeric vector. If it is a similarity matrix (i.e. a `dist` object, extract vector via `as.vector(x)` beforehand).
`y`	A `data.frame` containing numeric vectors to correlate `x` with. Number of rows has to equal the length of `x`
`method`	Method for correlation. Defaults to "pearson". See `cor` for other possibilities.
`permutations`	Number of permutations. Defaults to 1000, which gives reasonable results and allows to test against alpha = 0.001.
`...`	Further arguments passed to internal functions (i.e. to `cor`).

Details

`dfcor` is a wrapper for permcor2, which is usually called as a part of `pcol`. Here, the numeric vector in `x` is compared to each column vector of `y`.

Value

A list with the following:

`call`	The function call
`method`	P-value obtained by testing the initial correlation against the permuted correlation values.
`out`	A table with statistics. See details below.
`gesN`	The included number of cases.

`strata`	The number of variables against which `x` was tested.
`permutations`	The number of permutations.

The included printing method gives nice output (where information appears in a slightly different order) ending with the table of `out`. It is based on a data.frame with nrow = ncol(`y`) giving the statistics for the correlation between `x` and each column of `y` as follows.

`corr`	Correlation value (regarding to `method`).
`sig`	P-value obtained by testing the initial correlation against the permuted correlation values.
`nop`	Number of included pairs. The function tests for complete cases before calculation starts. Pairs containing NA's are not included.
`miss`	Number of missing pairs.

Note

Maybe `pcol` will get this functionality in future releases.

Author(s)

Gerald Jurasinski

References

Legendre, P, & Legendre, L. (1998) *Numerical Ecology*. 2nd English Edition. Elsevier.

See Also

For related functions of `simba` `permcor`, `permcor2`, `mancor`, `pcol`. Further see `mantel` of package `vegan` for a different implementation of permuted correlation on distance matrices.

Examples

`diffmean` *Calculate the difference in Mean between two vectors*

Description

The function can be used to calculate the difference in mean between two vectors. Statistical inference is obtained through permutation. F-ratio is also calculated. For data which is not normally distributed or lacks independence. The plotting method plots the actual values of the difference in mean and F against an histogram of the results of the permuted runs.

Usage

```
diffmean(x, y, permutations = 1000)
## S3 method for class 'dmn':
plot(x, which=3, two=2, ...)
```

Arguments

`x`	Numeric vector. For the plotting method the `dmn`-object which should be printed (results from a `diffmean` operation).
`y`	Numeric vector.
`permutations`	Number of permutations.
`which`	which histogram should be plotted? 1 triggers the histogram for difference in mean, 2 the one for F. It defaults to 3: both histograms are plotted. If it is changed from default, the next argument (`two`) is automatically set to 1!
`two`	Should the histograms be printed on a divided display? And how? Can only be set if `which` is set to 3. Defaults to 2, which means that the display is divided in two halfs and the histogram-plots are plotted side by side. 3 causes histograms to be plotted one on top of the other. If `two` = 1, the display is NOT automatically divided. Might be useful if more than one `dmn`-objekt is to be plotted on one display. Otherwise the function overrides the actual display settings.
`...`	Further arguments to the plotting method.

Details

The two vectors do not need to share the same length but they should not be too different. Otherwise the function might give spurious results.

Value

Returns a list giving the function call, the difference in Mean, the mean of vector x and y, the mean of means, the F-value, the significance of the difference in Mean and the significance of F, as well as the number of permutations. The results of the permutation runs can be retrieved with `result$bootsM` (for the difference in mean) and `result$bootF` (for the F-values). There is a plot method for easily illustrating the test. The difference is plotted against an histogram displaying the distribution of the permuted values.

Author(s)

Gerald Jurasinski

See Also

`diffslope`, `diffmich`

Examples

```
data(abis)

## create subsetting vector describing the belonging to different
## vegetationtypes
tcs.sub <- rep(0, 61)
tcs.sub[abis.env[,29]==1] <- 1
tcs.sub[abis.env[,30]==1] <- 2
tcs.sub[abis.env[,31]==1] <- 3

## check distribution
summary(as.factor(tcs.sub))
```

```
## compare vegetation types "shrubby vegetation" (shrub=2) and
## "protected by snowcover" (protect=3) regarding difference in
## similarities
abis2.soer <- sim(abis.spec[tcs.sub==2,])
abis3.soer <- sim(abis.spec[tcs.sub==3,])
abis.23cmp <- diffmean(abis2.soer, abis3.soer)
```

`diffmich` *Calculate the difference in parameters of a Michaelis-Menten kinetik fitted to (PAM) data*

Description

The function can be used to calculate the difference in the two parameters of the Michaelis-Menten Kinetik $y = \frac{a*x}{b+x}$ between two datasets containg each two vectors. Through permutation it is possible to compute significance of the difference. `fitmich` is used to calculate the Michaelis-Menten fit to the data. With the corresponding plot method a plot of the actual difference in the parameters against a histogram of the permuted values can easily be achieved.

Usage

```
diffmich(x1, y1, x2, y2, permutations = 1000, a=3, b=0.5, trace=FALSE, ...)
fitmich(x, y, a=3, b=0.5)
## S3 method for class 'diffmich':
plot(x, which=3, two=2, ...)
```

Arguments

`x1`	Vector containing an independent variable, for instance PAR measurements.
`y1`	Vector containing a variable dependent on `x1` (for instance ETR measurements). Must have the same length as `x1`.
`x2`	Vector containing a second independent variable (for instance PAR measurements).
`y2`	Vector containing a variable dependent on `x2` (for instance ETR measurements). Must have the same length as `x2`.
`permutations`	Number of permutations.
`a`	start value for parameter a, defaults to 3, usually there is no change necessary, but if the function gets trapped in the first run, changing the parameters might solve the problem.
`b`	Start value for parameter b, defaults to 0.5.
`trace`	set to TRUE for displaying the progress of the calculation
`...`	Arguments to other functions (for instance to `lm`, which is used to calculate the regression lines)
`x`	Vector containing an independent variable, for instance PAR measurements. Function `fitmich` is usually called only internally by `diffmich`. Plotting object in the plot method.
`y`	Vector containing a variable dependent on `x1` (for instance ETR measurements). Must have the same length as `x1`.

`which`	Which histogram should be plotted? 1 triggers the histogram for parameter a, 2 the one for parameter b. It defaults to 3: both histograms are plotted. If it is changed from default the next argument (`two`) is automatically set to 1!
`two`	Should the histograms be printed on a divided display? And how? Can only be set if `which` is set to 3. Defaults to 2, which means that the display is divided in two halfs and the histogram-plots are plotted side by side. 3 causes histograms to be plotted one on top of the other. If `two` = 1, the display is NOT automatically divided. Might be useful if more than one `diffmich`-objekt is to be plotted on one display. Otherwise the function overrides the actual display settings.

Details

As the function was initially built to easily calculate the difference of parameters of the Michaelis-Menten Kinetik for PAM measurements, the independent vectors are meant to contain PAR values whereas the dependent vectors should represent ETR values. But you can use it for anything else which can be fitted with Michaelis-Menten. The vectors belonging together are formed into a `data.frame`. For each permutation run the rows are interchanged randomly between the two `data.frame`s and the difference in the parameters is calculated and collected into a vector. The p-value is then computed as the ratio between the number of cases where the differences in Parameter exceed the difference in parameter of the inital configuration and the number of permutations.

As it uses a `for` loop it takes a while to calculate. So get a coffee while it is running, or set `trace` = TRUE to avoid boring moments ...

Value

Returns a `diffmich`-object with the function call, the difference in the two parameters and their significance. Furthermore the number of permutations. If you want to change the way `fitmich` is computed you can change the starting values. Per default it is calculated with starting values a=3 and b=0.5. There's no change needed unless the function gets trapped.

Author(s)

Gerald Jurasinski

See Also

`nls`, `sample`

Examples

`diffslope` *Calculate the difference in slope of two regression lines*

Description

The function can be used to calculate the difference in slope between two datasets containing each two vectors. Follows an idea of Nekola & White (1999) for calculating the statistical inference of the difference in slope between two regression lines. diffslope2 has the same purpose as diffslope but implementation is without for-loop. The plot method allows easy plotting of the actual difference in slope against the distribution of permuted values.

Usage

```
diffslope(x1, y1, x2, y2, permutations = 1000, resc.x = FALSE,
        resc.y = TRUE, trace=FALSE, ...)

diffslope2(x1, y1, x2, y2, permutations = 1000, resc.x = FALSE,
        resc.y = TRUE, ...)

## S3 method for class 'dsl':
plot(x, ...)
```

Arguments

`x1`	vector containing an independent variable (for instance distance between plots).
`y1`	vector containing a variable dependent on `x1` (for instance similarity between the plots. must have the same length as `x1`.
`x2`	vector containing a second independent variable (for instance distance between plots). can be the same as in x1.
`y2`	vector containing a variable dependent on `x2` (for instance similarity between the plots. must have the same length as `x2`.
`permutations`	number of permutations
`resc.x`	Shall the values of the independent variables be rescaled to a common mean?
`resc.y`	Shall the values of the dependent variables be rescaled to a common mean? Defaults to TRUE (Nekola & White 1999).
`trace`	Set to true if progress shall be printed with increasing numbers. Defaults to FALSE
`...`	Arguments to other functions (for instance to `lm`, which is used to calculate the regression lines).
`x`	`dsl`-object (given back by `diffslope`) which is to be plotted.

Details

As the function was initially build to easily calculate the difference in slope between the regression lines of distance decay plots, the independent vectors are meant to contain distance values whereas the dependent vectors should represent similarity values. But you can use it for anything else, as you wish. The vectors belonging together are formed into a data.frame. For each permutation run the rows are interchanged randomly between the two `data.frame`s and the difference in slope calculated thereafter is calculated and collected into a vector. The p-value is then computed as the ratio between the number of cases where the differences in slope exceed the difference in slope of the inital configuration and the number of permutations.

If the difference in slope returns negative, the slope (distance decay) of the second relationship is less pronounced, if it returns positive, the second relationship exhibits a stronger distance decay (slope) than the first. This holds for distance decay relationships. If `y` increases with `x`, it is vice versa.

As it uses a `for` loop, it takes a while to calculate. So get a coffee while it is running, or set `trace` to TRUE to avoid being bored ...

Value

Returns a list giving the function call, the difference in slope, the significance of this difference, and the number of permutations. If you want to change the way `lm` is computed you must send the arguments to `lm` via .... Per default it is calculated with the default arguments of `lm`.

Author(s)

Gerald Jurasinski

References

Nekola, J. C. and White, P. S. (1999) The distance decay of similarity in biogeography and ecology. Journal of Biogeography 26: 867-878.

Steinitz, O., Heller, J., Tsoar, A., Rotem, D. and Kadmon, R. (2005) Predicting Regional Patterns of Similarity in Species Composition for Conservation Planning. Conservation Biology 19: 1978-1988.

Steinitz, O., Heller, J., Tsoar, A., Rotem, D. and Kadmon, R. (2006) Environment, dispersal and patterns of species similarity. Journal of Biogeography 33: 1044-1054.

See Also

`lm`, `sample`

Examples

```
data(gaada.env)
data(coord)
names(gaada.env) ##take a look at the data
struc.dist <- 1-vegdist(gaada.env[,2:6])
##calculate the similarity (Bray-Curtis) between the plots
##regarding vegetation structure

soil.dist <- 1-vegdist(gaada.env[,7:8])
##calculate the similarity (Bray-Curtis) between the plots
##regarding soil parameters

coord.dist <- dist(coord) ##calculate geographical distance between plots

##transform all distance matrices into list format:
struc.dist.ls <- liste(struc.dist, entry="BC.struc")
soil.dist.ls <- liste(soil.dist, entry="BC.soil")
coord.dist.ls <- liste(coord.dist, entry="dist")

##create a data.frame containg plot information, geographical
##distance,similarity of soil parameters, and similarity of
##structural parameters:

df <- data.frame(coord.dist.ls, soil.dist.ls[,3], struc.dist.ls[,3])
names(df) ##see names

##give better names:
names(df)[4:5] <- c("soil","struc")
attach(df)

##prepare graphics device:
```

```
par(mfrow=c(2,1))

##plot and compare distance decay (decrease of similarity with
##distance):
plot(dist, soil)
plot(dist, struc)
##remove problematic zero entries:
df <- subset(df, soil != 0)

##plot again, this time with regression lines (in red for better
##visability):
detach(df)
attach(df)
plot(dist, soil)
abline(lm(soil~dist), col="red4")
plot(dist, struc)
abline(lm(struc~dist), col="red4")
##is the slope significantly different?
res <- diffslope(dist, soil, dist, struc)

##go for a coffee, as it takes a while...
```

`direct` *Obtain Direction Classes from Geographic Coordinates*

Description

The functions calculates direction classes from geographic coordinates (not lat/lon). All possible connections between these points are established and the direction of each link is calculated. This is followed by a designation of direction-classes.

Usage

```
direct(coord, listout=FALSE)

direct2(coord, listout=FALSE)
```

Arguments

`coord`	A `data.frame` containing coordinates. Should have the same number of points as the data for which the direction-classes are calculated.
`listout`	Logical value, indicating whether the result is given back in (`data.frame`)-format instead of returning a `dist`-object.

Value

Returns a matrix containing the direction-classes of the connections between the coordinates as a `dist`-object. If `listout` = TRUE, the result is given as a list (`data.frame`).

`direct` returns 4 directions (North-South, Northwest-Southeast, West-East, Northeast-Southwest).

`direct2` returns 6 directions.

Note

as with `mantel` it takes a while to calculate

Author(s)

Gerald Jurasinski

See Also

`mantel`, `cor.test`

Examples

```
data(gaada)
dirclass <- direct(coord)
dirclass
dirclass.ls <- direct(coord, listout=TRUE)
dirclass.ls
```

`gaada` *Vegetation and Environmental Data from a Transitional Ecosystem (semi-arid to mediterranean) of Northeastern Morocco*

Description

Vegetation and related data from field sites in North-Eastern Morocco. `spec.mtrx` holds presence/absence information of 358 species on 140 sites.

Usage

```
data(spec.mtrx)
data(spec.list)
data(gaada.env)
data(coord)
```

Format

spec.list	Contains the same information as `spec.mtrx` but in database format. It is organized as a `data.frame` with the columns `plot`, `species`, `presence`
gaada.env	contains some environmental variables from the Moroccan field sites as these are:

disturbance	Integer: indicating the severity of disturbance.
cov.asph	Numeric: the cover of *Aspodelus microcarpus*.
cov.trees	Numeric: the cover of trees.
cov.shrubs	Numeric: the cover of shrubs.
bare.soil	Numeric: the proportion of bare soil.
stones	Numeric: the proportion of open stones.
cn.ratio	Numeric: the CN ratio, gathered from soil samples.
pH.value	Numeric: the pH-value, gathered from soil samples.

coord	Contains the geographical coordinates of the Moroccan field sites:

x	Numeric: the x-value of the geographic coordinates.
y	Numeric: the y-value of the geographic coordinates.

Source

Jurasinski, G. and Beierkuhnlein, C. (2006) Spatial Patterns of Biodiversity - Assessing Vegetation using Hexagonal Grids. Proceedings of the Royal Irish Academy - Biology and Environment.

Examples

```
data(gaada)
```

`hexgrid` *Produces the nodes of an equidistant grid.*

Description

Given the coordinates of a starting point (left upper point of the grid), the function produces the nodes of an equidistant grid. Extent and distance between plots can be specified.

Usage

```
hexgrid(x, y, r = 100, nro = 10, nco = 20)
```

Arguments

`x`	`x`-value of the starting point. Defaults to 0.
`y`	`y`-value of the starting point. Defaults to 0.
`r`	Distance between nodes. Defaults to 100.
`nro`	Number of rows in the grid. Defaults to 10
`nco`	Number of columns in the grid. Defaults to 20. They are doubled (see the grid) compared to the rows. That's why 2*`nro` produces a quadratic grid.

Details

If the overall shape of the grid is not square, the user has to delete by hand the superfluous units. Might get more flexible in future versions.

Value

Returns a data.frame giving informations on the produced point/unit/plot locations with the following columns:

`ROW`	Number of row in the grid to which the point/unit/plot belongs.
`COL`	Number of column in the grid to which the point/unit/plot belongs.
`X`	x-coordinate of the point.
`Y`	y-coordinate of the point.

Author(s)

Gerald Jurasinski

References

http://homepage.mac.com/terhorab/gerald/downloads/whyhexaagons.pdf

Examples

```
## produces a grid with r=400:
test.grd <- hexgrid(456000, 7356700, r=400)
## for plotting the following is recommended as it preserves
## real positions:
library(geoR)
points.geodata(coords=test.grd[,3:4], data=test.grd[,1])
```

`liste` *Convert dist-objects and matrices to database format*

Description

Transposes `dist` objects to database list format (where each line represents a similarity value calculated between two plots, so the list has three columns containing information on plot x, plot y and information on similarity/dissimilarity). This might be useful if further database processing is intended. If the given matrix is not of class `dist`, the whole matrix is converted. This might be handy if species matrices are to be converted to database format.

Usage

```
liste(obj, x="NBX", y="NBY", entry=NULL, factorize=TRUE,
splist=FALSE)
```

Arguments

`obj`	A distance object as it is returned from `sim`, `dist`, `vegdist` or `dist.binary` or a similar matrix with class="dist". If the matrix is not of class `dist` a `data.frame` is expected and all entries are converted. Species matrices are assumed to contain sites (or plots) in rows and species in columns.
`x`	How the second column should be named, standard is that it contains "`NBX`" the neighbour X. Obsolete when `splist` = TRUE.
`y`	How the second column should be named, standard is that it contains "`NBY`" the neighbour Y. Obsolete when `splist` = TRUE.
`entry`	How the third column should be named. If there is nothing given, it is named "we" (whatever). Obsolete when `splist` = TRUE.
`factorize`	If naming (first two) columns should be given as factors. Defaults to TRUE.
`splist`	Set to TRUE if a species matrix is transformed to a database list format. Automatically removes entries with zero occurrence of the species' and names columns correspondingly (see Value).

Details

Column `x` represents the column names of the input matrix. So if you want to reshape a species matrix, `x` will be the species names and `y` will be the plot names. If it is needed vice versa, you have to change column order. For convenience you can set `splist` = TRUE and you will get a species list in database format with columns representing the plot, species and occurrence information. Furthermore zero occurrences are already omitted.

Value

Returns a `data.frame` with three columns:

`Col1`	The column names of the input matrix. If it is a `dist`-object only the lower triangle is used. Named `plot` when a species matrix is transformed with `splist` = TRUE.
`Col2`	The row names of the input matrix. Named `spec` when a species matrix is transformed with `splist` = TRUE.
`Col3`	The respective matrix entries. Named `occ` when a species matrix is transformed with `splist` = TRUE.

Author(s)

Gerald Jurasinski

See Also

`reshape`, `data.frame`. It resembles functionality of reshape - which is more flexible (but also more complex).

Examples

```
data(abis)
## there are empty species entries:
sum(colSums(abis.spec)==0)
## remove empty species
abis.spec <- abis.spec[,colSums(abis.spec)!=0]
abis.spec.ls <- liste(abis.spec, splist=TRUE)
```

`makead` *Create artificial data set (species matrix).*

Description

The functions allow for the automated creation of artificial data (species matrix). The user can choose between random organization or a gradient. The gradient can be defined via a gradient vector which allows for fine tuning of the gradient. `ads` has a different implementation and produces better results for gradients.

Usage

```
makead(nspec, nplots, avSR = NULL, anc = NULL, grad.v = NULL,
cf = 0.2, puq = 0.01)

ads(nspec, nplots, avSR = NULL, anc = NULL, grad.v = NULL,
reord = TRUE, cf = 0.2, puq = 0.01)

ads.hot(nspec, nplots, avSR = NULL, anc = NULL, grad.v = NULL,
frac=0.5, reord=TRUE, cf=0.2, puq=0.01)
```

Arguments

`nspec`	Numbers of species you want to be in the data-set. Meaningless if `anc` != NULL.
`nplots`	Numbers of plots you want to be in the data-set. Meaningless if `anc` != NULL.
`avSR`	Average species richness. If `anc` is given, it is calculated from the data when the default is not changed. If `avSR` != NULL, the given value is taken instead. In the actual version not implemented in `ads`.
`anc`	If a model species matrix is available (either a real data-set, or another artificial data-set) on which creation should be based, give it here. Rows must be plots and columns be species. The first three parameters are then obtained from this set. However average species richness (`avSR`) can still be given by the user.
`grad.v`	A numeric vector describing the gradient, or - in case of `ads.hot` - the hotspot. Must have the same length as `nplots` (or `nrow(anc)` respectively). See details.
`cf`	Determines the probability of the species to occur on the plots. In other words, it changes the shape of the species accumulation curve. Set to NULL if no natural species accumulation should be applied (may sometimes increase the visibility of the gradient)
`puq`	Percentage of ubiquitous species. Set to NULL if the produced gradients seem to be unclear or if you don't want ubiquitous species to be in the data-set. Only used if a gradient vector is given (which is then not applied to the given percentage of species).
`reord`	Triggers reordering of the columns in the produced gradient matrix (see details). May considerably change the resulting matrix. Defaults to TRUE.
`frac`	Numeric between 0 and 1 giving the percentage of species which should occur on the hotspot-gradient only (see details).

Details

There are three different implementations to create an artificial species matrix. `makead` first applies the **n**atural **s**pecies **a**ccumulation curve, the gradient for each species is represented by a vector containing numerics between 0 and 1. Both matrices are added so that values between 0 and 2 result. Through an iteration procedure a breakvalue is defined above which all entries are converted to 1. Values below are converted to 0 resulting in a presence/absence matrix. However the random element seems to be too strong to get evident gradient representations.

Therefore `ads` is implemented. It works different. First, a gradient is applied. As with `makead` the gradient is always applied in two directions so that half of the species are more likely to occur on plots on one side of the gradient, whereas the others are more likely to occur on the other side of the gradient. Subsequently, species occurrence for all species will oscillate around `nplots`/2.

If `puq` is specified the given percentage of species is divided from the whole matrix before the gradient is applied. With the parameter `cf` a vector is produced representing natural quasi-natural occurrence of the species on the plots: Most species are rare and few species are very common. This is described by a power function $y = \frac{1}{x^{cf}}$ with `x` starting at 2 and gives a vector of length `nspec` representing the number of times each species is occuring.

These numbers are applied to the gradient matrix and from the species occurrences only as many as specified by the respective number are randomly sampled. In cases were the occurrence number given by the vector exceeds the occurrences resulting from the gradient matrix, the species in the gradient matrix is replaced by a new one for which occurrence is not following the gradient and represents the number of occurrences given by the vector. The idea behind this is, that also in nature a species occuring on more than about half of the plots will likely be independent from a specific gradient.

In both cases (`makead` and `ads`) a totally random species matrix (under consideration of natural species occurrence, see `cf`) is obtained by randomly shuffling these occurrences on the columns (species) of the "natural species occurrence" matrix.

Contrarily to the other two functions, `ads.hot` allows for the creation of an artficial data-set including a hotspot of specis richness and composition. In this case, `frac` can be used to specify which proportion of the total number of species should only occur on the hotspot gradient. All other species occur randomly on the plots. However, with the hotspot-gradient (`grad.v`) you can influence the explicitness of the hotspot.

Value

Returns a species matrix with rows representing plots/sampling units and columns representing species.

Author(s)

Gerald Jurasinski, Vroni Retzer

See Also

Examples

```
## create a random data-set with 200 species on 60 plots
artda <- makead(200, 60, avSR=25)

## create a gradient running from North to South (therefore you
## need a spatially explicit model of your data which is obtained
## with hexgrid())
coor <- hexgrid(0, 4000, 200)
coor <- coor[order(coor$ROW),] #causes coordinates to be in order.
## then the gradient vektor can easily be generated from the ROW names
gradvek <- as.numeric(coor$ROW)
## check how many plots your array has
nrow(coor)
## create a data-set with 200 species
artda <- ads(200, 100, grad.v=gradvek)
## see the species frequency distribution curve
plot(sort(colSums(artda)))
```

`mama` *A (convenience) wrapper function to make matrix from a data.frame*

Description

The function `mama` uses `reshape` to transpose species data given in database list format (where each line represents a species in a plot, so the list has three columns containing information on plot, species and information on occurence) into a plot species matrix (where rows represent plots and columns represent species) for further use with other functions on vegetational data.

Usage

```
mama(dat)
```

Arguments

`dat`	Species data in list format. The columns have to represent plot, species, occurence information (presence/absence or abundances). Column names may differ but they must be in that order!

Details

You could reach the same result with `reshape`. I was just always quite confused with this. That's why i decided to do this little wrapper for convenience. It needs quite a while to run though, but this is due to `reshape`.

Value

Returns a `data.frame` which contains the presence/absence or abundance data of the species list. Rows represent plots, columns represent species. If you want to have it vice versa you have to use the function on a list with columns `species`, `plots`, `occurrence information` (in that order).

Author(s)

Gerald Jurasinski

See Also

`reshape`, `data.frame`

Examples

```
data(abis)
abis.spcls <- liste(abis.spec, splist=TRUE)
## see the list, it like what you get from a database
## and return to matrix-format:
abis.test <- mama(abis.spcls)
```

`occ.time` *Track species occurrence*

Description

Calculate the change in occurence of species on plots in general or on specific plots. Allows for the tracking of temporal changes in species abundance throughout an area or the simple quantification and comparison of species occurences between time steps.

Usage

```
occ.time(x, y, times = NULL, adjust = TRUE, gen.occ = FALSE,
perc = TRUE, nc.acc = FALSE, ...)

occ.tmp(x, y, adjust=TRUE, gen.occ=FALSE, perc=TRUE,
nc.acc=FALSE, ...)
```

Arguments

`x`	Species data in matrix or database-format representing species occurrence at time step one or throughout a time series. The latter means that you have a table with three columns where the columns represent `plots`, `species` and `occurence` information (in this order!). These are typically exported from a database. When `times` are given and data represents more than one time steps it has to be in database format. Conversion is handled automatically - if three columns are in the table it is assumed to be in database format. When there are only three species give the data in database-format. If there are many plots and/or species, internal matrix conversion might be quite slow.
`y`	Species data in matrix or database-format representing species occurrence at time step two. Obsolete when `times` are given. Otherwise the same as for `x` applies.
`times`	A vector describing the timesteps which has to be coercible to a factor. If your data comes from a database and contains species records for different time-steps, just export the time information with the species data. If you have single matrices for each time step, you could reshape them to database format via `liste` and concatenate these or calculate each time step alone.
`adjust`	Do not change the default behaviour (TRUE) unless you know what you do. Would spare some calculation time if set to FALSE, when your species data do not need adjustment, which means that in both or all time steps, there are exactly the same species and the same plots. However in most cases it will be more convenient to rely on the function (see details).
`gen.occ`	Triggers if general occurrence is regarded or specific occurrence. The latter is default (gen.occ=FALSE) and it means that it is calculated on which exact plots a species is changing. When set to TRUE only general occurence is regarded and it is calculated on how many plots a species occurs more or less then before. See details.
`perc`	If output shall be in percentage of species. Defaults to TRUE.
`nc.acc`	Per default, species which are not changing on a plot are counted as single species (also when they do not change on more than one plot). This can be changed when setting `nc.acc` = TRUE. Then each occurence of species which has not changed is counted.
`...`	Further arguments to functions.

Details

If you compare species data among time steps there will be most likely different numbers of species (and often also different numbers of plots for which information is available). The function takes care of this and you can give any species matrices you want. If one plot is the same, it will calculate what changed on this plot. There will be an error message if no plot is shared. The function relies on plot and species names!! As in a database - they must be unique!!

With the resulting named vector or table it is easy to draw a barplot tracking the changing occurrence of plants. Walter et al. (2005) used such plots to illuminate the changing (and increasing) occurrence of plant species on Alpine summits due to climate change.

However they only considered change in general occurrence. We added the possibility to track changes on the specific plots. If a species is occuring on 5 plots at time one and on 4 plots at time two one can't be shure that this species changed occurrence on only one plot. If it occurrs partly on different plots then before it will contribute to loss and gain respectively in this function when `gen.occ` is set to FALSE.

Value

Returns a named vector or a table (when multiple time steps are evaluated at once) with information on change in species occurence. The names tell on how many plots a certain species has changed. The values tell how many species (or percent of species) exhibit this change. Additionally the number of matching plots and species for each comparison are given back.

Per default nice output is given. However, the table can be accessed for printing whith *$bac (see Example for Details). A plotting method will be added in the near future.

Author(s)

Gerald Jurasinski ⟨terhorab@mac.com⟩ `http://homepage.mac.com/terhorab/gerald/`

References

Walther, G.-R., Beißner, S. & Burga, C. A. 2005. Trends in the upward shift of alpine plants. *Journal of Vegetation Science* **16**: 541-548.

See Also

to calculate similarity based on plant species occurrence between time steps see `sim.tmp`

Examples

`pcol` *Permuted Correlation (on strata)*

Description

The function is a wrapper for several functions related to the permuted correlation between matrices or vectors: It calls `permcor2` to calculate permuted correlation between vectors and `permcor` to calculate permuted correlation on strata. This can be useful to obtain data-points for a multivariate Mantel correlogram. Two matrices or vectors and a variable dividing these vectors into strata (levels) are to be specified. If the last is not given only permuted correlation between the two matrices (`dist`-objects) is done. If the second matrix/vector is a subsetting object the correlation can be done on the first object for each of the strata with `mancor`.

Usage

```
pcol(x, y, z = NULL, method="pearson", permutations=1000,
solo=FALSE, ...)

permcor(x, y, subsetter, method="pearson", permutations=1000,
alpha=0.05, trace=FALSE, ...)

permcor2(x, y, method="pearson", permutations=1000, subset=NULL,
complete=TRUE, ...)

mancor(dis, classes, width=NULL, method="pearson", permutations=1000,
alpha=0.05, trace=FALSE, ...)

## S3 method for class 'permcor':
plot(x, ...)
```

Arguments

`x`	Matrix (`dist`-objekt) or vector of numeric values (atomic) containing distances or similarities returned by `sim`, `vegdist`, `dist`, `dist.binary` or a similar matrix. Conversion is done automatically and triggered by `is.vector`. If it is not a vector it is assumed to be a `dist`-objekt or a similar matrix (with nrow==ncol). For the plotting method a `permcor`-object.
`y`	If `solo`=FALSE an object of the same qualities and dimensions (or length) as `x` to correlate to. See `Details` for the case `solo`=TRUE.
`z`	Vector or `dist`-objekt of a variable which defines the strata, or levels for which the permuted correlation shall be calculated. Doesn't have to be a factor but it has to be convertible into factor. see `Details` for more.
`subsetter`	Vector of a variable which defines the strata, or levels for which the permuted correlation shall be calculated. Usually conversion from `dist`-object to vector is done in `pcol`. If `permcor` is run separately it has to be a vector (same holds for `x`, `y`, and `z` if the background functions are run separately). Doesn't have to be a factor but it has to be convertible into factor. see `Details` for more.
`method`	Method of correlation, as it is done by `cor.test`, see help there for details. Defaults to Pearson correlation coefficients. Other options are Kendall and Spearman rank correlations.
`permutations`	number of permutations, defaults to 1000 to get a significance level of p = 0.001.
`solo`	If TRUE `y` is assumed to be a subsetting matrix, `dist`-object or vector giving strata to correlate `x` with and calculate the data-points for a Multivariate Mantel Correlogram for one distance-matrix.
`width`	If `solo`=TRUE the subsetting object is assumed to contain classes already. If `width` is specified (defaults to NULL), the classes are defined inside the function and `width` gives the class width.
`trace`	Set to TRUE to follow the runs of the for-loops in functions `permcor` and `mancor`. See `details` for when it is appropriate to set via `pcol`.
`complete`	Should only complete cases be considered? Defaults to TRUE.
`alpha`	The initial alpha-level against which should be tested. Depending on sub-function it is internally changed via Bonferroni-correction if necessary.

`subset`	If Case is 1 (see `details`) a subset of cases from `x` and `y` can be defined for correlation.
`dis`	Same as `x` for `mancor`.
`classes`	If `mancor` shall be run, second item is a vector or `dist`-objekt of a variable which defines the strata, or levels for which the permuted correlation shall be calculated. Doesn't have to be a factor but it has to be convertible into factor. see `Details` for more.
`permcor`	(In `plot.permcor`) an object returned by `permcor2` is easily plotted with `plot.permcor`. The actual correlation value is plotted against an histogram of the distribution of the permuted values.
`...`	Arguments to other functions, for instance to `cor.test` regarding specifications of the test, however only the correlation value is taken from this function. but here you could change from pearson to kendall for instance.

Details

`pcol` is a wrapper for the other functions. Depending on the input and the setting of `solo` the following functions are invoked (They can also be run separately. In this case `x`, `y`, and `z` must be given as vectors).

1. If `x` and `y` are `dist`-objects, or vectors containing distance or similarity values and everything else is set to defaults a simple permuted correlation with `permcor2` is run. This corresponds to a Mantel test. The two data-objects are correlated with `cor.test`, then the `y` is permuted and with `cor` the correlation is calculated again and written to a vector. This is repeated `permutation` times. Finally, the initial correlation value is compared to the permuted values. The number of times, the permuted values exceed the initial value is divided by the number of permutations to obtain a significance value. Thus, with 1000 permutations a minimum p of 0.001 can be tested.
2. If a `subsetter` is given in `z`, the permuted correlation is done for every stratum or level given by the subsetting object - this could e.g. be direction or distance classes flagging which plots share a similar distance and therefore fall into the same class. The resulting data-points can be used to plot a correlogram which allows for the analysis of non-stationarity in the relationships between `x` and `y`.
3. If `y` is itself a subsetting object (distance classes or so) you have to set `solo`=TRUE. Than the matrix or vector in `x` is correlated against this classes. This is handled by `mancor`. The parameter `width` allows for the calculation of classes inside the function. If for instance a distance-matrix with geographical distances is given, `width` specifies the width of the distance classes, they are computed and used to correlate the data in `x` against. This produces the data-points for a multivariate Mantel correlogram in the sense of Oden & Sokal (1986) (see also Legendre & Legendre 1998 for a comprehensive coverage of the subject).

Value

Returns different objects, depending on given arguments and triggers.

`case 1` a `permcor`-object with the following items is returned:

call	The call to the function.
method	The correlation method as used by `cor.test`.
statistic	The initial correlation value which is tested against the permuted values.
signif	The significance of the calculation.
n	The number of cases.

permutations	The number of permutations as specified by `permutations`.
perms	The result of the permuted runs. It is not printed by default but can be accessed via `result$perms`. The correlation value can be plotted against an histogram of the distribution of the permuted values to visualize the significance with the default plotting method.

`case 2` a `pclist`-object with the following items (in this case it might be nice to set `trace`=TRUE to display the progress of the calculation) is returned:

call	The call to the function.
method	The correlation method as used by `cor.test`.
gesN	The total number of cases.
strata	The number of strata (or levels) for which permutation has been done.
permutations	The number of permutations as specified by `permutations`.
out	A `data.frame` with 3 columns containing the result for each stratum in the rows: `statistic` contains the correlation values for the corresponding stratum, `sig` the obtained significance, and `nop` the number of cases found and used for permutation on this very level.

`case 3` a `pclist`-object with the same items as in Case 2 (in this case it might be as well interesting to set `trace`=TRUE to display the progress of the calculation) is returned.

Note

Depending on the background-function and the size of the matrices or vectors it may take a while to calculate. The slowest is `mancor` (case 3).

Author(s)

Gerald Jurasinski

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See Also

`mantel` for a different implementation of Mantel tests, and `mantell`, `cor.test`

Examples

```
data(abis)

## calulcate soerensen of species data
abis.soer <- sim(abis.spec)
## calculate distance (Euclidean) regarding some disturbance
## variables (feces counts)
abis.pert <- dist(abis.env[,19:25])
## are compositional similarity and dissimilarity of disturbance related?
pcol(abis.soer, abis.pert)
## the relationship is significant, but not very strong
```

`plot.mrpp` *plot an mrpp-object*

Description

There is no mrpp plotting function in the vegan package. For convenience it is provided here.

Usage

```
plot.mrpp(x, ...)
```

Arguments

`x`	a mrpp-object as computed with `mrpp`
`...`	Arguments to the plotting function

Value

Returns a histogram with the distribution of the permutation values plotted against delta: For explanations see `mrpp`

Author(s)

Gerald Jurasinski

See Also

`mrpp`, `anosim`

`sim` *Calculate similarities for binary vegetation data*

Description

One of 56 (dis)similarity measures for binary data can be set to calculate (dis)similarities. The vegetational data can be in either database (list) or matrix format. Same holds for the output. Simultaneous calculation of geographical distances between plots and the virtual position of the calculated similarity values between the parental units can be achieved if a `data.frame` with coordinates is given.

Usage

```
sim(x, coord=NULL, method = "soer", dn=NULL, normalize = FALSE,
listin = FALSE, listout = FALSE, ...)
```

Arguments

`x`	Vegetation data, either as matrix with rows = plots and columns = species (similarities are calculated between rows!), or as `data.frame` with first three columns representing plots, species and occurence information respectively. All further columns are dumped before calculation. Occurence is only considered as binary. If your list or matrix contains abundances or frequencies they are transformed automatically.
`coord`	A `data.frame` with two columns containing the coordinate values of the sampling units. If given, it triggers the simultaneous calculation of the geographical distances between the sampling units, the coordinates of virtual centre-points between all possible pairs of plots, and the geographical distances in either x- or y-direction. If `coord` is given, output is always in `database` format (no matrix).
`method`	Binary Similarity index (see `Details` for references and formulae), partial match to `"soerensen"`, `"jaccard"`, `"ochiai"`, `"mountford"`, `"whittaker"`, `"lande"`, `"wilsonshmida"`, `"cocogaston"`, `"magurran"`, `"harrison"`, `"cody"`, `"williams"`, `"williams2"`, `"harte"`, `"simpson"`, `"lennon"`, `"weiher"`, `"ruggiero"`, `"lennon2"`, `"rout1ledge"`, `"rout2ledge"`, `"rout3ledge"`, `"sokal1"`, `"dice"`, `"kulcz1insky"`, `"kulcz2insky"`, `"mcconnagh"`, `"manhattan"`, `"simplematching"`, `"margaleff"`, `"pearson"`, `"roger"`, `"baroni"`, `"dennis"`, `"fossum"`, `"gower"`, `"legendre"`, `"sokal2"`, `"sokal3"`, `"sokal4"`, `"stiles"`, `"yule"`, `"michael"`, `"hamann"`, `"forbes"`, `"chisquare"`, `"peirce"`, `"eyraud"`, `"simpson2"`, `"legendre2"`, `"fager"`, `"maarel"`, `"lamont"`, `"johnson"`, `"sorgenfrei"`, `"johnson2"`. See details.
`dn`	Neighbor definition. A geographic distance represented by a numeric or a two value vector defining a ring around each plot. Only takes effect when `coord` != NULL. If specified, the output does only contain similarities between neighboring plots. A plot is a neighbour to any given plot if it is within the range of the neighbor definition. See details.
`normalize`	Logical value indicating whether the values for `a`, `b` and `c` which are calculated in the process should be normalized to 100% (per row, which means per plot comparison). If normalize = TRUE an asymmetric index must be chosen (see details).
`listin`	if `x` is given in database (list) format this must be set to TRUE (there is no automatic detection of the format)
`listout`	If output is wanted in database format rather than as a `dist`-object set this to TRUE. Output is automatically given in database-format, when `coord` is specified.
`...`	Arguments to other functions

Details

All binary similarity indices are based on the variables `a`, `b` and `c` (or can be expressed as such). Some of them also use `d`. Where `a` is the number of species shared by two compared plots, `b` is the number of species found only in one of the compared plots, and `c` is the number of species only found in the other of the compared plots. `d` refers to species which are absent from both the compared plots but present in the whole dataset. Indices incorporating `d` are discussed critically by Legendre & Legendre (1998) and elsewhere. They are called symmetric and expose a "double zero" problem as they take species into account which are absent from both compared units. Absence of species from a sampling site might be due to various factors, it does not necessarily reflect differences in the environment. Hence, it is preferable to avoid drawing ecological conclusions from the absence of species at two sites (Legendre & Legendre 1998). The indices presented here come from various sources as indicated. Comparative reviews can be found in e.g. Huhta (1979), Wolda (1981), Janson & Vegelius (1981), Shi (1993), Koleff et al. (2003), Albatineh (2006)

The indices considerably differ in their behaviour. For classification purposes and in ecology, Jaccard and Sørensen have been found to give robust and meaningful results (e.g. Janson & Vegelius 1981, Shi 1993). For other purposes other indices might be better suited. However, you are invited to use (at least with the asymmetric indices) ternary plots as suggested by Koleff et al. 2003. The matching components `a, b,` and `c` can be displayed in a ternary.plot to evaluate the position of the plots in similarity space. When output is in database-format, the matching components are always given and `triax.plot` can be used to plot them into a triangle-plot. Koleff et al. (2003) used an artificial set of matching components including all possibilities of values that `a, b,` and `c` can take from 0 to 100 to display the mathematical behavior of indices. An artificial data-set with this properties - together with the values for the asymmetric indices included here - is part of this package (`ads.ternaries`) and can be used to study the behavior of the indices prior to analysis. See details and examples there.

If `coord` is given, the geographic distances between plots/sampling units are calculated automatically, which may be of value when the display or further analyses of distance decay (sensu Tobler 1970, Nekola & White 1999) is in focus. For convenience the `dn`-trigger can be used to tell the function to only return similarities calculated between neighboring plots. Similarities between neighboring plots in an equidistant array are not subjected to the problem of auto-correlation because all plots share the same distance (Jurasinski & Beierkuhnlein 2006). Therefore, any variation occurring in the data are most likely caused by environmental differences alone.

In the following formulae...

`a` = number of shared species

`b` = number of species only found on one of the compared units

`c` = number of species only found on the other of the compared units

`d` = number of species not found on the compared plots but in the dataset

`N` = $a + b + c + d$

with $(n_1 \leq n_2)$...

n_1 = number of species of the plot with fewer species $(a + b)$ or $(a + c)$

n_2 = number of species of the plot with more species $(a + b)$ or $(a + c)$

Computable asymmetric indices:

`soerensen`	$sim = \frac{2a}{2a+b+c}$	Soerensen (1948)
`jaccard`	$sim = \frac{a}{a+b+c}$	Jaccard (1912)
`ochiai`	$sim = \frac{a}{\sqrt{(a+b)(a+c)}}$	Ochiai (1957), Shi (1993)
`mountford`	$sim = \frac{2a}{(a(b+c)+2bc)}$	Mountford (1962), Shi (1993)
`whittaker`	$sim = \frac{a+b+c}{\frac{2a+b+c}{2}} - 1$	Whittaker (1960), Magurran (1988)
`lande`	$sim = \frac{b+c}{2}$	Lande (1996)
`wilsonshmida`	$sim = \frac{b+c}{2a+b+c}$	Wilson & Shmida (1984)
`cocogaston`	$sim = \frac{b+c}{a+b+c}$	Colwell & Coddington (1948), Gaston et al. (2001)
`magurran`	$sim = (2a + b + c)(1 - \frac{a}{a+b+c})$	Magurran (1988)
`harrison`	$sim = \frac{min(b,c)}{max(b,c)+a}$	Harrison et al. (1992), Koleff et al. (2003)
`cody`	$sim = 1 - \frac{a(2a+b+c}{2(a+b)(a+c)}$	Cody (1993)
`williams`	$sim = \frac{min(b,c)}{a+b+c}$	Williams (1996), Koleff et al. (2003)

`williams2`	$\frac{(bc)+1}{\frac{(a+b+c)^2-(a+b+c)}{2}}$	Williams (1996), Koleff et al. (2003)
`harte`	$1-\frac{2a}{2a+b+c}$	Harte & Kinzig (1997), Koleff et al. (2003)
`simpson`	$\frac{min(b,c)}{min(b,c)+a}$	Simpson (1949), Koleff et al. (2003)
`lennon`	$\frac{2\lvert b-c\rvert}{2a+b+c}$	Lennon et al. (2001), Koleff et al. (2003)
`weiher`	$sim = b + c$	Weiher & Boylen (1994)
`ruggiero`	$sim = \frac{a}{a+c}$	Ruggiero et al. (1998), Koleff et al. (2003)
`lennon2`	$sim = 1-\left[\frac{log\left(\frac{2a+b+c}{a+b+c}\right)}{log2}\right]$	Lennon et al. (2001), Koleff et al. (2003)
`rout1ledge`	$sim = \frac{(a+b+c)^2}{(a+b+c)^2-2bc}$	Routledge (1977), Magurran (1988)
`rout2ledge`	$toolong, seebelow$	Routledge (1977), Wilson & Shmida (1984)
`rout3ledge`	$sim = e^{rout2ledge}-1$	Routledge (1977)
`sokal1`	$sim = \frac{a}{a+2(b+c)}$	Sokal & Sneath (1963)
`dice`	$sim = \frac{a}{min((b+a),(c+a))}$	Association index of Dice (1945), Wolda (1981)
`kulcz1insky`	$sim = \frac{a}{b+c}$	Oosting (1956), Southwood (1978)
`kulcz2insky`	$sim = \frac{\frac{a}{2}(2a+b+c)}{(a+b)(a+c)}$	Oosting (1956), Southwood (1978)
`mcconnagh`	$sim = \frac{a^2-bc}{(a+b)(a+c)}$	Hubalek (1982)
`simpson2`	$sim = \frac{a}{a+b}$	Simpson (1960), Shi (1993)
`legendre2`	$sim = \frac{3a}{3a+b+c}$	Legendre & Legendre (1998)
`fager`	$sim = \frac{a}{\sqrt{n_1 n_2}} - \frac{1}{2*\sqrt{n_2}}$	Fager (1957), Shi (1993)
`maarel`	$sim = \frac{2a-(b+c)}{2a+b+c}$	van der Maarel (1969)
`lamont`	$sim = \frac{a}{2a+b+c}$	Lamont and Grant (1979)
`johnson`	$sim = \frac{a}{2b}$	Johnson (1971)
`sorgenfrei`	$sim = \frac{a^2}{(a+b)(a+c)}$	Sorgenfrei (1959)
`johnson2`	$sim = \frac{a}{a+b} + \frac{a}{a+c}$	Johnson (1967)

Computable symmetric indices (including unshared species):

`manhattan`	$sim = \frac{b+c}{a+b+c+d}$	Mean Manhattan, Legendre & Legendre (1998)
`simplematching`	$sim = \frac{a+d}{a+b+c+d}$	Sokal & Michener 1958
`margaleff`	$sim = \frac{a(a+b+c+d)}{(a+b)(a+c)}$	Clifford & Stevenson (1975)
`pearson`	$sim = \frac{ad-bc}{\sqrt{(a+b)(a+c)(d+b)(d+c)}}$	Phi of Pearson, Gower & Legendre (1986)
`roger`	$sim = \frac{a+d}{a+2(b+c)+d}$	Rogers & Tanimoto (1960), Gower & Legendre (1986)
`baroni`	$sim = \frac{\sqrt{ad}+c}{\sqrt{ad}+a+b+c}$	Baroni-Urbani & Buser (1976), Wolda (1981)
`dennis`	$sim = \frac{ad-bc}{\sqrt{(a+b+c+d)(a+b)(a+c)}}$	Holliday et al. (2002)
`fossum`	$sim = \frac{(a+b+c+d)\left(-\frac{a}{2}\right)^2}{(a+b)(a+c)}$	Holliday et al. (2002)
`gower`	$sim = \frac{a-(b+c)+d}{a+b+c+d}$	Gower & Legendre (1986)
`legendre`	$sim = \frac{a}{a+b+c+d}$	Gower & Legendre (1986)
`sokal2`	$sim = \frac{ad}{\sqrt{(a+b)(a+c)(d+b)(d+c)}}$	Sokal & Sneath (1963)
`sokal3`	$sim = \frac{2a+2d}{(a+d+(a+b+c+d)}$	Sokal & Sneath (1963)
`sokal4`	$sim = \frac{a+d}{b+c}$	Sokal & Sneath (1963)
`stiles`	$sim = \frac{(a+b+c+d)\left(\lvert ad-bc\rvert-\frac{a+b+c+d}{2}\right)^2}{(a+b)(a+c)(b+d)(c+d)}$	Stiles (1946)
`yule`	$sim = \frac{ad-bc}{ad+bc}$	Yule & Kendall (1973)
`michael`	$sim = \frac{4(ad-bc)}{(a+b)^2+(b+c)^2}$	Michael (1920), Shi (1993)
`hamann`	$sim = \frac{(a+d)-(b+c)}{N}$	Hamann (1961)
`forbes`	$sim = \frac{(aN-2n_2)}{(Nn_1-2n_2)}$	Forbes (1925), Shi (1993)

`chisquare`	$sim = \frac{2(ad-bc)^2}{(a+b)(a+c)(b+d)(c+d)}$	Yule & Kendall (1950)
`peirce`	$sim = \frac{(ad-bc)}{(a+c)(b+d)}$	Peirce (1984) in Shi (1993)
`eyraud`	$sim = \frac{a-(a+b)(a+c)}{(a+b)(a+c)(b+d)(c+d)}$	Eyraud (1936) in Shi (1993)

`rout2ledge` formula (Routledge, 1977; Koleff et al. 2003):

$$\beta_{R2} = \log(2a+b+c) - \left(\frac{1}{2a+b+c} 2a \log 2\right) - \left(\frac{1}{2a+b+c}((a+b)\log(a+b) + (a+c)\log(a+c))\right)$$

Value

If listout = FALSE a distance matrix of class `dist` is returned. If listout = TRUE, a `data.frame` is returned with 7 columns giving the names of the compared plots in the first two and the calculated similarity measure in the third column. The rest of the columns give the values for `a, b, c,` and `d` (in this order). Naming of the first three columns can be changed but defaults to `NBX` (one of the compared plots), `NBY` (the other one), `used index` (the values of the calculated index). If `coord` = NULL, the following columns are given in addition and the columns `a:d` shift to the end of the data.frame.

`distance`	Geographical distance between compared plots
`X`	For plotting purposes, the x-coordinate of the virtual position of the calculated similarity value in the center between the two compared plots
`Y`	For plotting purposes, the y-coordinate of the virtual position of the calculated similarity value in the center between the two compared plots
`xdist`	Geographical distance between compared plots, on the x-axis only
`ydist`	Geographical distance between compared plots, on the y-axis only

Note

In general, concepts of data-handling are taken from `vegdist` and the calculation of `a`, `b`, `c` and `d` is taken from `dist.binary`. Thanks to Jari Oksanen for his `vegan` package. The indices were collected from the literature and are applicable in different fields of research.

Author(s)

Gerald Jurasinski ⟨terhorab@mac.com⟩

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See Also

`vegdist`, `dist.binary`, `dsvdis`, `dist`

Examples

```
data(abis)
##calculate jaccard similarity and output as dist-object
jacc.dist <- sim(abis.spec, "jaccard")

##calculate Whittaker similarity (with prior normalisation) and
##output as data.frame
whitt.list <- sim(abis.spec, "whittaker", normalize=TRUE,
listout=TRUE)

##calculate similarity from a database list after Harte & Kinzig (1997)
##and output as dist-object
abis.spec.ls <- liste(abis.spec, splist=TRUE)
hart.dist <- sim(abis.spec.ls, "harte", listin=TRUE)

## calculate the geographic distances between sites simultaneously
## and return only similarities calculated between neighboring plots
abis.soer <- sim(abis.spec, coord=abis.env[,1:2], dn=100)

## in an equidistant array
## you can plot this nice between the original positions of the
## sites (with the size of the dots expressing number of species
## for the sites, and value of the Sørensen coefficient in between)
require(geoR)
points.geodata(coord=abis.env[,1:2], data=abis.env$n.spec,
cex.min=1, cex.max=5)
points.geodata(coord=abis.soer[,5:6], data=abis.soer$soerensen,
cex.min=1, cex.max=5, col="grey50", add=TRUE)
```

`sim.het` *Calculate a mean similarity to adjacent cells in an array*

Description

Useful for systematic sampling grids for calculating the mean similarity and its standard deviation between a focal unit and its surrounding units. Surrounding can be specified by the user.

Usage

```
sim.het(mat, coord=NULL, dn, method="soerensen", test=TRUE,
permutations=100, ...)

het2nbs(mat, coord=NULL, dn, method="soerensen", ...)
```

Arguments

`mat`	Species matrix or `dist` object resulting from similarity calculation.
`coord`	A `data.frame` with two columns containing the coordinates of the plots for which species data or a `dist` matrix is given. Defaults to NULL. Then, mean similarity and standard deviation of similarities from each plot to all other plots is calculated

`dn`	A numeric or a two value vector. In the first case it gives the distance until which sampling units should be considered as neighbors. In the second the two values define a ring around each plot. Plots which fall into the ring are considered as neighbors. Not necessary and skipped when `coord`=NULL
`method`	Only necessary when a species matrix is given. Specifies the method for calculating the similarity between plots with `sim`. For more details see the documentation of `sim`.
`test`	Shall significance be calculated? Defaults to TRUE which means that it is tested if the observed pattern is significantly different from random
`permutations`	Number of permutations for the significance test. Species are permuted on plots and the index is recalculated for each permuted species matrix. The initial values are then tested against the permuted values to obtain a significance level.
`...`	Further arguments passed to `sim`.

Details

If similarities (e.g. of species composition) are calculated between plots in a regular or irregular array (whereas the latter might be problematic because of spatial auto-correlation) the resulting values have no position. However they could be associated to a point in the centre between the compared plots (for each compared pair). Sometimes it is wanted to associate a dissimilarity value to the focal unit which comprises the similarities/dissimilarities of a focal unit to all surrounding units. One possibility is the calculation of a mean similarity (Williams 1996, Lennon 2001, Gaston 2001) out of the single similarities between a focal unit and its surrounding units. This might be problematic as the single similarity values might result from different sets of species. To include the variability of the single similarities between a focal unit and its neighbours as a measure of spatial heterogeneity the variation (sd) in the similarity values is included. See `sim.pat` for the calculation of similarity between a focal unit and its neighbours whilst preserving species identity.

Significance is tested against random expectations with a permutation procedure. After calculating the values for `mean` and `sd` the species/similarity matrix is permuted and the values are calculated again. This is done `permutation` times. Then the initial values are tested against the obtained distribution. If the initial values are under the mean of the respective values among plots they are tested against the lower tail of the permuted distribution. If they exceed the mean, they are tested against the upper tail of the permuted distribution. If a value is significant, this means that it is signifcantly different from a random distribution of species and therefore might likely be caused by underlying envrionmental patterns.

Value

A `data.frame` with the following columns

`nnbs`	Number of neighbours of the respective plot. Results from the neighbour definition `dn`.
`m.sims`	Mean similarity between plot and its neighbours.
`sd.sims`	Standard deviation of the similarity values calculated between the plot and its neighbours.
`sim.test.mean`	The p-value of the significance test for the `mean`-values.
`sig.mean`	The significance decision tested against alpha = 0.05. `"*"` indicates, that `mean` value is significantly different from random.

`sig.prefix.mean`	Marks against which tail significance of `mean` was tested. If the initial similarity value is lower than the mean of the permuted values the lower tail is tested (`sig.prefix = "-"`) and vice versa (`sig.prefix = "+"`).
`sim.test.sd`	The p-value of the significance test for the `sd`-values.
`sig.sd`	The significance decision tested against alpha = 0.05. `"*"` indicates, that `sd` value is significantly different from random.
`sig.prefix.sd`	Marks against which tail significance of `sd` was tested. If the initial similarity value is lower than the mean of the permuted values the lower tail is tested (`sig.prefix = "-"`) and vice versa (`sig.prefix = "+"`).

Author(s)

Gerald Jurasinski ⟨terhorab@mac.com⟩; Vroni Retzer ⟨vroni.retzer@uni.bayreuth.de⟩

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Williams, P. H. (1996) Mapping variations in the strength and breadth of biogeographic transition zones using species turnover. *Proceedings of the Royal Society of London Series B-Biological Sciences* **263**: 579-588.

See Also

See also `sim.pat` and `sim`

Examples

```
data(abis)
## calculate average similarity for the focal plots
abis.het <- sim.het(abis.spec, coord=abis.env[,1:2], dn=100)
```

`sim.pat` *Calculate pattern diversity*

Description

The function `sim.pat` uses `sima` to calculate compositional similarity between a focal sampling unit and all units in the data-set and `simn` to calculate compositional similarity between a focal unit and its surrounding units. Surrounding can be specified as a radius or a ring. Significance can be tested.

Usage

```
sim.pat(veg, coord = NULL, dn, presabs = TRUE, test = TRUE,
permutations = 100, ...)

sima(veg, presabs = TRUE, d.inc = FALSE, ...)

simn(veg, coord, dn, presabs = TRUE, d.inc = FALSE, ...)
```

Arguments

`veg`	A (species) matrix with rows representing plots/sampling units and columns representing species/variables. Up to now all values are transformed to presence/absence: all values > 0 are transformed to 1, all other values are 0.
`coord`	A two column `data.frame` defining the geographic positions of the sampling units. Should give (in this order) the x- and y-values in UTM or similar coordinates. Defaults to NULL. Triggers also if similarity to neighbours (when it is given) or to all units in the data-set (default) should be calculated.
`dn`	Neighbour definition. A positive numeric or a two value vector. In the first case it gives the distance from each sampling unit until which other sampling units should be seen as neighbours. In the second the two values define a ring around each plot. Plots which fall into the ring are considered as neighbors. See details. If `coord` is not given it becomes obsolete.
`presabs`	Triggers the calculation method. Should only the presence in the focal unit (FALSE) or also the absence in the focal unit (TRUE) be regarded?
`d.inc`	If species not occuring on the focal plot or its surroundings - but in the rest of the data-set should be considered, set it to TRUE. However, default behaviour is to do not. Note that when calling `sim.pat` without coordinates or `sima` this setting takes not effect unless there are non-occuring species in the matrix.
`test`	Should significance be tested? Defaults to true. See details.
`permutations`	If `test=TRUE`, how many permutations of the species matrix should be carried out? Defaults to 100. See details.
`...`	Further arguments to functions.

Details

The idea behind the function is the extension of available similarity measures by the possibility to calculate similarities between a focal unit and several other (surrounding) units at once whilst preserving species identities. In an equidistant grid one could also calculate the similarities between a focal unit and its six neighbours and then calculate a mean similarity value. However, this might be problematic as the values are based on the presence of different species. So the same similarity value can derive from a different set of species.

`sim.pat` is different as it respects species identities of all included units at once. It has two modes. If a coordinate file and a neighbour definition is given it calculates the similarity between each unit and its surrounding units. Neighbours are all units which fall into the specified radius or ring of radiuses (`dn`). On an equidistant grid the distance between grid units can simply be given if first hand neighbours shall be included, otherwise a ring has to be specified with a two value vector. If there is no `coord`, `dn` is obsolete. Then the similarity from each unit to all other units in the data-set is calculated.

The significance of the obtained similarity value can be tested in both cases. In the neighbour-case it is tested against a randomly rearranged species matrix `veg`. For each permuted matrix, `simn` is calculated for each unit and stored. The initial value is then tested against the resulting random values. If the initial value is lower than the mean of the permuted values (for each unit), the function looks at the lower end. If it is higher, the upper tail is tested. The test direction is given in the results file. Thus, for each unit it is known, whether the pattern is a deviation from random, if it is lower or higher than random, and if it is signifcantly different from random. In the all-case it is virtually the same but as a rearrangement of species on plots would change nothing, the function tests against an artificially produced data-set. This is done with `ads` and the key parameters resemble the original species matrix `veg`.

Value

Returns a `data.frame` with the similarity values calculated between the focal unit and its neighbours (`sim2nbs`) or all other units in the data-set (`sim2all`). In case of the first, the two first columns of the `data.frame` give the number of species on the focal plot (`n.spec`) and the number of neighbours (`nbs`) to which similarity was calculated based on the neighbour definition (`dn`).

If `test = TRUE` the following columns are given in addition:

`sim.test`	The p-value of the significance test.
`sig`	The significance decision, tested against alpha = 0.05. `"*"` means similarity value is significantly different from random.
`sig.prefix`	Marks against which tail significance was tested. If the initial similarity value is lower than the mean of the permuted values the lower tail is tested (`sig.prefix = "-"`) and vice versa (`sig.prefix = "+"`).

Author(s)

Gerald Jurasinski ⟨terhorab@mac.com⟩ `http://homepage.mac.com/terhorab/gerald/`,
Vroni Retzer ⟨vroni.retzer@uni-bayreuth.de⟩

References

Jurasinski, G. & Retzer, V. in prep. Measuring multi-plot similarity with presence-absence data. *Ecology* in prep.

See Also

`sim` from this package and the following functions of other packages for the calculation of similarities between two sites: `vegdist`, `dist.binary`, `dsvdis`, `dist`.

Examples

`sim.relt` *Calculate additive and relative partitioning.*

Description

Enables the calculation of three β-diversity measures closely related to each other: additive partitioning, multiplicative partitioning (Whittaker 1960), reverse multiplicative partitioning (Whittaker 1960, full change notion).

Usage

```
sim.relt(veg, coord = NULL, dn, method = "additive", test = TRUE,
permutations = 100, ...)

sim.rel(veg, coord=NULL, dn, method="additive", ...)
```

Arguments

`veg`	A species matrix. The function takes only presence/absence into account. However the translation is done automatically by assuming that zero means no occurrence, whereas any value > 0 is transformed to 1
`coord`	A two column `data.frame` defining the geographic positions of the sampling units. Should give (in this order) the x- and y-values in UTM or similar coordinates. Defaults to NULL. Triggers also if the similarity measures should only incorporate a focal plot and its neighbours (moving window) or if all units in the data-set (default) should be considered.
`dn`	A numeric or a two value vector. In the first case it gives the distance until which sampling units should be considered as neighbors. In the second the two values define a ring around each plot. Plots which fall into the ring are considered as neighbors. If `coord` is not given it becomes obsolete.
`method`	Which similarity measure should be calculated. Give a partial match to "`additive`", "`relative`" or "`reverse`". See details.
`test`	Shall significance be tested? Defaults to true. Does only make sense when `coord` and `dn` is given. In general `sim.relt` calls `sim.rel` to calculate the values. So the latter will rarely used by the user directly.
`permutations`	The number of permutations. Defaults to 100 which allows for a p-level of 0.01
`...`	Arguments to other functions.

Details

Three different diversity measures related to the concept of β-diversity can be calculated with this function. Besides the definition of β-diversity as the turnover in species composition (Whittaker 1960), Whittaker defined the *relation* between γ- and α-diversity as β-diversity where α is the mean species richness found on local plots or sampling units and γ-diversity is the species richness throughout a reference area (e.g. an investigation area). However, γ could also be defined for smaller units e.g. for a focal plot and its neighbours, which is done in the function when `coord` and `dn` are set. β-diversity in terms of *multiplicative* diversity is calculated when `method` is set to "`relative`". "`reverse`" simply means that the relation is calculated vice versa ($\frac{\bar{\alpha}}{\gamma}$) which results in numbers between 0 and 1 whereas the original formula gives results from 1 ($\bar{\alpha} = \gamma$) upwards. An upper end is not defined. However, increasing values indicate increasing heterogeneity in species composition.

The idea of "additive partitioning" (Lande 1996, Vellend 2001, Veech 2002) takes Whittakers approach further. Out of the criticism that β in Whittakers sense does not exhibit the same units (species numbers) as α- and γ-diversity here β-diversity results as the subtract of γ- and α-diversity. It expresses the average amount of diversity not found in a single, randomly-chosen sample. It is also rather calculated for a whole data-set. Here we apply it as well to a moving window of a focal plot and its neighbours if`coord` and `dn` are set.

The idea of γ-diversity might be questioned in general, as its quality is not different from α. Only the geographic extent is changed and often definition becomes problematic. Imagine a temporal study where different numbers of species are found throughout the years - Is γ then the overall species richness, or the species richness in one year? Furthermore β-diversity is not clearly defined. There are even more definitions to it then mentioned here (e.g. Qian et al. 2005) so it may be better to use 'differentiation-diversity' instead.

Significance is tested with a simple Monte-Carlo procedure. The initial value of the respective index is tested against a number of values which are calculated from a random reshuffling of the original species matrix. So the hypothesis tested is, that the observed pattern (for each focal plot) is different from random. This is meaningless when `coord` and `dn` are not set.

Value

The function returns either a named vector (if `coord` and `dn` are set) or a data.frame with the following items. The last three are only added if `test` = TRUE.

`nnbs`	Number of neighbours of the respective plot. Results from the neighbour definition `dn`. If this was not given it reflects the total number of plots in the data-set.
`n.spec`	Number of species on the focal plot. If `dn` and `coord` were not given it reflects the total number of species in the data-set
`value`	The calulated β-diversity. The name of the column changes respectively.
`sim.test`	The p-value of the significance test for the diversity values.
`sig`	The significance decision tested against alpha = 0.05. `"*"` means that the respective β-value is significantly different from random.
`sig.prefix`	Marks against which tail significance of β-values was tested. If the initial value is lower than the mean of the permuted values the lower tail is tested (`sig.prefix = "-"`) and vice versa (`sig.prefix = "+"`).

Author(s)

Gerald Jurasinski ⟨terhorab@mac.com⟩

References

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Veech, J. A., Summerville, K. S., Crist, T. O. & Gering, J. C. (2002) The additive partitioning of species diversity: recent revival of an old idea. *Oikos* **99**: 3-9.

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See Also

see also `sim.pat`, `sim.het`, `sim`, and for quantitative similarity measures `vegdist`, `dsvdis`, `dist`. More qualitative similarity indices can be calculated with `dist.binary`

Examples

`sim.tmp` *Calculate binary similarity in time*

Description

The function applies one of 56 similarity measures for binary data to calculate compositional similarity of plots between time steps.

Usage

```
sim.tmp(x, y, method = "soer", normalize = FALSE, adjust = TRUE, ...)
```

Arguments

`x`	Vegetation data, either as matrix with rows = plots and columns = species, or as `data.frame` with first three columns representing plots, species and occurence information respectively. All further columns are dumped before calculation. Occurence is only considered as binary. If your list or matrix contains abundances or frequencies they are transformed automatically.
`y`	Same as `x` for time-step two.
`method`	One of 42 similarity measures for binary data. The function uses the same indices as `sim`. See details there. Per default `soerensen` similarity is calculated.
`normalize`	Logical value indicating whether the values for `a`, `b` and `c` which are calculated in the process should be normalized to 100% (per row, which means per plot comparison). If normalize = TRUE an asymmetric index must be chosen (for details see `sim`).
`adjust`	Do not change the default behaviour (TRUE) unless you know what you do. Would spare some calculation time if set to FALSE, when your species data do not need adjustment, which means that in both or all time steps, there are exactly the same species and the same plots. However in most cases it will be more convenient to rely on the function (see details).
`...`	Other arguments to `sim`

Details

If you compare species data among time steps there will be most likely different numbers of species (and often also different numbers of plots for which information is available). The function takes care of this and you can give any species matrices you want. If one plot is the same, it will calculate what changed on this plot. There will be an error message if no plot is shared. The function relies on plot and species names!! As in a database - they must be unique!!

Value

Returns a named vector with the similarities for each site between time steps for each plot.

Author(s)

Gerald Jurasinski ⟨terhorab@mac.com⟩

References

See references in `sim`

See Also

See Also as `sim` (where you can find a much more elaborate see also section as well).

Examples

`simba-internal` *Internal functions of the package simba that are usually not called (or only implicitly) by the user*

Description

Mainly print functions for giving nice output.

Usage

```
## S3 method for class 'cslist':
print(x, digits = max(3, getOption("digits") - 3), ...)
## S3 method for class 'diffmich':
print(x, digits = max(3, getOption("digits") - 3), ...)
## S3 method for class 'dmn':
print(x, digits = max(3, getOption("digits") - 3), ...)
## S3 method for class 'dsl':
print(x, digits = max(3, getOption("digits") - 3), ...)
## S3 method for class 'occtmp':
print(x, digits = max(3, getOption("digits") - 3), ...)
## S3 method for class 'pclist':
print(x, digits = max(3, getOption("digits") - 3), ...)
## S3 method for class 'permcor':
print(x, digits = max(3, getOption("digits") - 3), ...)
```

Arguments

`x`	object to be printed
`digits`	number of digits
`...`	Further arguments.

Details

These are just printing methods to give nice output. Usually they are not to be called by the user.

Value

prints the output of a function and invisibly gives back the original object

Author(s)

Gerald Jurasinski

`simba-package` *Calculate similarity measures for binary data*

Description

Besides a function for the calculation of similarity measures with binary data (for instance presence/absence species data) the package contains some simple wrapper functions for reshaping species lists into matrices and vice versa and some other functions for further processing of similarity data.

Details

Package:	simba
Type:	Package
Version:	0.2-4
Date:	2007-04-09
License:	GPL version 2 or newer

The functions in this package can be used to calculate similarities between species records (in binary format). Functions related to the correlation of similarity matrices and some other useful functions for the analysis of spatial patterns and there change in time are included as well.

Author(s)

Gerald Jurasinski ⟨terhorab@mac.com⟩, with some help by Vroni Retzer ⟨vroni.retzer@uni-bayreuth.de⟩

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Wolda, H. (1981). Similarity indices, sample size and diversity. *Oecologia* 50, 296–302.

See Also

`vegdist`, `dist.binary`, `dsvdis`, `dist`, `reshape`, `cor.test`

Examples

```
##see functions for examples
```

Index

Appendix 8 - Species List recorded through the years of fieldwork in Morocco

	Latin Name	Genus	Count 2003	Count 2004	Count 2005	Count 2005b
1	Androcymbium gramineum (Cav.) Macbr. W	Amaryllidaceae	48	67	12	11
2	Narcissus cantabricus DC.	Amaryllidaceae	9	62	5	6
3	Pistacia lentiscus L.	Anacardiaceae		9		
4	Pistacia terebinthus L.	Anacardiaceae		1		
5	Anthriscus caucalis Bieb.	Apiaceae	17	17	3	4
6	Bifora testiculata (L.) Roth	Apiaceae		7		
7	Brachyapium dichotomum (L.) Maire	Apiaceae	15	26	3	4
8	Brachyapium pomelianum Maire	Apiaceae	43	70	3	3
9	Bupleurum lancifolium Hornem.	Apiaceae	3	10	1	1
10	Capnophyllum peregrinum (L.) Lag.	Apiaceae		6		
11	Caucalis platycarpos L.	Apiaceae	2	2		1
12	Eryngium campestre L.	Apiaceae	32	36	7	8
13	Ferula communis L.	Apiaceae	15	7		1
14	Hohenackeria bupleurifolia Fisch et. Mey.	Apiaceae	74	86	6	10
15	Petroselinum sativum Hoffm.	Apiaceae	19	20	1	1
16	Scandix pecten-veneris L.	Apiaceae	31	35	5	5
17	Thapsia garganica L.	Apiaceae		8		
18	Torilis leptophylla (L.) Reichenb.fil.	Apiaceae	75	91	10	9
19	Nerium oleander L.	Apocynaceae		1		
20	Ceterach officinarum DC. in Lam. et DC.	Aspleniaceae	1			
21	Achillea santolinoides Lag.	Asteraceae		2		
22	Anacyclus clavatus (Desf.) Pers.	Asteraceae	3	2		
23	Anacyclus pyrethrum (L.) Link	Asteraceae	73	86	12	13
24	Atractylis cancellata L.	Asteraceae		2		
25	Atractylis humilis L.	Asteraceae	6	4	1	1
26	Bellis annua L. ssp. minuta (DC.) Q. et S.	Asteraceae	3	10		
27	Bellis sylvestris Cyr.	Asteraceae	31	55	5	3
28	Bombycilaena discolor (Pers.) Lainz	Asteraceae	99	95	10	14
29	Calendula aegyptiaca Pers. ssp. eu-aegyptiaca Maire	Asteraceae		1		
30	Carduncellus pinnatus (Desf.) DC.	Asteraceae	44	55	12	12
31	Carduus nutans L. ssp. macrocephala	Asteraceae	36	74	12	14
32	Carduus tenuiflorus Curtis	Asteraceae	3	4		
33	Carlina involucrata Poir.	Asteraceae	94	116	13	15
34	Catananche caerulea L.	Asteraceae	51	45	5	4
35	Catananche cespitosa Desf.	Asteraceae	18	23	6	6
36	Centaurea boisserii spp. pomeliana (Batt. &. Trabut) Dostal	Asteraceae		5		
37	Centaurea boissieri DC	Asteraceae	67	72	10	9
38	Centaurea calcitrapa L.	Asteraceae		2		
39	Centaurea incana Desf. ssp. pubescens (Willd.) Maire	Asteraceae	5	3		
40	Centaurea maroccana Ball.	Asteraceae		7		
41	Cirsium echinatum (Desf.) DC.	Asteraceae	108	128	14	15

	Latin Name	Genus	Count 2003	Count 2004	Count 2005	Count 2005b
42	Crepis vesicaria L. ssp. haenseleri (Boiss. Ex DC.) P.D.Sell	Asteraceae	1	18	3	8
43	Crupina crupinastrum (Moris) Vis.	Asteraceae	3	3		
44	Cynara cardunculus L.	Asteraceae		15		1
45	Echinops spinosus L.	Asteraceae		1		
46	Evax argentea Pomel	Asteraceae	124	113	15	15
47	Filago germanica Presl.	Asteraceae	2	6	3	7
48	Filago pyramidata L.	Asteraceae	54	85	5	6
49	Hedypnois cretica (L.) Dum.-Courset	Asteraceae		15	1	1
50	Hyoseris radiata K. ssp. radiata	Asteraceae		10	1	
51	Hypochoeris achyrophorus L.	Asteraceae		26	2	
52	Hypochoeris glabra L.	Asteraceae		5	1	
53	Hypochoeris radicata L.	Asteraceae		31	2	2
54	Jurinea humilis (Desf.) DC.	Asteraceae	28	32	5	3
55	Lactuca viminea (L.) J. et C. Presl.	Asteraceae	16	43	1	2
56	Launaea arborescens (Batt.) Maire	Asteraceae		5		
57	Leontodon hispidulus (Del.) Boiss. ssp. muelleri (Sch-Bip) Maire	Asteraceae		23		
58	Leuzea conifera DC.	Asteraceae		5		
59	Mantisalca salmantica (L.) Briq. et Cavillier	Asteraceae	101	89	11	11
60	Micropus supinus L.	Asteraceae	8	26	5	6
61	Onopordon acanthium L.	Asteraceae	43	59	8	10
62	Onopordon acaule L.	Asteraceae	1	8	1	1
63	Pallensis spinosa (L.) Cass.	Asteraceae		7		
64	Phagnalon rupestre (L.) DC	Asteraceae		1		
65	Picnomon acarna (L.) Cass.	Asteraceae	119	124	15	15
66	Rhagadiolus stellatus (L.) Gaerten.	Asteraceae	4	13	1	
67	Rhaponthicum acaule L.	Asteraceae	8	15	4	3
68	Scolymus hispanicus L.	Asteraceae	2	1		
69	Scorzonera laciniata L.	Asteraceae	23	33	7	7
70	Scorzonera pygmaea Sibth. & Sm.	Asteraceae	20	43	8	8
71	Scorzonera undulata Batt	Asteraceae		15	5	6
72	Senecio gallicus L.	Asteraceae		9		
73	Senecio vulgaris L.	Asteraceae	9	10		1
74	Sonchus oleraceus L.	Asteraceae				
75	Taraxacum laevigatum (Willd.) DC.	Asteraceae	65	89	12	12
76	Taraxacum obovatum (Willd.) DC.	Asteraceae	56	86	12	12
77	Taraxacum zaunonii	Asteraceae	26	23	3	3
78	Urospermum picroides (L.) scop. Ex Schmidt	Asteraceae		3		
79	Xeranthemum inapertum (L.) Mill.	Asteraceae	95	83	13	13
80	Alkanna tinctoria (L.) Tausch	Boraginaceae	37	50	3	3
81	Anchusa officinalis L.	Boraginaceae	43	39	7	5
82	Lithospermum arvense L.	Boraginaceae	75	73	8	9

	Latin Name	**Genus**	**Count 2003**	**Count 2004**	**Count 2005**	**Count 2005b**
83	Myosotis ramosissima Rochel in Schultes	Boraginaceae	67	86	7	8
84	Neatostema apulum (L.) I.M.Johnston	Boraginaceae	95	105	11	12
85	Rochelia disperma (L.) Wettst.	Boraginaceae	118	118	13	13
86	Alyssum cochleatum Coss. et Dur.	Brassicaceae		1		
87	Alyssum granatense Boiss. Et Reuter	Brassicaceae		32	4	7
88	Alyssum linifolium Willd.	Brassicaceae		12	2	2
89	Alyssum montanum L.	Brassicaceae	114	126	15	13
90	Arabis auriculata Lam.	Brassicaceae	107	101	9	8
91	Arabis parvula Dufour in DC.	Brassicaceae	104	86	8	5
92	Arabis pubescens spp. pubescens (Desf.) Poiret	Brassicaceae		2	1	1
93	Arabis verna (L.) R.Br.	Brassicaceae		4		
94	Capsella bursa-pastoris (L.) Medicus	Brassicaceae	85	76	11	8
95	Cardamine parviflora L.	Brassicaceae	43	30		
96	Erophila verna (L.) Chevall.	Brassicaceae	49	68	11	8
97	Eruca vesicaria (L.) Cav.	Brassicaceae	1	2		
98	Erucastrum varium Dur.	Brassicaceae		7		
99	Erysimum incanum G. Kunze	Brassicaceae	114	113	6	10
100	Hornungia petraea (L.) Reichb.	Brassicaceae	92	99	6	8
101	Isatis tinctoria L.	Brassicaceae		1		
102	Lepidium draba L.	Brassicaceae		2		
103	Lepidium hirtum (L.) Sm. Ssp. calycotrichum (G.Kuntze) Thell.	Brassicaceae	79	76	8	9
104	Lobularia maritima (L.) Desv.	Brassicaceae		2		
105	Moricandia arvensis L.	Brassicaceae		2		
106	Sinapis arvensis L.	Brassicaceae		3		
107	Sisymbrium crassifolium Cav.	Brassicaceae	23	55	11	8
108	Sisymbrium runcinatum Lag. ex DC.	Brassicaceae	114	96	13	11
109	Teesdalia coronopifolia (J.P.Bergeret) Thell.	Brassicaceae	1			
110	Thlaspi perfoliatum L.	Brassicaceae	50	61	6	6
111	Legousia falcata (Ten.) Fritsch	Campanulaceae	80	91	6	7
112	Lonicera biflora Aiton	Caprifoliaceae		1		
113	Viburnum tinus L.	Caprifoliaceae		1		
114	Buffonia tenuifolia L.	Caryophyllaceae	112	106	13	13
115	Cerastium dichotomum L.	Caryophyllaceae	4	13	1	
116	Cerastium glomeratum Thuill.	Caryophyllaceae	81	89	10	10
117	Clypeola jonthlaspi L.	Caryophyllaceae		3		
118	Corrigiola littoralis L.	Caryophyllaceae	2	10	1	1
119	Dianthus sylvestris Wulfen	Caryophyllaceae	12	3		
120	Herniaria fontanesii Gay	Caryophyllaceae	2	1		
121	Herniaria hirsuta L.	Caryophyllaceae	116	118	11	12
122	Holosteum umbellatum L.	Caryophyllaceae			1	
123	Minuartia campestris L.	Caryophyllaceae	77	70	10	11

	Latin Name	Genus	Count 2003	Count 2004	Count 2005	Count 2005b
124	Minuartia geniculata (Poir.) Thell. var. maroccana (Batt.) Maire	Caryophyllaceae	10	6	2	4
125	Minuartia hamata (Hausskn. & Bornm.) Mattf.	Caryophyllaceae	10	8		1
126	Minuartia hybrida (Vill.) Schischkin in Komarov	Caryophyllaceae	36	45	1	3
127	Minuartia montana L.	Caryophyllaceae	72	93	4	7
128	Minuartia oberbuschig	Caryophyllaceae	10	4		
129	Moehringia trinervia (L.) Clairv.	Caryophyllaceae	117	120	11	14
130	Paronychia argentea L.	Caryophyllaceae	89	79	12	13
131	Paronychia capitata (L.) Lam.	Caryophyllaceae		5	2	3
132	Silene colorata Poiret	Caryophyllaceae	1	4		
133	Silene nocturna L.	Caryophyllaceae	45	51	6	5
134	Silene orepediorum Cosson	Caryophyllaceae	5	2		
135	Silene patula Desf.	Caryophyllaceae	15	22		
136	Silene rotblütig	Caryophyllaceae	4	19		1
137	Silene spec	Caryophyllaceae	1	8	1	
138	Silene vulgaris (Moench) Garcke ssp. commutata (Guss.) Hayek	Caryophyllaceae	18	31	2	3
139	Stellaria media (L.) Vill. s. str.	Caryophyllaceae		14	2	2
140	Vaccaria pyramidata Medicus	Caryophyllaceae		1		
141	Chenopodium foliosum (Moench) Aschers.	Chenopodiaceae	14	5		1
142	Chenopodium vulvaria L.	Chenopodiaceae	17	2	1	
143	Polycnemum fontanesii Dur. et Moq.	Chenopodiaceae	41	40	2	3
144	Cistus albidus L.	Cistaceae	26	39	1	1
145	Cistus incanus L.	Cistaceae		3	1	1
146	Cistus libanotis L.	Cistaceae		1		
147	Cistus salviifolius L.	Cistaceae		8		
148	Fumana thymifolia (L.) Spach ex Webb	Cistaceae		1		
149	Helianthemum cinereum (Cav.) Pers. ssp. rubellum (Presl.) Maire	Cistaceae	8	20	5	3
150	Helianthemum helianthemoides (Desf.) Gr.	Cistaceae	74	70	12	12
151	Helianthemum ledifolium (L.) Mill.	Cistaceae	68	101	14	13
152	Helianthemum lippii (L.) Pers.	Cistaceae	26	33		
153	Helianthemum pilosum (L.) Pers.	Cistaceae	5	7	2	1
154	Colchicum lusitanicum Brot.	Colchicaceae		33	5	6
155	Convolvulus altheoides L.	Convolvulaceae		1		
156	Convolvulus arvensis L.	Convolvulaceae	3	5	1	3
157	Convolvulus lineatus L.	Convolvulaceae	3	23	5	7
158	Sedum rubens L:	Crassulaceae	3	9		
159	Sedum sediforme (Jacq.) Pau	Crassulaceae		12		
160	Umbilicus rupestris (Salisb.) Dandy	Crassulaceae		1		
161	Juniperus oxycedrus L. ssp. oxycedrus	Cupressaceae	98	88	8	9
162	Tetraclinis articulata (Vahl) Masters	Cupressaceae		8		
163	Carex acuta L.	Cyperaceae		1		
164	Carex halleriana Asso	Cyperaceae	52	49	3	2

	Latin Name	Genus	Count 2003	Count 2004	Count 2005	Count 2005b
165	Carex otrubae Podp.	Cyperaceae		1		
166	Scirpus holoschoenus L.	Cyperaceae		3		
167	Tamus communis L.	Dioscoreaceae		2		
168	Scabiosa stellata L.	Dipsacaceae	8	4		
169	Euphorbia falcata L.	Euphorbiaceae	60	43	5	7
170	Euphorbia squamigera Lois.	Euphorbiaceae		2		
171	Euphorbia sulcata de Lens	Euphorbiaceae	17	23	4	7
172	Anthyllis vulneraria L. ssp. saharae (Zagorski) Beck	Fabaceae	47	44	2	2
173	Argyrolobium zanonii (Turra) P.W.Ball	Fabaceae	10	9		
174	Astragalus caprinus ssp. lanigerus (Desf.) Maire	Fabaceae	12	5	1	1
175	Astragalus echinatus Murray	Fabaceae	54	45	4	2
176	Astragalus gryphus Bunge	Fabaceae	6	29		1
177	Astragalus hamosus L.	Fabaceae	8	2	1	
178	Astragalus monspessulanus L.	Fabaceae		1		
179	Astragalus sesameus L.	Fabaceae	39	58	10	9
180	Astragalus spec.	Fabaceae		2		
181	Colutea arborescens L.	Fabaceae		2		
182	Coronilla minima L.	Fabaceae	31	22	2	4
183	Coronilla scorpioides (L.) Koch	Fabaceae	89	105	9	11
184	Coronilla valentina L. ssp. pentaphylla (Desf.) Batt.	Fabaceae		1		
185	Cytisus fontanesii Spach. ex Ball.	Fabaceae	1	5		
186	Genista erioclada Spach ssp. erioclada Emb. et Maire	Fabaceae	5	15		
187	Hippocrepis scabra DC.	Fabaceae	86	102	11	13
188	Lathyrus articulatus L. ssp. typicus (Fiori) Maire	Fabaceae		3	3	
189	Lathyrus sphaericus Betz	Fabaceae		1		1
190	Lens culinaris Medik.	Fabaceae	16	12	4	3
191	Lotus collinus (Boiss.) Heldr.	Fabaceae	23	41	1	2
192	Medicago arabica (L.) Hudson	Fabaceae		1		
193	Medicago minima (L.) Bartal	Fabaceae	122	126	14	15
194	Medicago orbicularis L.	Fabaceae		2		1
195	Medicago polymorpha L.	Fabaceae	1	4		
196	Medicago secundiflora Dur.	Fabaceae	86	100	8	13
197	Medicago turbinata (L.) Willd.	Fabaceae	47	73	8	9
198	Melilotus sulcatus Desf. ssp. brachystachys Maire	Fabaceae	3	8		
199	Ononis laxiflora Desf.	Fabaceae		1		
200	Ononis ornithopodioides L.	Fabaceae	44	44	4	7
201	Ononis reclinata L.	Fabaceae		10	3	1
202	Retama sphaerocarpa (L.) Boiss.	Fabaceae		1		
203	Trifolium campestre Schreb.	Fabaceae	63	80	7	7
204	Trifolium cherleri L.	Fabaceae	6	8	1	1
205	Trifolium pratense Schreb.	Fabaceae	109	116	14	14

	Latin Name	Genus	Count 2003	Count 2004	Count 2005	Count 2005b
206	Trifolium scabrum L.	Fabaceae	38	41	2	9
207	Trifolium stellatum L.	Fabaceae	10	2		2
208	Trifolium tomentosum L.	Fabaceae	23	27	4	5
209	Trigonella monspeliaca L.	Fabaceae	111	119	13	11
210	Trigonella polycerata L.	Fabaceae	77	95	8	13
211	Vicia hirsuta (L.) S.F.Gray	Fabaceae	45	57	2	5
212	Vicia lathyroides L.	Fabaceae	1	20	4	8
213	Vicia monantha Retz.	Fabaceae	84	70	9	7
214	Vicia onobrychioides L.	Fabaceae		4		
215	Vicia pannonica Crantz	Fabaceae		2		
216	Vicia sativa ssp. cordata (Wulfen ex Hoppe) Ascherson et Graebner	Fabaceae	91	93	10	9
217	Quercus rotundifolia L.	Fagaceae	118	105	10	11
218	Fumaria officinalis L.	Fumariaceae	9	15	1	1
219	Rupicapnos africana (Lam.) Pomel.	Fumariaceae		2		
220	Erodium cicutarium (L.) L'Her	Geraniaceae	95	129	15	15
221	Geranium lanoginosum L.	Geraniaceae	36	45	5	6
222	Geranium robertianum L.	Geraniaceae		5		
223	Geranium rotundifolium L.	Geraniaceae	95	99	12	13
224	Globularia alypum L. ssp. eu-alypum L.	Globulariaceae		4		
225	Crocus nevadensis Amo et Cam	Iridaceae		32	7	8
226	Gladiolus communis L. ssp. byzantinus (Miller) A.P.Hamilton	Iridaceae	14	41	4	5
227	Iris juncea Poir.	Iridaceae	11	25	7	5
228	Iris sisyrhinchum L.	Iridaceae	2			
229	Juncus acutus L.	Juncaceae		1		
230	Juncus pygmaeus Rich. (L.) Schinz et Thell.	Juncaceae		1		
231	Acinos alpinus (L.) Moench	Lamiaceae		6		
232	Ajuga chamaepitys (L.) Schreb. ssp.chamaepitys	Lamiaceae		1		
233	Ajuga iva (L.) Schreber	Lamiaceae	107	92	11	11
234	Lamium amplexicaule L.	Lamiaceae	62	59	7	6
235	Marrubium vulgare L.	Lamiaceae		8		
236	Nepeta nepetella L.	Lamiaceae		5		
237	Rosmarinus officinalis L.	Lamiaceae		10		
238	Salvia argentea L. ssp. patula (Desf.) Maire	Lamiaceae	33	22	7	7
239	Salvia verbenaca (L.) Briq.	Lamiaceae	47	58	11	11
240	Sideritis montana L.	Lamiaceae	24	45	3	2
241	Teucrium fruticans L.	Lamiaceae	7	12		
242	Teucrium polium ssp. capitatum (L.) Briq.	Lamiaceae		10	2	1
243	Teucrium pseudo-chamaepytis L.	Lamiaceae		7		
244	Thymus ciliatus Desf. ssp. coloratus (B. et R.) Batt.	Lamiaceae		3	1	
245	Thymus hirtus Willd.	Lamiaceae	24	14		
246	Thymus munbyanus Boiss. et Reuter ssp. coloratus (Boiss. et	Lamiaceae	69	71	11	11

	Latin Name	Genus	Count 2003	Count 2004	Count 2005	Count 2005b
247	Ziziphora hispanica L.	Lamiaceae	33	34	4	6
248	Allium paniculatum L.	Liliaceae	23	26	7	7
249	Allium rotundum L.	Liliaceae			1	
250	Allium subhirsutum spp. album (Santi) M. et W.	Liliaceae		6	1	2
251	Asparagus acutifolius L.	Liliaceae		4		
252	Asphodelus microcarpus Salzm. et Viv.	Liliaceae	86	78	8	8
253	Fritillaria lusitanica Wikstr. ssp lusitanica	Liliaceae	1	15	2	2
254	Gagea arvensis (Pers.) Dumont	Liliaceae		10	5	4
255	Muscari comosum (L.) Mill.	Liliaceae	1	35	2	2
256	Muscari neglectum Guss. ex Ten.	Liliaceae	30	79	15	14
257	Ornithogalum narbonense L.	Liliaceae		1		
258	Ornithogalum umbellatum L.	Liliaceae	23	65	12	6
259	Tulipa sylvestris L. ssp. australis (Link) Pamp.	Liliaceae		8		4
260	Urginea maritima (L.) Baker	Liliaceae		4		
261	des Bupleurum-Ding des	Liliaceae?		5		
262	Linum narbonense L.	Linaceae		2		
263	Malva aegyptiaca L.	Malvaceae	1	2		
264	Malva rotundifolia L.	Malvaceae	54	56	4	3
265	Jasminum fruticans L.	Oleaceae		5		
266	Phillyrea angustifolia L. spp. intermedia	Oleaceae		8		
267	Phillyrea angustifolia ssp. eu-angustifolia	Oleaceae		13		
268	Ophrys tenthredinifera Willd.	Orchidaceae		1		
269	Orchis langei Richter	Orchidaceae		1		
270	Hypecoum pendulum L.	Papaveraceae	2	6	1	1
271	Papaver argemone L.	Papaveraceae		16	2	1
272	Papaver dubium L.	Papaveraceae	48	22		
273	Papaver hybridum L.	Papaveraceae	1	6		
274	Papaver pinnatifidum Moris	Papaveraceae	35	82	9	6
275	Papaver rhoeas L.	Papaveraceae		2		
276	Roemeria hybrida (L.) DC.	Papaveraceae	1	7		1
277	Plantago afra L.	Plantaginaceae		4	4	4
278	Plantago albicans L.	Plantaginaceae	10	4	1	1
279	Plantago coronopus L.	Plantaginaceae	8	11	2	3
280	Aegilops geniculata Roth	Poaceae	88	86	13	15
281	Aegilops ovata L.	Poaceae	1	2		
282	Aegilops ventricosa Tausch	Poaceae	1	2		1
283	Alopecurus arundinaceaus Poir. in Lam.	Poaceae	2			
284	Anthoxanthum odoratum L.	Poaceae	4	10	1	9
285	Arrhenaterum elatius (L.) Beauv.ex J. et C.Presl ssp. bulbosum	Poaceae	35	12	2	4
286	Avena barbata Pott. Ex Link in Schrader	Poaceae	5	10	1	
287	Avena fatua L.	Poaceae		16		

	Latin Name	Genus	Count 2003	Count 2004	Count 2005	Count 2005b
288	Avena sterilis L.	Poaceae	56	65	12	11
289	Avenula bromoides (Gouan) H.Scholz	Poaceae	27	12		
290	Brachypodium distachyon (L.) Beauv	Poaceae	56	57	9	11
291	Bromus lanceolatus Roth	Poaceae	5	1	1	1
292	Bromus rubens L.	Poaceae	96	120	14	15
293	Bromus tectorum L.	Poaceae	102	109	15	14
294	Cynosurus elegans Desf.	Poaceae	65	91	10	8
295	Dactylis glomerata L. ssp. hispanica (Roth.) Nyman	Poaceae	98	116	14	14
296	Desmazeria rigida (L.) Tutin in Clapham	Poaceae	100	97	12	11
297	Echinaria capitata (L.) Desf.	Poaceae	95	113	13	13
298	Festuca cynosuroides Desf.	Poaceae	30	56	8	12
299	Festuca ovina agg.	Poaceae	5	39	3	4
300	Festuca triflora Desf.	Poaceae	38	54	5	6
301	Hordeum murinum L.	Poaceae	113	116	14	14
302	Koeleria phleoides (Vil.) Pers.	Poaceae	13	36	4	6
303	Lamarckia aurea (L.) Moench	Poaceae	9	13		
304	Lolium rigidum Gaudin	Poaceae	4	2		
305	Melica uniflora Retz.	Poaceae	1	5		
306	Parapholis incurva (L.) C.E. Hubb.	Poaceae		1		
307	Pennisetum ciliaris (L.) Link	Poaceae		1		
308	Poa bulbosa L. s. str.	Poaceae	16	4		3
309	Poa bulbosa L. ssp. vivipara (Koeler) Arcangeli	Poaceae	98	110	15	15
310	Poa trivialis L.	Poaceae	3	3		
311	Psilurus incurvus (Gouan) Schinz et Thell.	Poaceae	1	9		
312	Schismus barbatus (L.) Thell.	Poaceae	98	71	9	12
313	Stipa barbata Desf. - O Medit.	Poaceae	38	48	6	8
314	Stipa capensis Thunb.	Poaceae		3		
315	Stipa fontanesii Parl.	Poaceae		3		
316	Stipa lagascae E. et S.	Poaceae	28	24	6	6
317	Stipa parviflora Desf.	Poaceae	2	5		
318	Stipa tenacissima L.	Poaceae		10		
319	Tetrapogon villosus Desf.	Poaceae	42	50	1	3
320	Trisetaria nitida (Desf.) Maire	Poaceae	29	9		
321	Vulpia bromoides (L.) S.F. Gray	Poaceae	67	79	10	11
322	Vulpia geniculata (L.) Link.	Poaceae	1	5		
323	Vulpia unilateralis (L.) Stace	Poaceae	95	115	15	14
324	Polygala rupestris Pour.	Polygalaceae		1		
325	Polygonum balansae Boiss et Reut	Polygonaceae		7	1	
326	Rumex bucephalophorus L.	Polygonaceae	1	2		
327	Rumex thyrsiflorus Fingerh.	Polygonaceae	13	36	5	6
328	Anagallis arvensis ssp. caerulea (Schreb.) Hartm.	Primulaceae		14		

	Latin Name	Genus	Count 2003	Count 2004	Count 2005	Count 2005b
329	Androsace maxima L.	Primulaceae	25	59	7	6
330	Asterolinon linum-stellatum (L.) Duby in DC.	Primulaceae	44	42	3	5
331	Cytinus hypocystis L. spp. kermesinus	Rafflesiaceae		2		
332	Adonis aestivalis L.	Ranunculaceae		2		
333	Adonis microcarpa DC.	Ranunculaceae	2	16	3	2
334	Ceratocephalus incurvus Stev.	Ranunculaceae	28	48	9	8
335	Ranunculus arvensis L:	Ranunculaceae		2		
336	Ranunculus paludosus Poiret	Ranunculaceae	8	20	5	6
337	Reseda alba L.	Resedaceae	13	17	4	6
338	Reseda lutea L.	Resedaceae		5		
339	Reseda luteola L.	Resedaceae	42	52	6	8
340	Rhamnus lycioides (L.) Cam.	Rhamnaceae		3		
341	Aphanes arvensis L.	Rosaceae	20	38	5	7
342	Rosa canina agg. L.	Rosaceae		1		
343	Rubus caesius L.	Rosaceae		1		
344	Sanguisorba ancistroides (Desf.) Cesati	Rosaceae	48	68	9	10
345	Asperula arvensis L.	Rubiaceae		3	1	
346	Asperula hirsuta L.	Rubiaceae	43	75	8	12
347	Crucianella angustifolia L.	Rubiaceae	90	74	7	8
348	Galium aparine L.	Rubiaceae	100	100	10	10
349	Galium mollugo L.	Rubiaceae		23		
350	Galium parisiense L.	Rubiaceae	41	57	7	4
351	Galium verrucosum Hudson	Rubiaceae	6	2	1	1
352	Sherardia arvensis L.	Rubiaceae	1	1	1	1
353	Saxifraga globulifera Desf.	Saxifragaceae		2		
354	Chaenorrhinum rubrifolium (Robill. Et Cast. Ex DC.) Fourr.	Scrophulariaceae		5		
355	Linaria heterophylla Desf.	Scrophulariaceae	87	99	9	8
356	Linaria laxiflora Desf.	Scrophulariaceae	4	11	2	1
357	Parentocellia latifolia (L.) Caruel	Scrophulariaceae	2	3		
358	Verbascum sinuatum L.	Scrophulariaceae	9	4		
359	Veronica arvensis L.	Scrophulariaceae	101	91	12	12
360	Veronica hederifolia L.	Scrophulariaceae	35	40	8	7
361	Veronica polita Fries	Scrophulariaceae	1	4		
362	Thymelaea velutina Cosson et Dur.	Tymelaeaceae	5	8	2	1
363	Urtica dioica L.	Urticaceae	1			
364	Centranthus calcitrapae (L.) Dufr.	Valerianaceae	26	43	2	4
365	Valerianella coronata (L.) DC.	Valerianaceae	110	123	14	15
366	Viola tricolor L.	Violaceae	7	4	1	1

Appendix 9 Additional information on climatic characteristics of the Investigation Area in Northeastern Morocco

Temperature

In summer, the Northeastern part of Morocco is influenced by subtropic anticyclones. The climate is then characterized by drought, heat and strong insolation. For the High Plateaus the Azores anticyclone often causes very stable weather conditions but sometimes hot winds from the Sahara bring very dry and hot air (up to 45°C) as well as dust and sand-storms (chergui, Direction Regionale des Eaux et Forêts de l'Oriental 1996). At the Gaada average annual temperature equals 14°C. However, throughout the field campaigns (from april to may) average temperature differed considerably between the years (2003 = 14°, 2004 = 9°, 2005 = 16°, see also Figure 3.5 in main text), which indicates that there can also be large fluctuations.

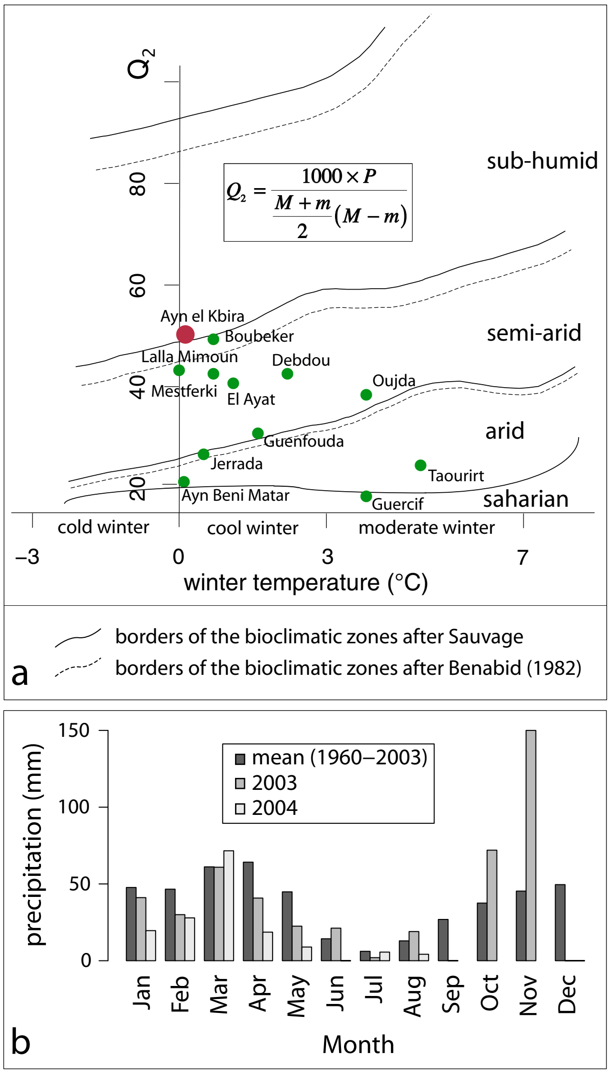

Figure A9.1. Climate diagrams of the Investigation Area. **a)** Bioclimatic classification of the district of Oujda after the pluvio-thermic coefficient of Emberger (1955)[1]. M and P are taken from the forest management plan (Direction Regionale des Eaux et Forêts de l'Oriental, 1996). **b)** Average monthly temperatures based on precipitation data from 1960-2003 compared to the monthly averages of the years 2003 and 2004 (measured at Ayn El Kbira).

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[1]) Based on the plant geographic knowledge which he accumulated during its work in North-Africa, the botanist Emberger (1955) developed a methodology to characterize Mediterranean vegetation incorporating the variables temperature and precipitation (Barbéro et al. 1992; Dufour-Dror & Ertas 2004), see Formula in Figure A9.1a). As the extremes are much more important than yearly averages, he included the average temperature of the hottest (M) and coldest month (m) additional to the variable precipitation (P) in the calculation of the pluviothermic coefficient Q. The x-axis of the diagram represents the average temperature during winter, whereas the y-axis represents the calculated Q. Thus the classification of a given region into the bioclimatic zones depends on the mean winter temperature and Q. The bio-climatic zones which are distinguished are the saharian, arid, semi-arid, subhumid, humid, and perhumid zones (the two latter are not displayed in the diagram).

In winter, cyclonic weathers from Northern regions prevail due to the equatorial shift of the climate circulation system: Cool and wet air from the atlantic regions or from the Mediterranean delivers precipitation (Müller-Hohenstein 1978). Often, two precipitation peaks occur throughout the year (autumn and spring (Le Houérou 2002), see Figure A9.1 b). At the escarpment of the Gaada frost occurs regularly in winter. Therefore there are two non-growing seasons, during summer caused by heat and dryness, during winter caused by cold temperatures.

Precipitation

Throughout the Mediterranean, climate is highly variable (Evans & Geerken 2004; Gritti et al. 2006). Therefore average precipitation estimates regarding both frequency and amount are of limited validity (Laounia 1990; Lázaro et al. 2001) and should be backed up by actual measurements. However on average 40 rain days and 4 to 10 snow days can be assumed per year (Müller-Hohenstein 1978, compare to 6 - 7 snow days after Direction Regionale des Eaux et Forêts de l'Oriental (1996)). The Gaada obtains on average about 600 mm/a. This is much more than the Moulouya plains (which receive about 200 mm/a, see Chapter 3.1). After Emberger (1955) the plains are arid, whereas the slopes of the Gaada are semi-arid to sub-humid (Figure A9.1 a, see Figure caption for details). Note, that the precipitation assessed with a simple rain gauge on Ayn el Kbira does only include rain. Snow and fog are not measured although at least the latter might bring a considerable amount of additional deposition which is of high importance for the plants in the region (Deil 2003).

This part of Morocco suffers from episodic drought with dry periods varying in duration from 2 to 13 years (Davis 2005) which is assumably triggered by a shift of the Azores high to the North. The field campaigns started at the end of a medium length dry period (M'Hamdi, pers. comm., Figure 3.5 c in main text). Therefore it was much wetter in 2003 and 2004 than in the years before (see also Figure 3.5). However, in 2005 it was relatively dry again. Furthermore the winter of 2005, albeit cold, brought very few snow (Bezzot, pers. comm.) and during the field work it rained only on two days.

Wind is as well an important factor at the Gaada. Because of the exposed situation, only few days are without considerable winds (personal experience). Its climatic effect depends on the direction where it is coming from. The summer winds and storms from the South and East bring very dry, hot air, drawing humidity off the soils, whereas the atlantic winds in spring and autumn bring wet air from the Seas (Mediterranean and Atlantic), increasing the moisture balance. However, they already leave most of their loads at the Rif mountains, the Middle Atlas mountains or the coastal mountains of Beni-Snassen (Direction Regionale des Eaux et Forêts de l'Oriental, 1996).

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Appendix 10 Patterns of similarity caused by various asymmetric binary similarity coefficients, compared to the respective ternary plots

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Appendix 11
Curriculum Vitae, Gerald Jurasinski

Dipl.Ing., PhD-Student, Research Associate

Birthday: 03/24/1975
Place of Birth: Quedlinburg
Nationality: German
Marital status: Married

Profile

- Landscape Ecology, Vegetation Ecology, Basic and Applied Research.
- Assessment and analysis of spatio-temporal patterns of vegetation and their drivers on landscape- and ecosystem-scale
- Method development for the assessment and analysis of vegetation patterns on different spatial and temporal scales
- Planning and monitoring for nature conservation

Work Experience

from 04/2002 — Research Associate, Department of Biogeography, University of Bayreuth, Germany

- from 04/2003 working on PhD thesis; organizing associated Diploma theses
- Acquisition, administration, and realization of the research project *Biodiversity and Disturbance - Raster based Investigations in Semi-Arid Ecosystems*, progress and final reporting for other research projects of the department
- Contributing to further fund-raising activities of the department (DFG, EU, BMBF)
- Preparing and holding courses for Bachelor, Master and Diploma students of the study courses Geoecology, Geography and African Developments Studies (courses include, *inter alia*, Plant Taxonomy and Identification, Geoecological Field Course, Vegetation Classification, Island Biogeography, Geobotany)
- Website developement and maintenance for the *Arbeitskreis Biogeografie* (2002-2004)

from 02/2001 — Occasional Freelance Work

- Contributions to research projects of the UFZ Leipzig (literature research, data analyses, method description)
- Consulting (environmental impact assessment for a flint mining site in Lower Saxony)

04/2001 - 03/2002 — Research Associate, Insitute for Land Management and Landscape Ecology, University of Rostock, Germany

- Fund raising, course preparation, teaching assistant in the courses Vegetation Science (field course) and Plant Taxonomy and Identification, website development and maintenance for the working group *Landscape Ecology*

Education

Spring 2007 — PhD in Geoecology, University of Bayreuth (scheduled graduation)

- Subject: *Spatio-Temporal Patterns of Biodiversity and their Relation to Disturbances in a Transitional Ecosystem in North-Eastern*

09/2003 — AVEC Summer School, Peyresq, Alpes des Hautes de Provence, France

- Subject: *Integrated Assessment of Vulnerable Ecosystems under Global Change*

Autumn 2000 — Engineering Degree (very good) in Landscape Management and Environmental Protection, University of Rostock

- Diploma thesis (short title): *Conservation Management and Development Plan for the Nature Reserve ‚Nüssenberg' near Weischütz (Burgenlandkreis)*
- Major fields of study: Special Geosciences, Applied Ecology, Waste and Sewage Treatment, Environmental Chemistry and Ecotoxicology

09/1997 - 09/1998 — Study accompanying training, StAUN (National Board for Environment and Nature), Rostock

- Project: *Evaluation of the Rewetting Potential of the Peat Bog „Steinfelder Niederung"*

1994 — A-levels (very good), Gymnasium Stephaneum, Aschersleben

- Major courses: Biology and English

Erklärung zur vorgelegten schriftlichen Leistung

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dass ich die vorliegende Dissertationsschrift selbständig und ohne fremde Hilfe verfasst, andere als die angegebenen Quellen und Hilfsmittel nicht benutzt und die den benutzten Werken wörtlich oder inhaltlich entnommenen Stellen als solche kenntlich gemacht habe.

Hiermit erkläre ich an Eides statt,

dass ich weder die vorliegende noch eine gleichartige Doktorprüfung an einer anderen Hochschule endgültig nicht bestanden.

(gez. Gerald Jurasinski)