Proceedings IAVS Symposium, pp. 186-189, 2000

The gradient structure of Swiss forest vegetation: Evaluation of the traditional Swiss forest classification

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Abstract. Abrupt spatial changes in species composition of Swiss forests reflect small-scale patterns in topographical and geological site factors as well as management influences. Therefore, it has always seemed appropriate to define discrete forest units, i.e. plant associations or vegetation units generated by clustering, rather than by the arrangement of plots along underlying environmental gradients. Well-defined forest units are essential for mapping projects aimed at management applications. After having revised the old classification system of Ellenberg & Klötzli (1972) on the basis of new data, we faced a lively resistance to the new classes, primarily by people who had classified forests in specific regions. In search of a solution to the problem, we tested the old classification system by using direct and indirect gradient analyses on more than 6000 relevés. We found that these forest relevés are arranged continuously. We compared the resulting gradients with secondary site factors. Previously described vegetation units were reviewed by displaying them in ordination space.

Keywords: Complementary Analysis; Correspondence Analysis; Forest gradient; Revision.

Introduction

In Switzerland, a multitude of geological formations as well as different climates meet on a small area of only 40 000 km^2. Consequently, the resulting vegetation varies considerably. The real vegetation was classified into numerous types and there was also good reason to distinguish between many different species assemblages.

It is widely believed that large areas of the forests are in a rather natural state and it is a declared objective of forestry departments to maintain or to re-establish this state. Also in the federal forest law, site or vegetation classification is declared mandatory as a basis for all forest projects.

A cornerstone in forest vegetation classification was set by Ellenberg & Klötzli (1972). The authors divided the total forest vegetation of Switzerland into 71 units by applying the so-called relevé punch card method on 5000 relevés (Ellenberg & Christofolini 1964; Mueller-Dombois & Ellenberg 1974). This procedure corresponded to some extent to a modern computer classification. Since this publication appeared, the new system has been applied to numerous regional forest vegetation surveys (e.g. Schmider et al. 1993; Frey 1995; Ott et al. 1997). The old classification is in fact still used today, even though the data base has increased meanwhile to as many as 15 000 relevés.

We established a data base consisting of 15000 available relevés in order to revise the old classification system (Wohlgemuth 1992; Wildi et al. 1996). The most obvious weakness of the data collection is that there has never existed an underlying statistical sampling design. This led to various problems such as over- and under-representation of types, limited reliability in the determination of species, different homogeneity of the different relevé plots. Data from ca. 300 different sources of publications were compiled in the data base. Many of these studies were based on preferential sampling, which generally reinforces the discrete view of vegetation. On the other hand, we hoped that the large number of relevés would compensate for some of the weaknesses.

We faced a lively resistance to our new classification system, primarily by people who had classified forests in specific regions of Switzerland earlier. In particular, they did not agree with the proposed new units. In search of a solution to the problem, we tested the old classification system by using direct and indirect gradient analyses. Evaluating a classification system is a delicate task because classification is often considered an art rather than a scientific method and hence influenced by personal preferences. In this paper we address the following questions:
1. Are Swiss forest communities discrete units?
2. Which are the predominant gradients in Swiss forests?
3. Does the traditional classification system of Swiss forests need a revision?

Material and Methods

In order to test the traditional alliances and associations, we created an ordination space using as many relevés as possible (CANOCO, version 4; ter Braak & Šmilauer 1998). Two data sets served as test data: 'Switzerland' with nationwide data (6525 relevés) and 'N Switzerland' (6266 relevés) consisting of relevés from Swiss areas north of the Alps (Table 1). A majority of the relevés of the data base describe natural forest stands, i.e. the vegetation is considered close to the potential natural vegetation (PNV; Tüxen 1956; Westhoff & van der Maarel 1978). The data sets include a considerable number of core relevés which were originally used by Ellenberg & Klötzli (1972) to define the 71 old units. In order to test the quality of the old classification we visualized the core relevés in ordination space built by the large data sets. This procedure is also known as complementary analysis (Kent & Ballard 1988).

Apart from the species information, we also included secondary environmental variables. According to Walter (1960), we defined the following easily measurable variables as secondary factors: climate (radiation, rainfall, temperature), relief (slope, aspect), soil (type, structure, chemical properties, water storage), biotic factors (man, animals, plants). Ecologically relevant factors with a direct effect on plants are considered primary: warmth, light,

Table 1. Data sets used in the analyses.

Data set	Switzerland	N Switzerland
Data constraints	- tree cover > 50 % - coordinates available - plot size 50 to 300 m^2 - date > 1950	- tree cover > 50 % - coordinates available - located in Jura Mts, Central Plateau or Northern Prealps (Wohlgemuth 1996)
No. of relevés	6525	6266
No. of species in layers	1820	1563

water, chemical factors (nutrients) and mechanical factors (wind, snow, disturbance).

In order to detect discrete relevé groups as well as primary site factors which often are revealed by species positions along the axes, we conducted Correspondence Analysis (CA) on both data sets (percent coverage of species, downweighting of rare species). In an additional analysis – not presented here – we ran Canonical Correspondence Analysis (CCA) including environmental variables.

Results

In the CA-ordination diagrams of the relevés, no discrete groups are detectable (Fig. 1). The relevés are arranged along gradients. Distinct arcs are visible in the ordinations of both data sets. In addition, the ordination displays reflect unbalanced distribution of relevés.

According to the positions of the species along the axes, we interpreted the first two axes in ecological terms i.e. with primary factors. CA-axis 1 corresponds best with the mean availability of nutrients and, partly, with warmth and soil acidity (geological substrate). CA-axis 2 corresponds best with drought stress or water demand, or more commonly, moisture.

Core relevés are displayed in the CA-ordination space based on the data set N Switzerland. Their assignment to different traditional units is indicated with different symbols, following the classification hierarchy in Ellenberg & Klötzli (1972), i.e. alliances, associations and subassociations. With respect to the system of alliances, ordination results correspond with the traditional classification, i.e. groups of core relevés overlap only partly in ordination space. With respect to the system of associations and subassociations, the units overlap considerably (Fig. 2).

Discussion

Discreteness and continuum

Our CA-ordination results revealed a continuous gradient system of Swiss forest vegetation. This, on the one hand, is not very astonishing because the large number of relevés involved presumably could blur discrete patterns. On the other hand, even in the highly structured landscape of Switzerland, the expected discreteness of at least few

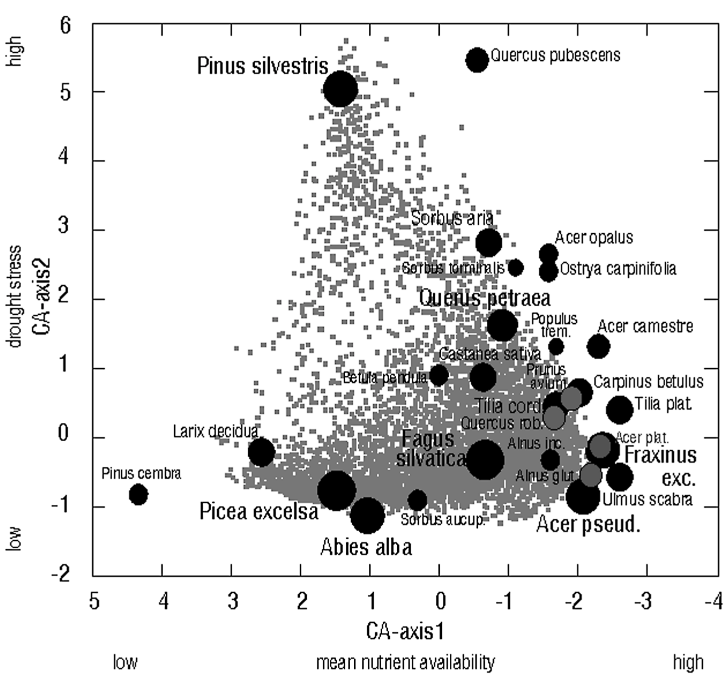

Fig. 1. CA-ordination of 6525 relevés and 28 tree species of data set 'Switzerland'. Species symbols reflect the log transformed weights resulted from CA. Axes are labeled according to the interpretation that is based on the relative positions of the tree species. In order to compare the CA-ordination with the ecogram for Central Europe (Ellenberg 1963, 1988), the first CA-axis is reversely displayed.

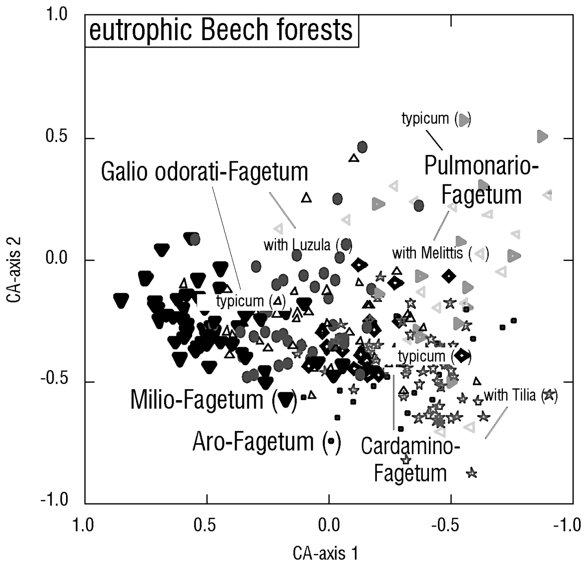

Fig. 2. CA-ordination of core relevés which were used by Ellenberg & Klötzli (1972) to define forest associations and sub-associations (data set). Ordination space was built using the data set 'N Switzerland'. The display shows core relevés of the alliance *Eu-Fagion* (eutrophic beech forests).

associations is not visible. This in turn raises the question about the delimitation of vegetation types. While in early 1970, the data available (ca. 5000 relevés) did not cover the entire ecological variation and therefore reflected more discreteness, today we face three times more data resulting in more difficulties for classification because the patterns are more continuous now. Future classifications need to emphasize gradients and reference relevés within the vegetation continuum rather than preferentially sampled data which until recently served as core units.

Gradients

The CA-ordination of the data set Switzerland revealed the primary factors: mean nutrient availability (CA-axis 1) and drought stress – moisture (CA-axis 2). Nutrient availability is strongly dependent both on water availability and warmth, though. A proper distinction between the factors, nutrient availability and moisture, is almost impossible. This effect is expressed exactly by the tree species in ordination space. We compared the CA gradient system with the ecogram of Ellenberg (1963, 1988). The ecogram is considered a direct ordination (Wildi 1986) using the two axes of acidity and moisture. In contrast to our results, the ecogram was designed with expert knowledge of the region. The species positions along the axes of the CA-ordination correspond fairly well with the ones in Ellenberg's ecogram, although the first axis of the ecogram is originally defined as acidity. Ellenberg & Klötzli (1972) adopted the ecogram concept but replaced 'acidity' as the denomination of the first axis with 'nutrient richness', which in turn corresponds to our first CA-axis. This implies that the meaning of the well-accepted and widely applied ecogram is ambivalent with respect to the first axis. In a different study we paid special attention to this problem (Wohlgemuth et al. 1999).

The predominant gradients in Swiss forest vegetation are nutrient availability and moisture in terms of primary factors. In terms of secondary factors, the forest vegetation is best explained by the factors degree days, annual rainfall and soil skeleton. Soil acidity i.e. the geological substrate, is masked by the availability of nutrients (Fig. 1, CA-axis 1). Low availability of nutrients corresponds to sites at higher altitudes where the substrate is not of primary importance. In contrast, floristic differences of sites at low altitudes can be well explained by the geological substrate. However, these differences again are strongly related to nutrient availability.

Evaluation of the traditional classification system

Results of complementary analyses confirm the problems that emerge in all the new regional classification projects concerning forest vegetation in Switzerland. These problems include the fact that many of the defined vegetation units overlap, and hence, there are considerable difficulties of distinction, not only between, but also among regional associations. Generally, associations are well defined within the alliances at the end of the vegetation gradients (low availability of nutrients, high drought stress; e.g. mixed oak forests). In beech forests, in contrast, only about 50% of the associations are well-defined. In the centre of the CA-ordination, distribution patterns of many associations overlap considerably. We consider mainly two reasons for that. 1. For methodological reasons, CA-ordinations result in a dense centre with many relevés and a scattered periphery consisting of few relevés with different species composition. 2. Mesic sites in lowlands are suitable for almost all trees in Switzerland, resulting in an increased competition pressure. Small ecological differences in these sites result in considerable differences of tree, shrub and herb species composition. Ecological differences may be, in addition, caused by large plot size or differences in forest management. Taking into account additional random variation, the ecological interpretation of the units in terms of species is difficult. We conclude that it is not a coincidence that exactly the mesic forest units are the ones leading to the most distinct contradictions in actual mapping projects. Our results show that some parts of the traditional system need to be revised. To generalize rather than divide vegetation units would often be justified.

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