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Alpha and Beta Diversity in Central European Beech Forests

W. Willner, D. Moser & G. Grabherr
Institute of Ecology and Conservation Biology, University of Vienna, Althanstr. 14, A – 1090 Vienna, Austria; e-mail: wolfgang.willner@univie.ac.at

Abstract
Recently, the beech forests of southern Central Europe (including large parts of the Illyrian region) have been syntaxonomically revised, using a TURBOVEG database containing more than 5800 relevés, mainly from Austria, Switzerland, Germany, the Czech Republic, Hungary, Slovenia and Croatia. The same TURBOVEG database was used to calculate patterns of alpha and beta diversity within beech forests. A strong correlation between local species richness and soil pH was found. Beta diversity is related with area and the number of associations therein.

Keywords: Diversity calculations, *Fagus sylvatica*, phytosociology, species pool hypothesis.

Zusammenfassung
Alpha- und Beta-Diversität in mitteleuropäischen Buchenwäldern. In einer kürzlich vorgelegten Studie wurden die südmitteleuropäischen Buchenwälder (unter Einschluss großer Teile der illyrischen Region) syntaxonomisch revidiert, basierend auf einer TURBOVEG-Datenbank mit mehr als 5800 Aufnahmen, hauptsächlich aus Österreich, der Schweiz, Deutschland, Tschechien, Ungarn, Slowenien und Kroatien. Dieselbe Datenbank wurde benutzt, um Muster der Alpha- und Beta-Diversität innerhalb der Buchenwälder zu berechnen. Es wurde eine starke Korrelation zwischen dem lokalen Artenreichtum und dem pH-Wert des Bodens festgestellt. Die Beta-Diversität hängt einerseits von der Größe des betrachteten Gebiets, andererseits von der Anzahl der darin vorkommenden Assoziationen ab.

Schlagworte: Diversitaets-Berechnungen, *Fagus sylvatica*, Pflanzensoziologie, Species-Pool-Hypothese.

Introduction

The main gradients determining the floristic composition of Central European beech forests are soil reaction and altitude (Moor, 1952; Tüxen, 1960; Lausi & Pignatti, 1973; Ellenberg, 1996; Willner, 2002). The classical conception of Tüxen (1955), who established three alliances reflecting these gradients (thermophilous beech forests = *Cephalanthero-Fagion*, mesophilous beech forests = *Asperulo-Fagion* and acidophilous beech forests = *Luzulo-Fagion*), was supported by a TWINSPAN of 5815 relevés (Willner, 2001). Geographic gradients, although strongly emphasized by many authors (e.g. Soó, 1964; Török *et al*., 1989; Rivas-Martínez *et al*., 1991; Dierschke, 1998), have been proved less important, at least in Central Europe.

In the present study we examine how the local species richness (alpha diversity) of beech forests is influenced by these environmental factors. Furthermore, we look for patterns in the average species turnover (beta diversity).

Materials and methods

We used 5131 relevés from Austria, Switzerland, Germany, the Czech Republic, Hungary, Slovenia, Croatia, and from a small part of Italy (Friuli Venezia Giulia). The data are stored in a TURBOVEG database (Hennekens & Schaminée, 2001).

Alpha diversity is defined as the number of vascular plant species occuring in one relevé. For no direct measurement of soil reaction was available, we calculated avarage not-weighted Ellenberg indicator values for all relevés (Ellenberg *et al*., 1991).

Correlations between alpha diversity and environmental factors can be shown on two different levels: 1. on the level of single relevés (which is the usual approach), 2. on the community level. For the latter we calculated means of alpha diversity, altitude and average Ellenberg indicator values for 41 beech forest communities distinguished by Willner (2002), corresponding to associations or lower syntaxonomic units.

Beta diversity is understood in the original sense, i.e. variation of species composition within a region according to Whittaker's formular beta = gamma / mean alpha where gamma is the total species number, and mean alpha the average alpha diversity within a certain region (Whittaker, 1972; Vellend, 2001). We distinguished 11 biogeographic regions of Central European beech forests which are more or less homogeneous in their syntaxonomic content (Fig. 1). A special problem was how to calculate gamma diversity for the 11 regions. We defined gamma as the regional „habitat-specific" species pool (Dupré, 2000), i.e. the total number of vascular plant species occuring in beech forests in the respective region. To avoid sampling bias, in each region a random selection of 100 relevés was made. For the dinaric region of Slovenia and Croatia only 92 relevés were available in the database.

Results

1. Alpha diversity

The species number per relevé is significantly correlated with the mean Ellenberg R (reaction) value (Fig. 2a). The higher the soil pH, the more species can be found. This is the best relationship between alpha diversity and any single factor examined. There is also a positive correlation between species richness and mean Ellenberg L (light) value, although the explained variance is much lower (Fig. 2b). However, the best explanation is obtained when species richness is related with the product of mean R and mean L (Fig. 3). There is no significant linear correlation between species richness and altitude or between species richness and any other Ellenberg value.

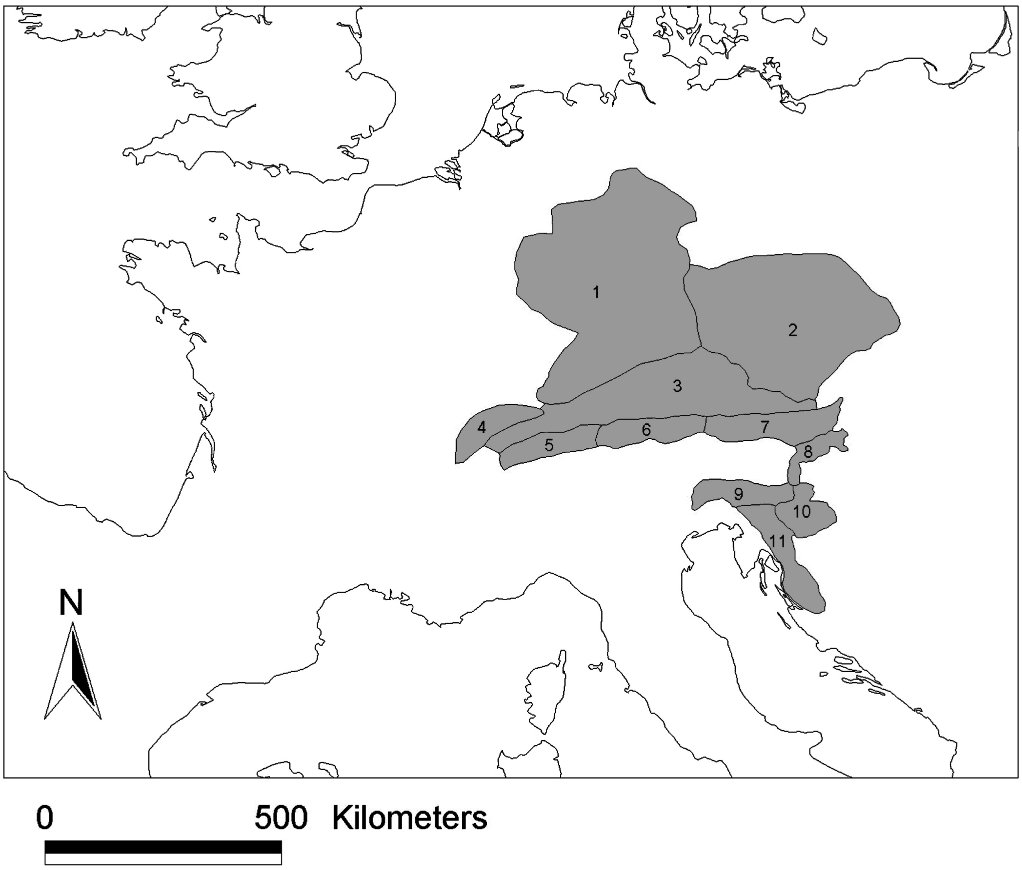


Fig. 1 – Biogeographical regions of Central European beech forests which were used for calculation of beta diversity

On the community level, the results are very similar, but the explained variance is higher. Soil reaction alone explains already almost two thirds of the variance in average species richness (Fig. 4). If we add light value in the same manner as above, r^2 increases but slightly (from 0.6 to 0.67).

Changes in local species richness along geographical gradients are difficult to detect, because all other factors should be hold constant. When mean alpha diversity of ecologically analogous but geographically vicariant associations is compared, no obvious trend can be found (Tab. 1).

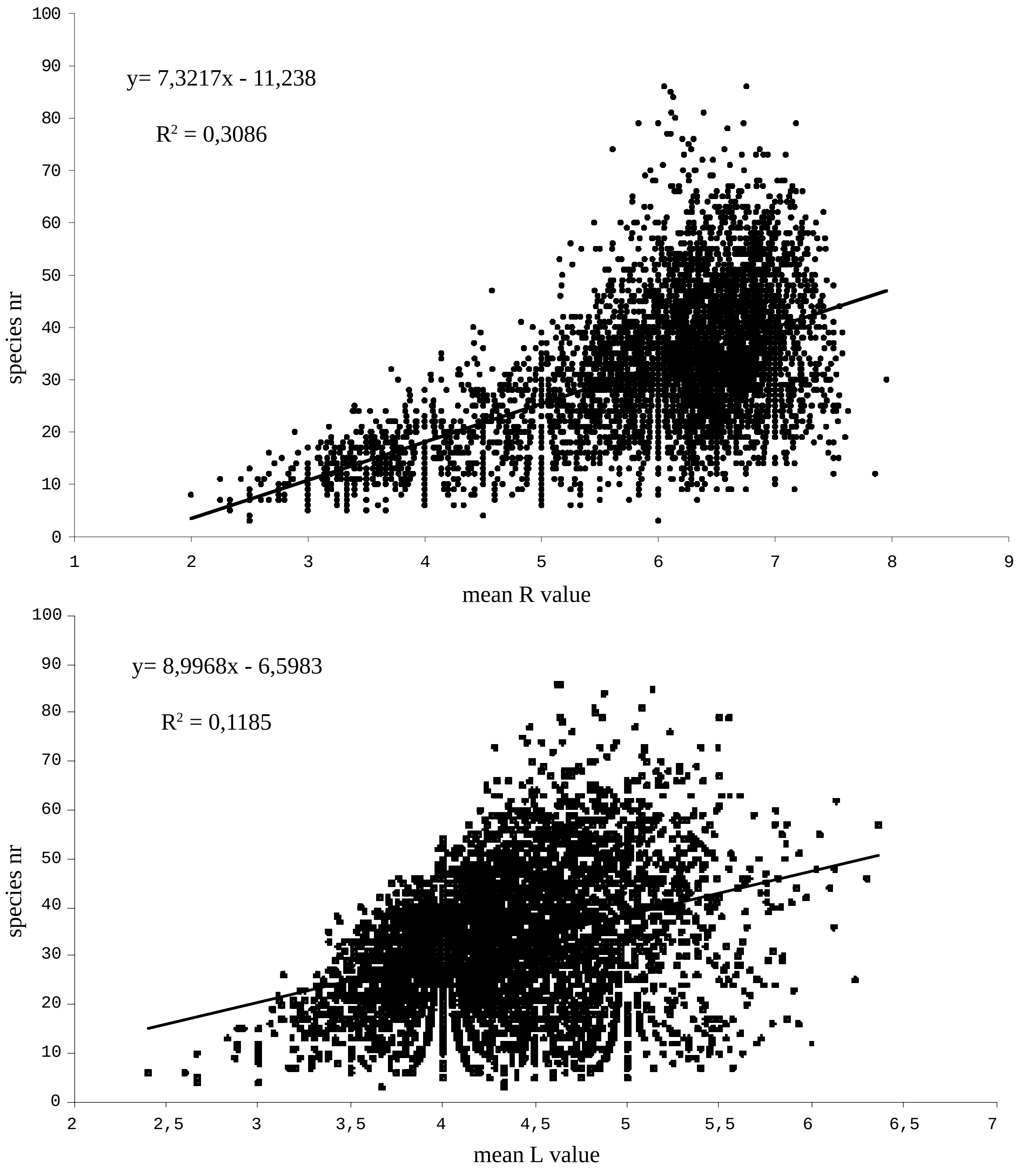


Fig. 2 – Relationship between species number and (a) mean Ellenberg R value and (b) mean Ellenberg L value. Dots are single relevés

Tab. 1 – Scientific name, region and mean number of vascular plant species per relevé in seven vicariant beech communities on loamy soils (nomenclature following Willner, 2002)

ASSOCIATION	REGION	MEAN SPECIES NR.
Hordelymo-Fagetum	W Germany	27,76
Hordelymo-Fagetum	Bohemian Massif	33,83
Lonicero alpigenae-Fagetum	NW Alps	30,64
Cardamino trifoliae-Fagetum	E Alps	29,34
Dentario pentaphylli-Fagetum	S Alps	33,35
Isopyro-Fagetum	E Slovenia	29,03
Omphalodo-Fagetum	Dinaric Mountains	35,11

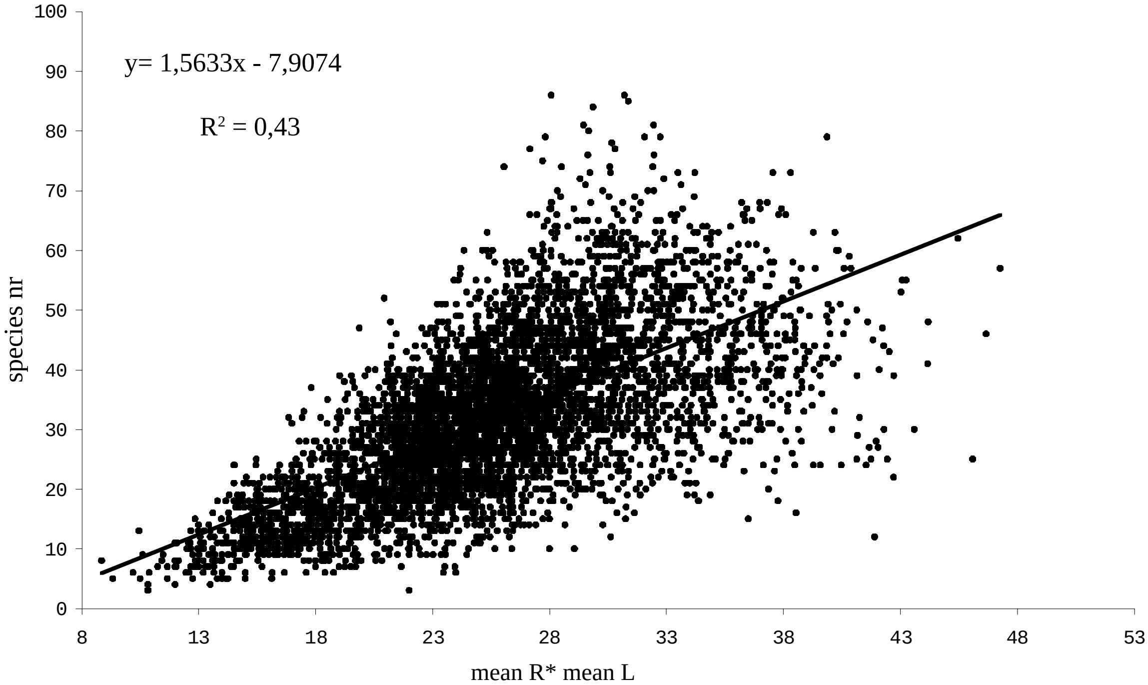


Fig. 3 – Relationship between species number and the product of mean Ellenberg R value and mean Ellenberg L value. Dots are single relevés

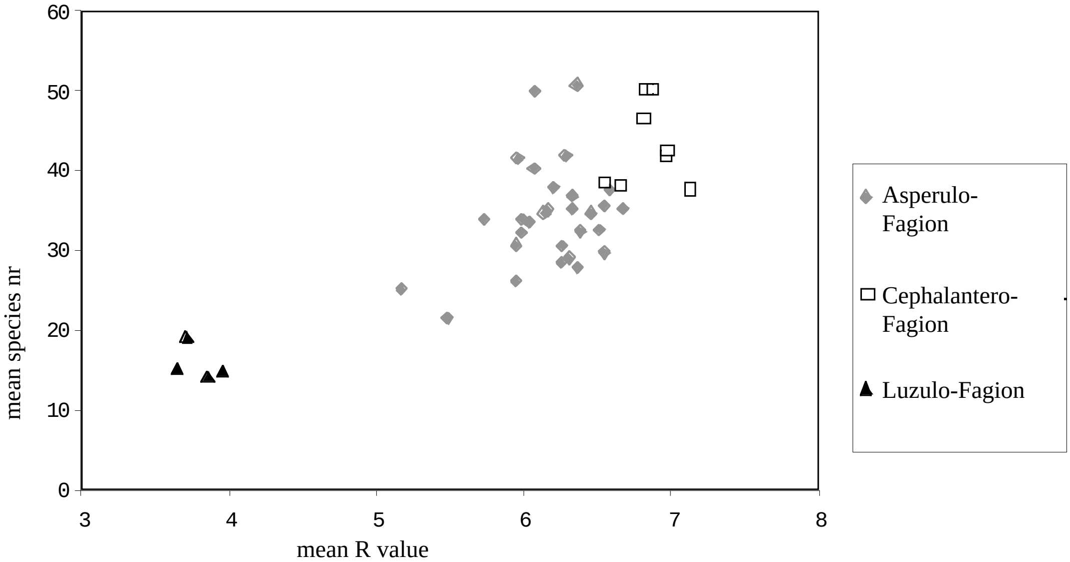
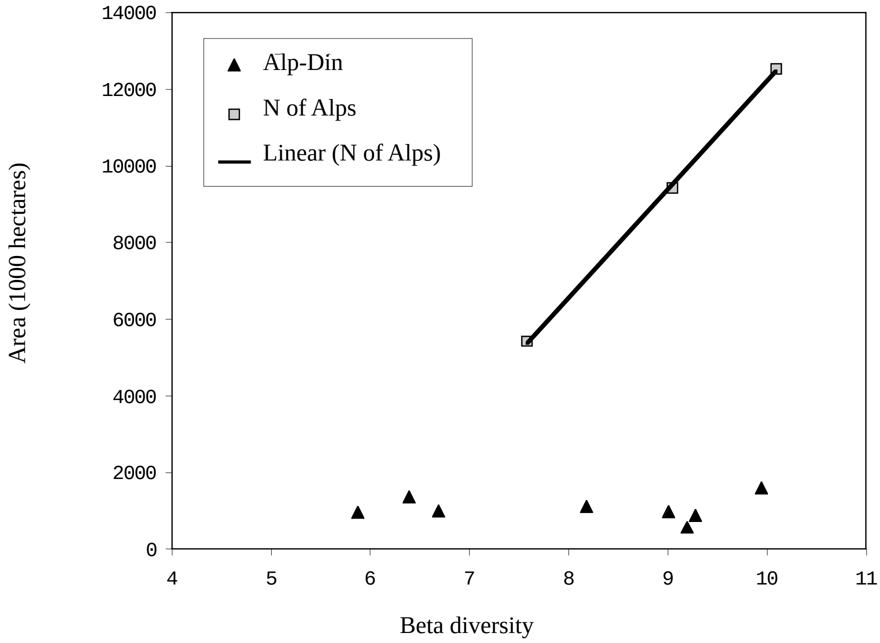


Fig. 4 – Relationship between local species richness and soil reaction on the community level: the mean species number per relevé is plotted against the mean of mean Ellenberg R values



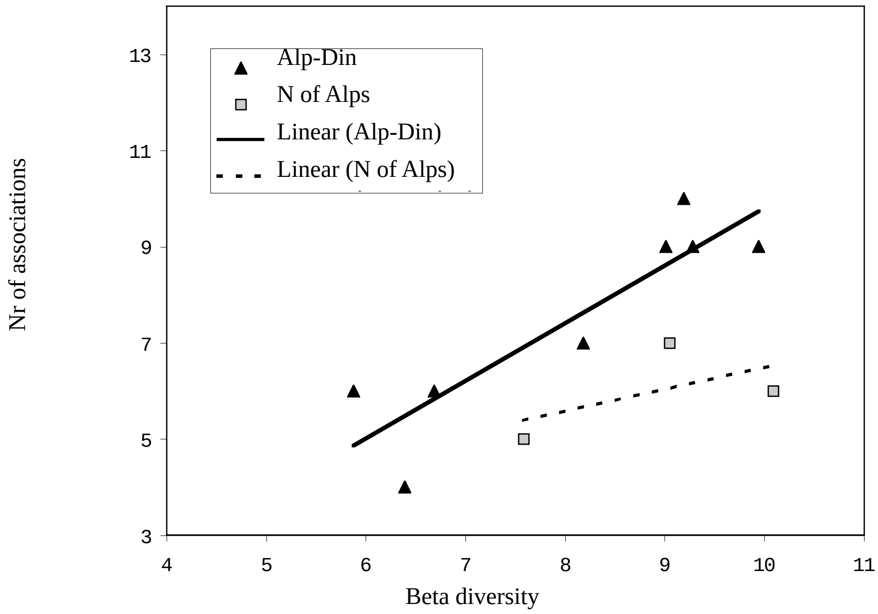


Fig. 5 – Relationship between beta diversity of beech forests and (a) region area and (b) number of beech forest associations within the region

2. Beta diversity

Beta diversity of the 11 regions varies from 5.88 in Swiss Jura to 10.09 in German central mountain ranges. The three largest regions, which are situated north of the Alps (northern foreland of the Alps, German „Mittelgebirge“ and Bohemian massif), show an almost perfect linear relationship between region area and beta diversity (Fig. 5a). For the 8 regions of the Alpin-dinaric range no relationship with area can be found, but with the number of beech forest associations occuring in the respective region (Fig. 5b).

Discussion

Many studies have found positive correlations between species richness and soil pH. Explanations go in two main directions: 1. species richness increases with pH because high Ca-concentration means also higher productivity (Pausas & Austin, 2001; Dupré *et al.*, 2002), 2. the pool of species that is suited for high pH soil is larger than the pool of species that is suited for low pH soil due to evolutionary history (Pärtel, 2002).

The first explanation is valid only for a part of the gradient. On dry carbonatic soils pH is high but productivity is low, nevertheless the beech forests on these sites (*Cephalanthero-Fagion, Adenostylo glabrae-Fagetum*) have the highest species numbers. One reason might be that on dry soils the tree canopy is less closed and therefore the understorey gets more light. But we think, there is also evidence for the species pool concept: The European beech forests have been subjected to a couple of bottle neck situations during the Pleistocene glacial periods. In the refugia on the Balcan peninsular carbonatic bedrocks are predominant (Horvat *et al*., 1974), and it is doubtful if any acidophilous beech forest (*Luzulo-Fagion*) existed there. Thus, it is not surprising to find hardly any species with an ecological optimum in this alliance. On the other hand, the flora of Central Europe is characterized by an unusually large portion of calciphilous species (Ewald, in press). Although most of these species have their optima in grasslands or pioneer vegetation, they contribute also to the species pool of limestone forests.

Beta diversity increases with area and the number of associations therein. The latter, reflecting environmental heterogeneity, is obviously the predominant factor. Only in phytosociologically homogeneous data sets, like beech forests in Central Europe north of the Alps, the species-area relationship can easily be detected (cf. Rosenzweig, 1995).

References

Dierschke H., 1998. Syntaxonomical survey of European Beech forests: some general conclusions. Annali di Bot. 55 (1997): 17-26.

Dupré C., 2000. How to determine a regional species pool: a study in two Swedish regions. Oikos 89: 128-136.

Dupré C., Wessberg C. & Diekmann M., 2002. Species richness in deciduous forests: Effects of species pools and environmental variables. J. Veg. Sci. 13: 505-516.

Ellenberg H., 1996. Vegetation Mitteleuropas mit den Alpen in ökologischer, dynamischer und historischer Sicht. 5. Aufl. Ulmer, Stuttgart.

Ellenberg H., Weber H. E., Düll R., Wirth V., Werner W. & Paulißen D., 1991. Zeigerwerte von Pflanzen in Mitteleuropa. Scripta Geobot. 18: 1-248

Ewald J., in press. The calcareous riddle: Why are there so many calciphilous species in the Central European flora? Folia Geobotanica.

Hennekens S. M. & Schaminée J. H. J., 2001. TURBOVEG, a comprehensive data base management system for vegetation data. J. Veg. Sci. 12: 589-591.

Horvat I., Glavac V. & Ellenberg H., 1974. Vegetation Südosteuropas. Geobotanica selecta 4, Gustav Fischer Verlag, Stuttgart.

Lausi D. & Pignatti S., 1973. Die Phänologie der europäischen Buchenwälder auf pflanzensoziologischer Grundlage. Phytocoenologia 1 (1): 1-63.

Moor M., 1952. Die Fagion-Gesellschaften im Schweizer Jura. Beitr. Geobot. Landesaufn. Schweiz 31: 1-201.

Pärtel M., 2002. Local plant diversity patterns and evolutionary history at the regional scale. Ecology 83: 2361-2366.

Pausas J.G. & Austin M.P., 2001. Patterns of plant species richness in relation to different environments: An appraisal. J. Veg. Sci. 12: 153-166.

Rivas-Martínez S., Báscones J.C., Díaz T.E., González F.F. & Loidi J., 1991. Sintaxonomía de los hayedos del suroccidente de Europa. Itinera Geobot. 5: 457-480.

Rosenzweig M.L., 1995. Species diversity in space and time. Cambridge University Press, Cambridge, UK.

Soó R., 1964. Die regionalen Fagion-Verbände und Gesellschaften Südosteuropas. Studia Biol. Hung. 1, Akadémiai Kiadó, Budapest.

Török K., Podani J. & Borhidi A., 1989. Numerical revision of the Fagion illyricum alliance. Vegetatio 81: 169-180.

Tüxen R., 1955. Das System der nordwestdeutschen Pflanzengesellschaften. Mitt. Florist.-Soz. Arbeitsgem. N. F. 5: 155-176.

Tüxen R., 1960. Zur Systematik der west- und mitteleuropäischen Buchenwälder. Bull. Inst. Agronom. Stat. Rech. Gembloux, Hors série 2: 45-58.

Vellend M., 2001. Do commonly used indices of ß-diversity measure species turnover? J. Veg. Sci. 12: 545-552.

Whittaker R.H., 1972. Evolution and measurement of species diversity. Taxon 21: 213-251.

Willner W., 2001. Neue Erkenntnisse zur Synsystematik der Buchenwälder. Linzer biol. Beitr. 33: 527-560.

Willner W., 2002. Syntaxonomische Revision der südmitteleuropäischen Buchenwälder. Phytocoenologia 32: 337-453.