BIODIVERSITY OF THE HERCYNIAN MOUNTAINS OF CENTRAL EUROPE

JAN JENÍK

Faculty of Science, Charles University, Benátská 2, CZ-12801 Praha 2, Czech Republic

SUMMARY.- The vegetation of temperate Central Europe north of the Alps is mainly of low diversity broadleaf and conifer forest. The occurrence of three azonal habitat types: mires with their numerous microhabitats, the georelief of the karst and its deeply-cut river valleys, and ecological islands with a distinct vegetation near the treeline of the middle-mountains causes local areas of high diversity. These high species diversity spots are the result of an interplay between physical, biotic and historical factors. A model of an anemo-orographic system with its underlying factors is described to explain the high plant and animal diversity in the corries (glacial cirques) of the Hercynian mountains.

RÉSUMÉ.-La végétation de l'Europe Centrale temperée au nord des Alpes nous montre surtout des forêts à de feuillues et de connifères à faible diversité. Cependant, la présence de trois types d'habitats azonaux peut produire une haute diversité au niveau local: zones humides avec leur nombreux microhabitats, reliefs karstiques et leur profonds défilés fluviaux, et enfin des îles écologiques avec une végétation particulière situées près de la limite supérieure des arbres (treeline). Ces secteurs riches en espèces peuvent s'expliquer par l'interaction des facteurs physiques, biotiques et historiques. Dans ce domaine nous proposons un système anémo-orographique avec ses facteurs inféodés qui pourrait expliquer la haute diversité animale et végétale dans les cirques glaciaires des montagnes hercyniennes.

RESUMEN.-Al N de los Alpes, la vegetación de la Europa Central templada está constituida fundamentalmente por bosques de baja diversidad, bien sean de hoja ancha o de coníferas. No obstante, la presencia de tres tipos de hábitats azonales aumenta la diversidad: charcos con sus numerosos microhábitats, el relieve kárstico con sus desfiladeros y las islas ecológicas con vegetación diversa cerca del límite superior del bosque en las montañas medias. Estas áreas de gran diversidad específica son el resultado de la interacción de factores físicos, bióticos e históricos. Para explicar la elevada diversidad vegetal y animal de los circos glaciares de las montañas Hercínicas proponemos un modelo anemo-orográfico con sus factores subordinados.

Key words: Hercynian mountains, species diversity, anemo-orographic system

1. Introduction

Biodiversity is manifested at all levels of the biological hierarchy: from genes to species, communities and ecosystems (SOLBRIG, 1991; GROOMBRIDGE, 1992). Whilst studies of diversity at the gene level require experimental procedures which can only be applied to a limited number of model organisms, at the species and community levels diversity is studied using observational-comparative methods (MAYR, 1982). The latter enables a satisfactory evaluation of regional and global diversity, and the management and conservation of biotic resources. An assessment of biological diversity in practice is therefore often reduced to observations and comparisons of species presence or absence. Identification of the centres of biodiversity (WWF & IUCN, 1994) and various hotspots of species biodiversity have received much attention lately. Most mountain regions, owing to their physical and biotic diversity, belong to the species-rich centres and hotspots.

The priorities identified at the ESF Workshop at Monte Bondone in 1995 for European mountain biodiversity research were: (1) a synthesis of current data with regard to the biodiversity in mountain habitats in Europe, (2) an identification of gaps in scientific knowledge and (3) the initiation of co-operative research programmes.

The availability of data for synthesis is a result of centuries long natural history research in Europe. A cursory look at the data would reveal that both plants and animals showed a contrast between lowlands and uplands with regard to the number of species and variety of community types per unit area and how impacts of present-day immigrations and historical factors affected the speciation, immigration and survival of viable populations. In a wider context, the importance of mountain diversity for human society and in general, its influence on the development of natural history can be shown (JENÍK, 1996).

In Europe, the highest biological diversity is associated with the Pyrenees, Alps and Caucasus; i.e. the high-mountain systems situated at the transition zones between the temperate and submediterranean zones (MEUSEL *et al.*, 1965). The Alps have a particularly long history of scientific exploration in western Europe (OZENDA, 1988) with an active natural history research predating the Linnaeus period. The geomorphological and plant diversity of the Alps with their c. 350 endemic species of vascular plants (PAWLOWSKI, 1970) has much attracted botanists and plant sociology and the syntaxonomy

84

of communities of the Zürich-Montpellier School were born in these mountains (BRAUN-BLANQUET, 1951).

In the scientific shadow of the Alps remain the so called middle-mountains of Central Europe. These lower ranges (see map on the inner side of the cover in OZENDA, 1994) belong geologically to a much older Hercynian (Variscan) system than the Alps. They stretch from the Massif Central in France to the westernmost outliers of the Western Carpathians in Poland and Czechia. They rise only marginally above the altitude of natural tree growth today and provide excellent examples of refuges of arctic-alpine populations of the present Post-glacial era. They offer, in the absence of strong human impacts, a system to study the interaction between physical and biotic factors. These middle-mountains have also played an important role in the development of universities and other learned institutions of Germany, France, Austria, Czechia and Poland.

2. Brief historical notes

The exploration of species diversity in the Central European middle-mountains began by the activities of herbalists L. Camerarius and P. Jesenius in the Ore Mountains at the end of the 16th century (HEYNERT, 1964). C. SCHWENCKFELDT first published enumerations of biota occurring in the Sudetes in 1600. After the 30-year war, in the second half of the 18th century floristic research became active again (e.g.: MATTUSCHKA, 1776-1777). A unique scientific expedition of the Royal Bohemian Society into the Giant Mountains in 1786 (JIRASEK et al., 1791) returned with long lists of plants from species-rich sites. It also discovered new species for science, e.g. *Poa laxa*, a species later recognised as a typical component of the distant North American mountains (JENÍK, 1986). Numerous flora works covered the northern (Silesian) side of the Sudetes (for a list see JENÍK, 1961).

Comparative studies in the 19th century highlighted essential differences in species composition between lowlands and uplands and described the distribution of various formations (today's biomes) in certain mountain ranges. Botanical research had always been more advanced than zoology, mainly owing to the efforts of physicians, herbalists and apothecaries searching for medicinal herbs. Early exploration of wildlife was made by hunters and naturalists, who described game and predatory mammals, birds and reptiles, but modern zoological research can only be dated back to the beginning of the 19th century. The study of the invertebrate fauna —concentrating on some groups of insects— started much later (KIESENWETTER, 1847) and slowly, the difference in

85

biodiversity between high-mountains and particular middle-mountain ranges became more apparent.

During the 20th century, a number of taxonomic summaries reconfirmed the high species-richness in some of the Hercynian ranges, particularly in those which rise above the timberline. A summary of their characteristics is given in the Appendix. Progress in animal and plant taxonomy and the availability of floristic data with a good coverage over the whole of Central Europe enabled comparative studies and the compilation of plant distribution maps (MEUSEL *et al.*, 1965; 1978). Other developments included small-scale vegetation mapping (MIKYSKA, 1968), description of communities (by using phytosociological relevés) and a classification of syntaxonomic units (OBERDORFER, 1977-1992; MORAVEC *et al.*, 1983), and comparative ecological evaluations of mountain ecosystems, based on the latter (JENÍK, 1961).

Presenting an overview of the biodiversity is fraught with difficulty arising from Central Europe's centuries long political fragmentation. Administrative boundaries dividing ridges into sovereign territories have constrained field studies, separated collections of specimens and forced unnatural boundaries in mapping. For example, individual geographic (landscape) units were often divided and each side's biotic communities were described in local publications at opposite sides of borders, sometimes in different languages with the information seldom crossing the border. Research has been fraught with semantic inconsistencies, and topographic names, nomenclature of plants and animals, and mapping units of vegetation have varied much. In addition, about half the 20th century has been affected by militarisation, the two World Wars and later by the erection of the Iron Curtain.

Biogeographical research suffered from the absence of unified toponyms and relevant topographical maps. The Central European middle-mountains still lack a consensus on oronyms (JENÍK, 1998). For example, the prominent range situated along the border dividing Austria, Germany and Czechia is called Böhmerwald in German speaking Austria, but Hinterer Bayerischer Wald in Germany, and Sumava in Czechia. The usage of these oronyms often overlaps and much confusion is caused in the relevant data banks, regional literature and when an English equivalent is required (a suitable one for the above may be Bohemian Forest). Another lower range to the NW along the same national boundary is called Oberpfälzerwald on the German side, yet the Czech side bears the name Cesky les, a homonymous equivalent of the Austrian name Böhmerwald. It is worth noting that in the maps of Claudius Ptolemaios the same area was called Silva Gabreta, a forgotten unifying name only recently reintroduced for a new natural history book series.

86

Owing to the above, information about the diversity of species, communities and ecosystems, is scattered in the scientific literature of the four neighbouring countries: Austria, Czechia, Germany and Poland. Only a few large-scale synthetic works, such as those of HEGI *et al.* (1966 *et seq.*), TUTIN *et al.* (1964-1983), FIRBAS (1949; 1952) and ELLENBERG (1996) provide integrated information over the entire area. Two recent publications by UNESCO and IUCN (PRICE, 1995; IUCN, 1995) have also given a transboundary treatment of the Hercynian middle-mountains.

3. Species diversity in Central Europe

There are about 80000 known species of all organism groups (Table 1) in the Czech part of Central Europe (e.g. VAVROUSEK & MOLDAN, 1989; PLESNÍK, 1999). This is only about 5 % of the world total number of species described so far (GROOMBRIDGE, 1992). In temperate Europe, the most species rich groups (fungi and invertebrates) are associated with old growth forests and can have a high richness within a single community, i. e. high alpha diversity (sensu WHITTAKER, 1970). However, old growth forest stands are rare and the majority of the remaining woodlands have been transformed into monodominant stands with few tracheophyte species. Azonal non-forest ecosystems, whose species composition substantially varies along environmental gradients and over patchy soils (beta diversity *sensu* Whittaker, 1970), also have a high biodiversity. The diversity of autotrophic tracheophytes may be used as an estimator of overall biodiversity and the non-forest forbs and graminoids with their numerous associates can provide a proxy in estimating species-richness in the mountains.

Closed woodlands covered > 90 % of the landscape north of the Alps (domaine Centre-Européeen, *sensu* OZENDA, 1994) by the end of the late-Holocene. Three forest formations dominated: (1) mixed broad-leaved

Plants		Animals	
Tracheophytes	2000	Mammals	70
Bryophytes	1000	Birds	170
Algae (incl. blue-greens)	6000	Reptiles	10
Lichens	1000	Fishes	50
Fungi	30000	Amphibians	20
		Invertebrates	40000
Total	40000	Total	40300

Table 1. Estimated numbers of indigenous species in Czechia. Data are from various sources.

87

woodlands in the lowland and colline belt, (2) closed beech and fir forests in the lower montane belt, and (3) monodominant spruce taiga in the upper montane belt. The forest formations comprised about 35 tree species, 300 vascular herbs, and correspondingly low numbers of consumers at the lower trophic levels. Actual and potential composition of these forests is described in detail in the phytosociological (e.g., OBERDORFER, 1977-1992; ZLATNÍK, 1959; ELLENBERG, 1996; MUCINA et al., 1993; MORAVEC et al., 1983) and palynological literature (FIRBAS, 1949; 1952; HUNTLEY & BIRKS, 1983). The Pleistocene glacial periods inhibited migration and the flora and fauna became relatively impoverished in Central Europe in contrast to the more species-rich Eastern Forests of North America.

The floodplain woodlands and colline oak-hornbeam woods at lower and warmer altitudes have been reported to contain 50 vascular plant species per relevé (about 400 m² in size), however, most of the zonal vegetation in the foothills of Hercynian mountains consists of oligotrophic oak forests, beech forests and spruce taiga, with < 20 vascular plant species per relevé. There is a high beta diversity in azonal woodlands along deeply-cut river valleys and on limestone (karst). On hill sides, the north facing slopes tend to host psychrophilous beech (*Fagus sylvatica*) communities, whilst the warm southern slopes on limestone host durmast-oak (*Quercus pubescens*) woods where plant and animal species of a diverse geographical origin occur together.

The biodiversity of the Central European landscape is higher in patchy and treeless azonal habitats, where plants and animals do not face the adversity of closed-canopy shade and root competition by trees is reduced.

The closed woodlands of Central Europe become patchy naturally in extreme environments such as the dry and hot south-facing slopes along the river valleys, in the karst areas and on exposed cliffs of volcanic hills. These xero-thermic habitats are found along the large rivers, such as the Berounka, Danube, Sázava, Saale, Vltava and Weser, on limestone, e.g.: Swabian Jura, Bohemian Karst, Moravian Karst, in the basaltic Doupov Hills and on the neovolcanic cones of NW Bohemia (Ceské Stredohorí) in the rain shadow of the Ore Mountains. The treeless patches are dominated by *Festuco-Brometea* grasslands, containing a mixture of relics and forerunner species, including some continental elements left from the Late Glacial when this biome was widespread in Central Europe.

Waterlogging, particularly in depressions and areas of permanent springs and mires produces a variety of wetlands which may occur locally in forests. There is a variety of life forms present in wetlands which interact with the physical environment and influence microhydrology and microtopoclimate, and thus create favourable conditions for enhanced beta diversity. Soligenous mires of the *Scheuchzerio-Caricetea fuscae* class (fens) and ombrogenous mires

of the *Oxycocco-Sphagnetea* class (bogs) make remarkable contribution to biodiversity in Central Europe, particularly with regard to bryophytes and invertebrates. For example, on the Cervené Blato bog in South Bohemia, SPITZER & JAROS (1993) identified 570 species of butterflies over an area of less than 3 km². The drying out of these wetlands creates favourable conditions for tree growth, and thus a high reduction in beta diversity. The adverse effects of waterlogging on trees may combine with effects of low temperature in the montane and subalpine belts of the Hercynian mountains. This is the case for mires and flushes in the High Sudetes (particularly in the Giant Mts.), where numerous arctic-alpine plant and animal species have survived the pressures of forest succession in the Holocene and contribute to today's biodiversity.

Cold wind-exposed habitats, particularly at high altitude with a short growing season can prevent the successful establishment of trees by delaying the hardening of the xylem tissues. Common in the neighbouring Alps and Western Carpathians, this treeless bald or alpine tundra is a rarity in the Hercynian middle-mountains. They mostly occur as small treeless islands on top of some ridges and peaks, in snowbeds and corries. Some of them can be viewed merely as azonal islands within the montane belt: e.g. Plesné Lake, Cerné Lake, Certovo Lake and Gross Arber-See corries in Bohemian Forest, the Zechengrund in the Ore Mts., or the summit bald of the Harz. However, the larger treeless areas on top of the Vosges, Black Forest, Giant Mts., Snow Mts. and Jeseník Mts. form a true altitudinal belt, sometimes referred to as subalpine or even alpine. Their diversity is best reflected by the number of habitats and communities. For example, in the three ranges of the High Sudetes, about 70 plant communities have been distinguished in 11 phytosociological classes (habitats): *Asplenietea trichomanis* (crevices), *Thlaspietea rotundifolii* (scree), *Juncetea trifidi* (summit tundra), *Salicetea herbaceae* (snow beds), *Mulgedio-Aconitetea* (tall-herb communities), *Montio-Cardaminetea* (flushes), *Scheuchzerio-Caricetea fuscae* (fens), *Oxycocco-Sphagnetea* (bogs), *Nardo-Callunetea* (mat-grass and heath communities), *Betulo carpaticae-Alnetea virids* (subalpine scrub), and *Vaccinio-Piceetea* (krummholz). The species richness of these habitats is well documented in floristic and faunistic works; SOUREK (1969) enumerated 1150 vascular species in a single range of the Giant Mountains, which equals half the total estimated for Czechia (Table 1).

4. The human vegetation history of the Hercynian mountains

Human-induced fragmentation of the continuous forest cover in the warm lowlands of Central Europe began in the Neolithic, about 5,000 B.P. resulting

89

in today's mosaic of natural, semi-natural and cultivated forests, pastures, meadows, arable land and patches of treeless clearings (for a summary see ELLENBERG, 1996). Forest clearing and the expansion of agriculture have progressively moved into the montane belt and to the ridges of the Hercynian mountains. Pasturing at the summits of the Vosges has been mentioned as early as the 9th century (SCHMITT, 1963), whilst the uplands of the High Sudetes were not exploited until about the 16th century (LOKVENC, 1978). Using the evidence of archives and old charts, JENÍK & HAMPEL (1992) pointed out some differences in the exploitation of summit tundra on various estates in the Jeseník Mts., where the 16th century, too, appeared to be the beginning of pasturing. The application of artificial forest regeneration, cultivation of monodominant stands of Norway spruce (*Picea abies* (L.) Karsten) and Scots pine (*Pinus sylvestris*), and the introduction of exotic tree species such as *Pseudotsuga menziesii, Pinus strobus, Robinia pseudoacacia* for example have caused large changes in the foothills of Hercynian mountains over the past 200-300 years. The intensive management has not caused forest loss in the montane belt in most of the Hercynian ranges, but species diversity has declined mainly through the expansion of coniferous stands.

Altitudinal zonation in the Hercynian mountains differs in the west from that in the east. In the Vosges and in the Black Forest, European beech (*Fagus sylvatica*) and silver fir (*Abies alba*) had primarily dominated much of uppermost montane belt up to the tree-limit, however following tree cutting, burning and air pollution it has been transformed into monodominant plantations. In contrast, in the Bohemian Forest, the Ore Mts. and Sudetes, beech forests seldom reached an altitude of > 1000 m and coniferous taiga with Norway spruce predominated up to about 1300 m. However, forest clearing and logging, followed by either natural regeneration or plantation in the last 300 years have resulted in monodominant spruce stands over most of these mountains today. The loss of broadleaf stands caused an impoverishment of soils and reduced both below- and aboveground species richness (preliminary data on fungi and bacteria are available at Charles University). Windthrows followed by bark beetle outbreaks were another factor in changing forest composition with prominent effects on biodiversity.

Norway spruce, European beech and silver fir form a krummholz in the transition towards the treeline in many Hercynian ranges where there is no naturally occurring dwarf pine (*Pinus mugo*). Monodominant stands of *P. mugo* form a krummholz only in the Giant Mountains with small patches also in the Bohemian Forest and Iser Mts. Remarkably, the Jeseník Mts. were never colonised by dwarf pine, though it is widespread to the west, in the Giant Mts. and to the east, in Babia Góra (the westernmost Carpathian range with

90

Pinus mugo). The are no altitudinal limits to tree growth in the Ore Mts. and their species-rich Zechengrund is probably only a small island in the snow-rich leeward side (see below).

The position of the treeline and the presence or absence of the competitive dwarf pine have played an important role in the development of biodiversity in the Hercynian mountains (JENÍK & LOKVENC, 1962). Not only altitude, but general relief and topoclimate (irradiation, wind action, duration and distribution of snow, snow creep and avalanches) have diversified the pattern of the alpine-like belt with its wide range of plant and animal species from either the Alps and the boreal/subarctic region (SOUKUPOVÁ *et al.*, 1995). In the mid-Holocene period, marked by the expansion of Central European woods above their current altitudinal limits, only the highest summits, steep flanks and corries remained treeless. Treelessness has been a prerequisite for the development and maintenance of fragile plant populations and communities of alpine character. In a similar context, CARBIENER (1966) prefers to write about subalpine vegetation in the Vosges, and BOGENRIEDER *et al.* (1982) have coined the term subalpine island for the highest area of Feldberg in Black Forest.

The long-term maintenance of the local alpine-like areas without relict forest species and their continued treelessnes remain a puzzle for the palaeo-ecologist. Palynological data have suggested that during the climatic optimum, about 5,000 years ago, forest vitality in Central Europe increased and the alpine timberline ascended 200 to 400 m above its present-day position (FIRBAS, 1952; de VALK, 1981; HÜTTEMANN & BORTESCHLÄGER, 1987). This means that all Hercynian ranges would have been covered by forests and their heliophilous arctic-alpine populations should have become extinct. Also, there would have been no place for the microevolutionary processes which resulted in the differentiation of some non-forest plant taxa in the Holocene period (for details see JENÍK, 1983).

5. The causes of the distribution pattern of biodiversity

As a whole, the Hercynian mountain ranges lack high altitude, the diversity of rocks, large areas of limestone, and complexity of relief, they only exceptionally surpass the natural tree-limit, and their acid, nutrient-poor parent rocks seldom create a fertile substratum for eutrophic ecosystems. This is reflected in the species-poor zonal vegetation with a small number of tree species and few competitive ferns and grasses, ericaceous shrubs and a modest cryptogamic flora. The fauna is similarly species poor. However, there are some localised centres of high biodiversity in certain localities which harbour enhanced numbers of

species, many infraspecific taxa, and curious hybrids between parents derived from ecologically distant habitats.

An example of localities which repeatedly appear in floristic and faunistic lists is the three ranges of the High Sudetes. The corries (or cirques) of Kotelné Jámy, Labské Jámy, Sniezne Kotly, Kotly of Great and Little Staw in the Giant Mts, or Velká Kotlina corrie in the Jeseník Mts. have several hundreds of vascular plant species, whilst the species-poor communities on neighbouring slopes are composed of only a dozen vascular species (JENÍK et al., 1983a; b). The above corries also have a high number of mosses, hepatics, molluscs and insects. Environmental and phytosociological analyses (JENÍK 1961; JENÍK et al., 1980) have identified some common features in the topographical position of these species-rich sites. They are mainly (i) on east-facing slopes at the eastern margin of large summit plateaux or on the eastern side of prominent saddles, (ii) across the summit plateaux on the adverse side of a prominent funnel-shaped valley, (iii) in the hollows of corries or snowbeds, (iv) situated under prominent cornices, covered regularly by deep snow drifts and affected by frequent avalanche action (JENÍK, 1990).

The driving force behind this special biodiversity pattern is the prevailing westerly winds, a feature well documented by summit meteorological stations on Snezka Peak and Szrenica (MIGALA et al., 1995). The westerlies are streamlined and accelerated in funnel shaped windward valleys, and sweep across the corresponding summit plateau or saddle areas. This wind action is documented by flag-trees, unilaterally eroded turf and ablation forms in the snow surface in winter. Over the sheltered lee slopes, the laminar air flow changes to turbulent eddies, a process clearly detectable by the movement of clouds, airborne snow crystals and by the deposition of drift snow (STURSA et al., 1973). In summer, deposition of other airborn particles, such as soil, litter and seeds has also been documented. Similar topographical configuration and related air currents appear in the summit areas of all Sudetic ranges and there are 10 prominent areas of enhanced species diversity related to them. JENÍK (1961) has described a model called anemo-orographic system, which consists of three interdependent components: (1) windward funnel-shaped valley, (2) acceleration summit zone, and (3) leeward turbulence zone. The validity of this model has later been confirmed in the Vosges (CARBIENER, 1966; 1969; de VALK, 1981), in the Bohemian Forest (SOFRON & STEPAN, 1971) and in the Feldberg region in Black Forest (JENÍK, unpublished). It is the leeward turbulence zone that coincides with the centres of high biodiversity. Current weathering and locally outcropping base-rich rocks, which are kept bare by the secular action of avalanches and water erosion improve nutrient availability at these sites. In the summer, dissected turf and exposed soil are invaded by seed and spores transported

92

sometimes from afar, thus further increasing the richness of flora and fauna. Treelessness has been maintained by avalanches, which even occurred during the climatic optimum of the mid-Holocene due to snow swept from the large summit plateaux.

Despite the avalanches and erosion by melt water the leeward habitats of the anemo-orographic systems have maintained a stable microhabitat diversity and, in the course of millenia, accumulated a genetically diverse assemblage from rather different mountain and sometimes lowland ecosystems. Relicts from the Late Glacial and early-Holocene grow together with sub-thermophilous species of the mid-Holocene. These sites function as micro-evolutionary workshops where gene recombination and hybridization produce new infraspecific taxa or microspecies (JENÍK, 1983). The corries of the Sudetes, for example, have been the speciation centres for the apomictic *Hieracium* genus (20 endemic species). The Velká Kotlina in the Jeseník Mts., is in the lee of a double anemo-orographic system, and has accumulated about 500 vascular plant species (some of them have recently become extinct). It also has a rich vertebrate and invertebrate fauna, which makes this place the most species rich locality in the whole of the Hercynian mountains of Central Europe (JENÍK *et al.*, 1983a; b). Similarly, a prominent anemo-orographic system makes possible the presence of biogeographically outstanding species in the back wall of the corrie near Great Arber Lake in the Bohemian Forest (JENÍK *et al.*, 1998).

References

BARTSCH, J. & BARTSCH M. (1940). *Vegetationskunde des Schwarzwaldes.* Verlag G. Fischer, 229 pp., Jena.

BOGENRIEDER, A. *et al.* (1982). *Der Feldberg im Schwarzwald: Subalpine Insel im Mittelgebirge.* Landesanst. Umweltschutz Baden-Würtenberg, 526 pp., Karlsruhe.

BRAUN-BLANQUET, J. (1951). *Pflanzensoziologie,* 2nd ed. Springer-Verlag, 631 pp., Wien.

CARBIENER, R. (1963). Un remarquable groupement végétal des Hautes Vosges: La Calamagrostidiaie subalpine. *C.R. Acad. Sciences, Paris,* 256: 4967-4969.

CARBIENER, R. (1966). *La végétation des Hautes Vosges dans ses rapports avec les climats locaux, les sols et la géomorphologie - Comparaisons avec la végétation subalpine des moyennes montagnes d'Europe occidentale et centrale.* Thèse, Centre d'Orsay, Paris.

CARBIENER, R. (1969). Subalpine primäre Hochgrasprärien im Herzynischen Gebirgsraum Europas, mit besonderer Berücksichtung der Vogesen, und der Massif Central. *Mitteilungen Flor. Soz. Arbeitsgem., N.F. Heft*, 14: 322-345.

ELLENBERG, H. (1996). *Vegetation Mitteleuropas mit den Alpen, 5th ed.* Eugen Ulmer, 1095 pp., Stuttgart.

FIRBAS, F. (1949). *Spät- und nacheiszeitliche Waldgeschichte Mitteleuropas nördlich der Alpen.* Volume 1. G. Fischer Verlag, 480 pp., Jena.

FIRBAS, F. (1952). *Spät- und nacheiszeitliche Waldgeschichte Mitteleuropas nördlich der Alpen.* Volume 2. G. Fischer Verlag, 256 pp., Jena.

GROOMBRIDGE, B. (Ed.) (1992). *Global Biodiversity: Status of the Earth's Living Resources.* Chapman & Hall, 585 pp., London.

HEGI, G. *et al.* (1966 *et seq.*). *Illustrierte Flora von Mittel-Europa, 3te* Ausgabe. München.

HEYNERT, H. (1964). *Das Pflanzenleben des Hohen Westerzgebirges.* Verlag Theodor Steinkopf, 141 pp., Dresden.

HUNTLEY, B. & BIRKS, H. J. B. (1983). *An Atlas of Past and Present Pollen Maps for Europe 0-13,000 Years Ago.* Cambridge University Press, 667 pp., Cambridge.

HÜTTEMANN, H. & BORTESCHLÄGER, S. (1987). Beiträge zur Vegetationsgeschichte: Riesengebirge, Hohe Tatra, Zillertal. *Ber. Nat.-Med. Verein*, Innsbruck, 24: 81-112.

IUCN (1995). *The Mountains of Central and Eastern Europe.* IUCN, 139 pp., Gland, Switzerland.

JAEGER, P. (Ed.) (1963). *Le Hohneck: Aspects physiques, biologiques et humains.* Ass. Philom. D'Alsace et de Lorraine, 448 pp., Strasbourg.

JAHN, A. (Ed.) (1985). *The Polish Giant Mountains* [in Polish]. Wydaw. Polskiej Akademii Nauk, 566 pp., Wroclaw.

JENÍK, J. (1961). *Alpine Vegetation of the High Sudetes: Theory of Anemo-Orographic Systems,* [in Czech.]. Naklad. CSAV, 409 pp., Praha.

JENÍK, J. (1983). Evolutionary stage of the Sudetic corries [in Czech.] *Biologické Listy,* 48: 241-248.

JENÍK, J. (1986). Bicentennary of the Czech Science Society's expedition to the Krkonoše mountains [in Czech.] *Opera Corcontica,* 23: 53-76.

JENÍK, J. (1990). Large-scale pattern of biodiversity in Hercynian massifs. In: *Spatial processes in plant communities* (Eds. F. Krahulec, A. D. Q. Agnew, S. Agnew, J. H. Willems). Academia, pp. 251-259, Praha.

JENÍK, J. (1996). Europe's mountains: landmarks in natural and cultural history. In: *Sustainable Mountain Development.* The Scottish Office, pp. 19-26, Edinburgh.

94

JENÍK, J. (1998). The names of the Central European mountains shared by national boundaries [in Czech.] *Geografie-Sborník Czech Geographical Society*, Praha, 103/2: 101-107.

JENÍK, J., BURES, L. & BURESOVÁ, Z. (1980). A syntaxonomic study of the vegetation in the Velká Kotlina cirque, Sudeten mountains. *Folia Geobotanica & Phytotaxonomica*, 15: 1-28.

JENÍK, J., BURES, L. & BURESOVÁ, Z. (1983a). A revised flora of the Velká Kotlina cirque, Sudeten mountains: part 1. *Preslia*, 55: 25-61.

JENÍK, J., BURES, L. & BURESOVÁ, Z. (1983b). A revised flora of the Velká Kotlina cirque, Sudeten mountains: part 2. *Preslia*, 55: 123-141.

JENÍK, J. & HAMPEL, R. (1992). *Die waldfreien Kammlagen des Altvatergebirges-Geschichte und Ökologie.* Mährisch-Schlesischer Sudetengebirgsverein, 104 pp., Kirchheim/Teck, Deutschland.

JENÍK, J. & LOKVENC, T. (1962). Die alpine Waldgrenze im Krkonoše Gebirge. *Rozpravy Cs. Akad Ved, series Mat. Prír.*, Praha, 72/1:1-65.

JENÍK, J., SOUKUPOVÁ, L. & VANA, J. (1998). Vegetation diversity in the backwall of the Great Arber-Lake corrie, High Bohemian Forest. *Silva Gabreta*, 2: 20-27.

JIRASEK, J., HAENKE, T., GRUBER A. & GERSTNER, F. (1791). *Beobachtungen auf Reisen nach dem Riesengebirge,* Waltherische Hofbuchhandlung, 309 pp., Dresden.

KIESENWETTER, E. A. H. (1847). Das Riesengebirge in entomologischer Beziehung. *Deutsche Natur. Zeitung.*, 2: 161-164.

KUNSKY, J. (1968). *Physical geography of Czechoslovakia* [in Czech]. Stát. Pedag. Naklad., 537 pp., Praha.

LOKVENC, T. (1978). *Wanderings in the Giant Mountains' History* [in Czech.] Kruh, 267 pp., Hradec Králové.

MATTUSCHKA, H. G. (1776-1777). *Flora Silesiaca, vols. 1 et 2.* W.G. Korn, Leipzig.

MAYR, E. (1982). *The Growth of Biological Thought: Diversity, Evolution and Inheritance.* Harvard University Press, 974 pp., Cambridge.

MEUSEL, H., JÄGER, E., & WEINERT, E. (1965). *Vergleichende Chorologie der zentraleuropäischen Flora*, volume 1, Gustav Fischer, 583 + 258 pp., Jena.

MEUSEL, H., JÄGER, E., & WEINERT, E. (1978). *Vergleichende Chorologie der zentraleuropäischen Flora*, volume 2, Gustav Fischer, 710 + 170 pp., Jena.

MIGALA, K., PEREYMA, J. & SOBIK, M. (1995). Current climatic factors and topoclimatic differentiattion of the Giant Mts. [in Polish]. In: *Ecological issues of the high-mountain part of the Giant Mts.* (Ed. Z. Fischer), pp. 51-78, Inst. Ekologii PAN, 371 pp., Warszawa.

MORAVEC, J. et al. (1983). *Plant Communities of the Czech Socialist Republic and their Conservation Status.* [in Czech.], Okresní Vlatived. Museum, 206 pp., Litomerice.

95

MIKYSKA, R. (1968). *Geobotanical Map of Czechoslovakia*, [in Czech.]. Academia, 204 pp., Praha.

MUCINA, L., GRABHERR, G. & WALLNÖFER, S. (Eds.) (1993). *Die Pflanzengesellschaften Österreichs*. Pars 3, Gustav Fischer, 353 pp., Jena.

OBERDORFER, E. (1977-1992). *Süddeutsche Pflanzengesellschaften*, Volumes 1-4. Gustav Fischer, 311, 355, 455, 282 pp., Jena.

OZENDA, P. (1988). *Die Vegetation der Alpen im europäischen Gebirgsraum*. G. Fischer Verlag, 353 pp., Stuttgart.

OZENDA, P. (1994). *Végétation du continent européen*. Delachaux et Niestlé, 271 pp., Lausanne.

PAWLOWSKI, B. (1970). Remarques sur l'endémisme dans la flore des Alpes et des Carpates. *Vegetatio*, 21: 181-243.

PLESNÍK, J. (1999). *National Biodiversity Conservation Strategy and Action Plan in the Czech Republic*. Unpublished, Ministry of Environment, Praha, Czech Republic.

PRICE, M. F. (1995). *Mountain Research in Europe: an Overview of MAB Research from Pyrenees to Siberia*. Parthenon, 230 pp., London.

SCHMITT, R. (1963). Regard vers les cimes vosgiennes. In: *Le Hohneck*, pp. 349-360, Ass. Philom. D'Alsace et de Lorraine, 448 pp., Strasbourg.

SCHWENCKFELDT, K. (1600). *Stirpium et fossilium Silesiae catalogus*. Lipsiae.

SENDTNER, O. (1860). *Vegetations-Verhältnisse des Bayerischen Waldes nach den Grundgesätzen der Pflanzengeographie*. Literarisch-artistische Anstalt, 505 pp., München.

SOFRON, J. & STEPAN, J. (1971). Vegetation of the cirques in the Bohemian Forest [in Czech.]. *Rozpr. Cs. Akad. Ved, series Mat.-Prír.*, 81/1: 1-57.

SOLBRIG, O.T. (Ed.) (1991). *From Genes to Ecosystems: a Research Agenda for Biodiversity*. International Union Biological Sci., 124 pp., Cambridge, Mass.

SOUKUPOVÁ, L., KOCIÁNOVÁ, M., JENÍK, J. & SEKYRA, J. (Eds.) (1995). Arctic-alpine tundra of the Krkonoše, the Sudetes. *Opera Corcontica*, 32: 5-88.

SPITZER, K. & JAROS, J. (1993). Lepidoptera associated with the Cervené Blato bog, Central Europe. *European Journal of Entomology*, 90: 323-336.

SYKORA, B. *et al.* (1983). *Krkonoše National Park* [in Czech]. Stát. Zemed. Naklad., 276 pp., Praha.

SOUREK, J. (1969). *Flora of the Giant Mountains*. [in Czech.]. Academia, 451 pp., Praha.

STURSA, J., JENÍK, J. *et al.* (1973). Snowpack of the Western Giant Mts. in the abnormal winter of 1969/1970 and its ecological impact [in Czech]. *Opera Corcontica*, 10: 111-146.

TUTIN, T., G. *et al.* (Eds.) (1964-1983). *Flora Europaea*, vols.1 - 5. Cambridge University Press, Cambridge.

96

de VALK, E.J. (1981). *Late Holocene and Present Vegetation of the Kastelberg (Vosges, France)*. Labor. Palaeobot. Palynol., State Univ., 294 pp., Utrecht.

VAVROUSEK, J. & MOLDAN, B. (Eds.) (1989). *Status of the Environment in Czechoslovakia* [in Czech]. Cesky Geol. Ustav, 110 pp., Praha.

WHITTAKER, R. H. (1970). *Communities and Ecosystems*. Macmillan, 158 pp., London.

WWF & IUCN (1994). *Centres of Plant Diversity. A Guide and Strategy for their Conservation*. Volumes 1-3. IUCN Publication Unit, 354 pp., Cambridge.

ZLATNÍK, A. (1959). *An Overview of the Slovak Forests According to Forest Types* [in Czech]. Vys. Skol. Zemed., 195 pp., Brno.

Appendix

Brief characteristics of selected ranges in the Hercynian mountains; A, highest peaks with altitude, B, extent, C, climate, D, lithology of the summit area, E, georelief, F, position in relation to immigration, G, evidence of microevolution, H, disturbance factors impacting on biodiversity, and J, selected references.

The Vosges

A: Hohneck 1362, Kastelberg 1346

B: about 100 km in length and 40 km in width

C: annual precipitation > 1900 mm, eu-maritime pluviometric regime, suboceanic thermal regime

D: mainly porphyroid granite

E: flat-topped summit area, gentle slopes towards west, deeply cut corries on the east-facing slopes

F: rather solitary within the Hercynian Arch, calcareous Jura to the south

G: numerous apomictic microspecies, e.g. in the *Sorbus* genus

H: grazing in the summit area, wood cutting, air pollution

J: JAEGER (ED.), 1963; CARBIENER, 1963; 1966; 1969; DE VALK, 1981.

Black Forest

A: Feldberg 1493

B: about 160 km in length, 50 km in width

C: annual precipitation > 2000 mm, difference between wind exposed and lee slopes

97

D: mainly gneiss and bunter sandstone, small areas of granite

E: mostly smooth and undulating surface, with a number of corries and snowbeds

F: close to the calcareous Jura and the Alps

G: infraspesific taxa, e.g., within *Gnaphalium supinum*, differing from populations in the Alps

H: wood cutting, coniferous plantations, air pollution

J: BARTSCH & BARTSCH, 1940; BOGENRIEDER *et al.*, 1982.

Bohemian Forest

A: Great Arber 1456

B: about 130 km in length and 70 km in width

C: annual precipitation > 1400 mm, warmer NE flanks

D: mainly gneiss, smaller summit areas of granitic rocks

E: moderate slopes, a large upland plateau with few precipitous walls in corries

F: member of a chain of ranges of the Bohemian Massif with the Alps lying across the Danube valley

G: infraspecific varieties of *Picea excelsa* (Sumava provenance), endemic *Gentiana bohemica* subsp. *gabretae*

H: wood cutting for glass industry, spruce plantations of alien provenance, insect population explosions, and peat exploitation

J: KUNSKY, 1968; SOFRON & STEPAN, 1971.

Giant Mountains

A: Snezka Peak 1602

B: about 35 km in length and 10 km in width and connected to a massif of the Jizera Mts.

C: cool and oceanic climate; high proportion of precipitation is as snowfall

D: granite in the main Silesian ridge, gneiss and phyllite in the Bohemian ridge

E: two parallel ridges connected by two large upland plateaux with polygonal soils and numerous corries and snowbeds

F: highest range of the Sudetes stretching along W to S direction

G: 30 endemic vascular taxa, mainly microspecies of the *Hieracium* genus, a population of *Sorbus sudetica* derived from two vanished parents (*S. chamaemespilus, S. aria*)

98

H: cutting of wood, cattle grazing, tourism, air pollution
J: JENÍK, 1961; SOUREK, 1969; SYKORA *et al.*, 1983; JAHN, 1985.

Jeseník Mountains

A: Pradìd 1492
B: about 25 km in length and 4 km in width
C: cool suboceanic climate with high maximum wind speeds and abundance of snow
D: phyllite, amphibolite, gneiss
E: a funnel-shaped ridge with smooth summits, a few snowbeds and a prominent corrie (Velká Kotlina)
F: easternmost range of the Sudetes connected with a few low Sudetic ridges
G: infraspecific endemics of vascular plants (*Plantago atrata* ssp. *sudetica* , *Dianthus carthusianorum* ssp. *sudeticus* AUTH) and *Hieracium* microspecies.
H: grass cutting, wood cutting, monospecific spruce plantations
J: JENÍK, 1961; JENÍK & HAMPEL, 1992.

99