Can the Functional Stability of Forest Ecosystems be Evaluated from the Spatial Analysis of Stands? A Case Study from the Bialowieza Primeval Forest (Poland)

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Abstract.—Variability of external and internal factors entails specific spatial patterns and functional dynamics of communities. The study of the oak-lime-hornbeam (*Quercus robur-Tilia cordata-Carpinus*) forest in the Bialowieza Primeval Forest supports the concept of silvatic unit, determining the minimal structural area. To find out if the dynamics of a stand can be inferred from its spatial pattern, and to compare the structural properties of natural and managed hardwoods, detailed mapping of developmental phases in natural and managed stands was performed. While the mosaic composition in Bialowieza National Park indicates a stable character of the natural oak-lime-hornbeam forest, the managed forest reveals a considerable deficit of optimal and senescent phases and simplification of the mosaic texture. An absolute ban on cutting in remaining old-growth stands should be a basic rule for restoration management.

MOSAIC STRUCTURE, AN INHERENT FEATURE OF FOREST COMMUNITIES

Complexity of Natural Systems Makes Biodiversity

Composition, spatial structure, and dynamics are three aspects of biodiversity (Crow *et al.* 1994, after Roberts and Gilliam 1995). Any particular biological community is not only an assembly of components, but also a structural and dynamic system. Both external static factors (climate, slope, bedrock, etc.), and biotic components (species) will determine the spatial structure of a community and its dynamics. Also, the influence of external dynamic factors, such as windfalls, heavy snow, and fire, depends on species composition. On the other hand, a considerable modification of spatial pattern or dynamics of the system may lead to compositional changes. For instance, the alteration of natural dynamics in the Bialowieza Primeval Forest through forest management has resulted in a significant increase in fast-growing pioneer species there.

Dynamics and Structure: Inseparable Aspects of Forest Communities

A good example of mutual relationships of species composition, spatial structure, and dynamics is a forest community with trees as prominent components. Trees influence the lower vegetation through overshading (e.g., Beatty 1984, Tyler 1989), supplying differentiated litter (Pallant and Riha 1990, Peterson and Campbell 1993, Peterson and Facelli 1992), influencing chemical properties of stemflow and canopy throughfall (Boerner and Koslowsky 1989, Koch and Matzner 1993), and creating gaps (e.g., Clebsch and Busing 1989, Cho and Boerner 1991, Kubota 1995, Kuuluvainen 1994). The most common disturbances in the natural forest that determine the ecosystem's dynamics are windfalls (e.g., Stone 1975, Beatty 1984, Falinski 1986, Ulanova 1991). The annual number of wind-blown trees (>7 cm dbh) in the rich deciduous communities of oak-lime-hornbeam (*Quercus robur-Tilia cordata-Carpinus betulus*) forest in the Bialowieza National Park (BNP) ranges from 200 to 450 per 100 ha (Falinski 1986). With its superficial root system, spruce (*Picea abies*) is recognized as the species most prone to windfalls (Falinski 1986).

Under natural conditions, a community-specific pattern of structure and dynamics should develop. The most conspicuous structural feature of natural forests is the mosaic of regeneration units or eco-units (Oldeman 1983). The community of oak-lime-hornbeam forest is a collection of patches, representing different phases of stand development after disturbance. Dynamics and structure of stands are of great interest to ecologists and foresters, but because of methodological difficulties, the two aspects have often been treated separately. On the one hand, stand measurements led to stand development models with defined phases (Leibundgut 1959), neglecting, however, the spatial distribution of eco-units. On the other hand, most descriptions of forest communities are based on observations and measurements carried out in so-called "representative" plots. Figures reported by many authors indicate that the plots (phytosociological releves or structural plots) usually avoided gaps or larger assemblages of young trees and represented mainly the optimal (or biostatic) phase (e.g., Falinski 1986;

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Sokolowski 1980, 1993). Two opposite, but complementary, approaches to forest dynamics have been developing: simulation and description. The first, based on data concerning functions and physiological reactions of particular components of ecosystem, aims at construction of a computer model, that simulates the functions of the natural system (like JABOWA and derivatives; Botkin *et al.* 1972, Fulton 1991, Shugart 1984). The second approach aims at a steady improvement of tools of forest description, enabling a better interpretation of observed phenomena and the role of different components of a community (e.g., SILVI-STAR; Koop 1989).

The Bialowieza Primeval Forest as a Reference Site

Unlike tropical rain forests and remote taiga, where the mosaic structure of a community stand[1] can still fully develop (e.g., the mosaic investigation in French Guyana forest; Pelissier and Riera 1993, Riera 1995), there are few natural lowland forests left in the temperate zone of the Northern Hemisphere. In Europe, the only exception is the 47 km^2 of the strict nature reserve of BNP, the best preserved part of the Bialowieza Primeval Forest (BPF), northeastern Poland (Falinski 1986).

Forestry management, an activity focusing on trees, modifies stand structure and dynamics. The biggest changes can be observed when natural old-growth is cut and replaced by plantation. In Europe, BPF offers an exceptional opportunity to directly compare recently managed forest with preserved natural communities. The information received from the comparative studies provides a background for decisions and practical measures in the field of restoration management and nature conservation.

General Physiographic Data

The BPF (52° 43'N, 23° 50'E) is the best preserved lowland forest in the European temperate zone. Abiotic conditions in the forest are: (1) the influence of a continental climate (mean annual precipitation 641 mm, ranging from 426 to 940 mm, 85 percent as rain; mean annual temperature 6.8 °C, ranging from 5.1 to 8.8 °C, with the mean temperature ranging from 15.2 to 21.6 °C in July and from -13.4 to 1.8 °C in January; Olszewski 1986, the meteorological data from 1948 to 1983), (2) the old post-glacial formation (vast plains with altitudes ranging from 134 to 202 m above sea leavel), and (3) the watershed location (dependence on precipitation water; Falinski 1986).

[1] Futher called "mosaic," which corresponds with "silvatic mosaic" by Oldeman (1990).

Historical Traces

Protected since the 15th century as a royal hunting ground, the 1,500-km^2 BPF remained preserved until World War I (1914-1918), when intensive timber exploitation began. The most famous part of the forest is the strictly protected nature reserve of BNP (47 km^2), established in 1921 (fig. 1). Since then any commercial activity in BNP has been forbidden, except for limited tourism. Most of the area (ca. 1,200 km^2) was commercial forest (CF) until World War II. In 1945, the BPF was split into a Polish part (ca. 600 km^2), where timber exploitation had been continued, and a Soviet (today Belorussian) one, preserved as a hunting grounds.

In the Polish forest, the negative effects of the large clear-felling system forced the forestry authorities to change management methods in the late 1970's. The principle of the new forestry rules (presented as sustainable or multifunctional forestry) was reduction in the size of clearcuts to 0.25 ha. There was an increasing awareness of the role of natural regeneration, albeit planting remained the main reforesting method. As a result, the commercial forest (CF, ca. 80 percent of the Polish part of BPF) constitutes a patchwork of even-aged, usually single-species plantations; isolated remnants of natural and seminatural stands (approximately 20 percent of CF); and large areas of 60- to 80-year-old pioneer, mainly birch stands, that developed spontaneously on the clear-felling areas left without artificial reforestation.

The Main Focus: Oak-Lime-Hornbeam Forest

The predominant community of BPF is oak-lime-hornbeam forest (*Tilio-Carpinetum*), occurring in three closely related variants: *typicum* (on slightly wet sites, with low participation of maple in the stand layer and nitrophilous species in the herbaceous layer, as well as with poor geophyte flora), *caricetosum* (on wetter sites, with a considerable portion of *Carex remota* in the herbaceous layer) and *stachyetosum* (the richest variant, with significant participation of maple in the stand layer and nitrophilous species with *Stachys sylvatica* and geophytes in the herbaceous layer, Sokolowski 1993). It primarily occupies the ground moraine plains formed by boulder clay. Under the conditions of runoff-gleyey type of water circulation, the mesotrophic leached brown soils (browned lessive soils) were established (Kwiatkowski 1994). Originally, the oak-lime-hornbeam forest occupied about 45 percent of today's area of the Polish part of BPF, and it still remains the major community type in the restricted area of BNP. Rich in species, the forest's prominent components are hornbeam (*Carpinus betulus*), lime (*Tilia cordata*), maple (*Acer platanoides*), spruce (*Picea abies*), and pedunculate oak (*Quercus robur*). The most common shrub is hazel (*Corylus avellana*), sometimes overshading entire gaps. The most influential

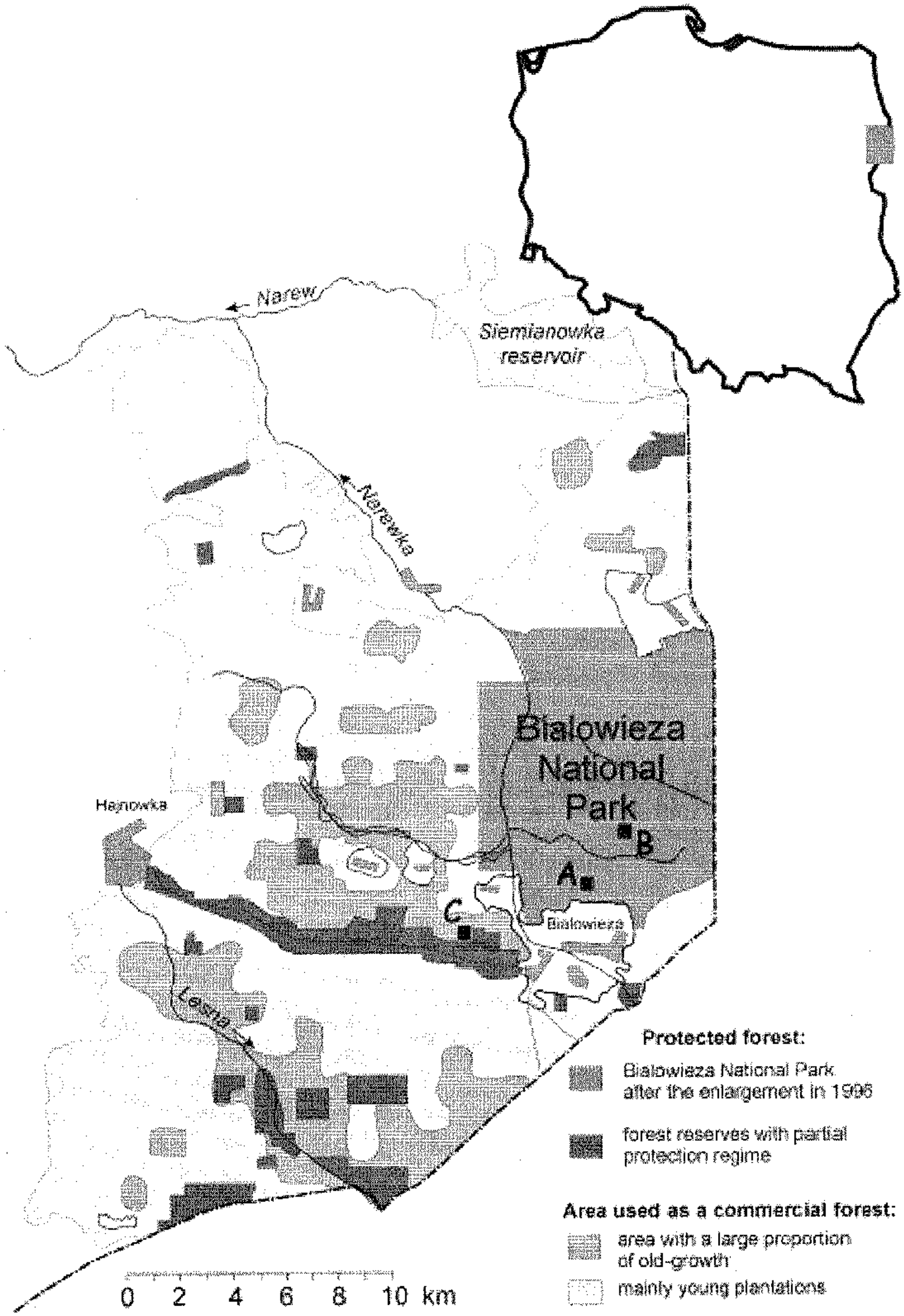

Figure 1.—*Study area location: Polish part of the Bialowieza Primeval Forest with the Bialowieza National Park. Black squares with letters A, B (natural forest—BNP), and C (commercial forest—CF) represent 25-ha plots, where mapping of silvatic mosaic was performed.*

dynamic factors in this almost non-flammable forest—namely tree aging, diseases and death, windfalls, and outbreaks of insects—lead to structural heterogeneity.

Definition and Description of Developmental Phases

Several developmental phases were proposed by Leibundgut (1959) and reviewed by Miscicki (1994). On the basis of preliminary observations of natural deciduous forest in BNP and tree measurements in sample plots (900-1,200 m^2 in young homogeneous stands and 2,500-5,000 m^2 in heterogeneous old growth, arbitrarily distributed in the most "typical" fragments of the forest representing pre-defined developmental phases), the following phases were distinguished:

1. Young phase (Y): Averaged data describing the phase: 25 trees per 100 m^2; dbh from 1 to 15 cm; height up to 10 m; most trees are 10-25 years old; very dense, single layer, usually established in larger gaps; floor vegetation weakly developed due to poor light conditions; usually large amount of partly decayed woody debris; dominating species at this stage of *Tilio-Carpinetum* forest are hornbeam and lime.
2. Pole phase (P): 10 trees per 100 m^2; dbh 10-30 cm; height up to 25 m; 25-40 years old; usually developed from Y, single layer or with gradually disappearing subordinated layer of outcompeted trees; full canopy coverage prevents the development of floor vegetation; woody debris less abundant and more decayed.
3. Young optimal phase (P+): 6.5 trees per 100 m^2; dbh 25-40 cm; height up to 35 m; 40-60 years old; usually single-layer cohorts of lime; emerging gaps in the canopy coverage allow better development of the floor vegetation; quantity of woody debris depends on events in neighboring eco-units.
4. Optimal phase (O): 4.5-6.5 trees per 100 m^2; dbh 2-70 cm, with individual trees exceeding 150 cm; height up to 42 m (lime, oak, and ash - *Fraxinus excelsior*) and 55 m (spruce); 60-200 years old (some trees may exceed 450 years); complex vertical structure, usually three distinct layers of trees with the intermediate one being the most dense; highly variable canopy covers 75-100 percent of the area and contributes to the uneven development of floor vegetation and recruitment of new saplings from the seedling bank; amount of dead wood is variable in space.
5. Terminal phase (T): Disconnected canopy coverage, the complex of small gaps and solitary, mainly aging, sick, or dying trees; with poor renewal or the brushes of saplings steadily grazed by ungulates; abundant herbaceous layer; usually great amount of woody debris.
6. Regeneration phase (R): 15-20 trees per 100 m^2; dbh of most of trees from 2 to 25 cm, with few old and large specimens, whose canopies cover less than 50 percent of the area; highly variable vertical structure (tree heights from 4 to 40 m) indicates a long-lasting renewal period; R can seemingly grow optimal or steadily homogenize and transform into P.

According to the terminology of Oldeman (1990), phases Y, P, P+, and R correspond to the "aggradation phase," phase O to the "biostatic phase," and phase T is an equivalent of the "degradation phase." Because our measurements neglected trees below 1.3 m in height, the present classification does not distinguish the "innovation phase," defined by Oldeman (1990). As long as young saplings do not reach the measurement threshold, the open units are being classified as either gaps (G) or phase T.

RESULTS: MAPPING AS A BASIC TOOL IN MOSAIC APPROACH

Mapping for Managing

The main criterion used by the routine forest inventory, carried out in the BPF in 1989-1993, was the forest site classification, based on edaphic and humidity site characteristics. Within every forest subcompartment, representing the forest type, relascope (Bitterlich 1947) samplings (one per 0.84 ha on average) were performed in order to describe the stand characteristics (species composition and percent canopy coverage, age of the dominant species). The survey resulted in a map of stands at the scale of 1:10000 (fig. 2). This kind of data provides important background information on the forest variability determined by abiotic and static factors. However, it is not sufficiently informative in terms of stand structure and dynamics.

Mapping for Learning: The Field Example

To approach the texture (variability of eco-unit sizes, grain size structure) of the oak-lime-hornbeam forest community, detailed mapping (based on preliminarily described characteristics of the developmental phases) of 25-ha plots representing oak-lime-hornbeam forest was performed. Preliminary observations and trials of direct mapping of developmental phases in the field showed patches delimitation as a most difficult and unreliable operation. The use of regular 10 x 10-m pixels (100-m^2 units) avoids the dilemmas accompanying the drawing of arbitrary limits. The decision is restricted to the classification of pixels, based on the above listed characteristics of the developmental phases (fig. 3).

The pattern revealed by the developmental phases shows no relationship with the areas depicted by the techniques used during the forest inventory survey (figs. 2 and 3). There is a striking divergence of the spatial pattern determined by the forestry management in CF from the

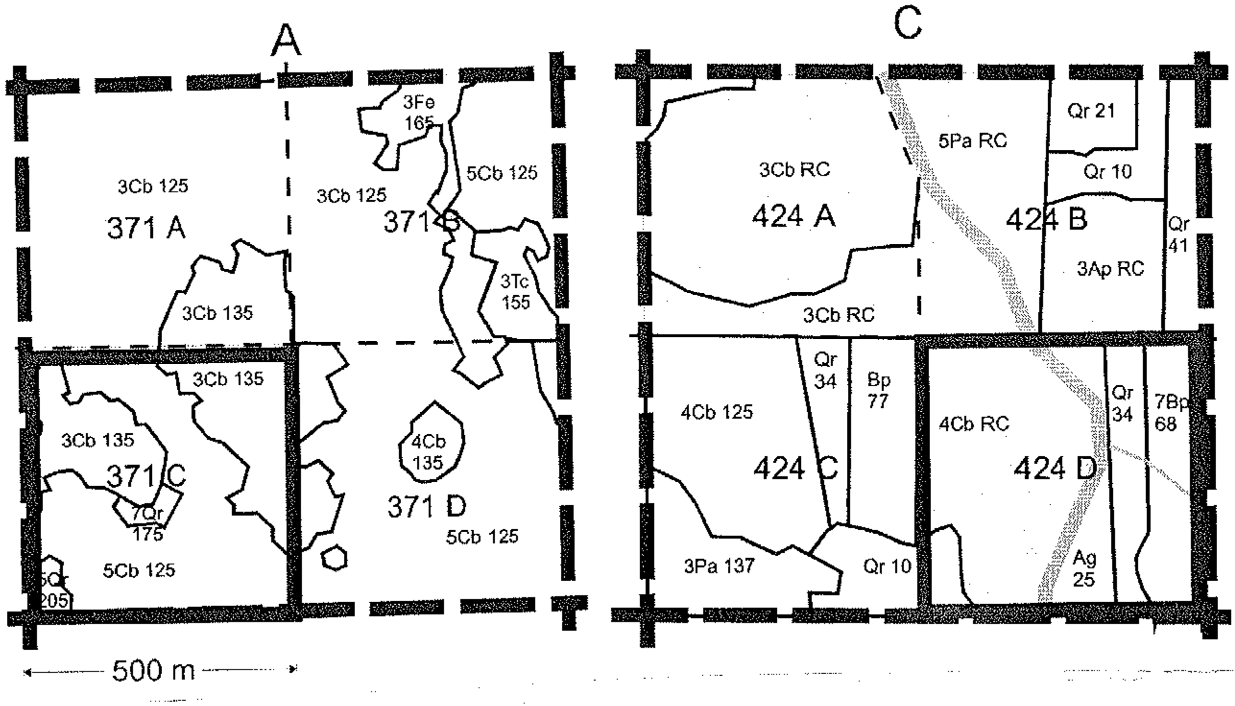

Figure 2.—*Two fragments of the map produced by the forest inventory in 1989-1993, representing natural and managed forest (letters A and C- the names of plots refer to the map in figure 1). Numbers before the abbreviations of dominant species names stand for their relative participation in stand (10=100 percent). Numbers after the names correspond with the average age of a dominant species. The gray line denotes roads, and the gray-striped area refers to the so-called "regeneration class" (RC), where cutting began recently. Ag* - Alnus glutinosa, *Ap* - Acer platanoides, *Bp* - Betula pendula, *Cb* - Carpinus betulus, *Pa* - Picea abies, *Qr* - Quercus robur.

mosaic developed under natural conditions in BNP. The discrepancy is in both the mosaic composition (percent participation of particular phases) and its texture. The most conspicuous compositional difference is a total lack of phase T and a clearly lesser participation of phase O (20 percent) in the plot representing CF in comparison with the plots in BNP (33 and 40 percent). In the natural oak-lime-hornbeam forest, the area covered by gaps and phase T is similar in size to the area occupied by stands of the future: phases Y, P, P+, and R (table 1). The analysis of linear dimensions of the eco-units, along the rows and columns of plots, displayed two different types of distribution: (1) one-tailed, geometric distribution - referring to the plots in BNP, and (2) asymmetrical two-tailed distribution, with the extra peak at the large eco-unit classes (fig. 4).

DISCUSSION

Hierarchy of Mosaics

The investigation of stand structure, carried out in the oak-lime-hornbeam forest of Bialowieza, fully supports the concept of silvatic mosaic, as proposed by Oldeman (1990). The basic assumption is that the silvatic mosaic is a supersystem developed on a relatively homogeneous site, i.e., within the limits of a community. Its components, eco-units (regeneration units), are pieces of the area, "on which at one moment in time a vegetation development has begun, of which the architecture, ecophysiological functioning and species composition are ordained by one set of trees until the end" (Oldeman 1990, p. 165). Depending on the character of the so-called "zero event" (vast and intensive disturbance that destroys most of the stand) initializing a new eco-unit, it can develop as even-aged or uneven-aged (Oldeman 1990). In the present study, young and pole phases reveal mostly even-aged character, while the eco-units representing regeneration, optimal, and terminal phases are uneven-aged. The mosaics studied clearly differ from the forest mosaics, which reflect variability among the sites determined by the abiotic factors ("edaphic mosaic," according to Lertzman *et al.* 1996). Forest mosaics are systems of higher level organization and are composed of actual silvatic mosaics. The forestry maps prepared during the standard inventory show forest mosaics determined by the site characteristics and very general parameters describing stands as basic management units. This kind of data matches the traditional forestry approach based on strict rules of silvicultural methods and tools ascribed to a given site type. It provides, however, no information on spatial structure and dynamic trends of the community.

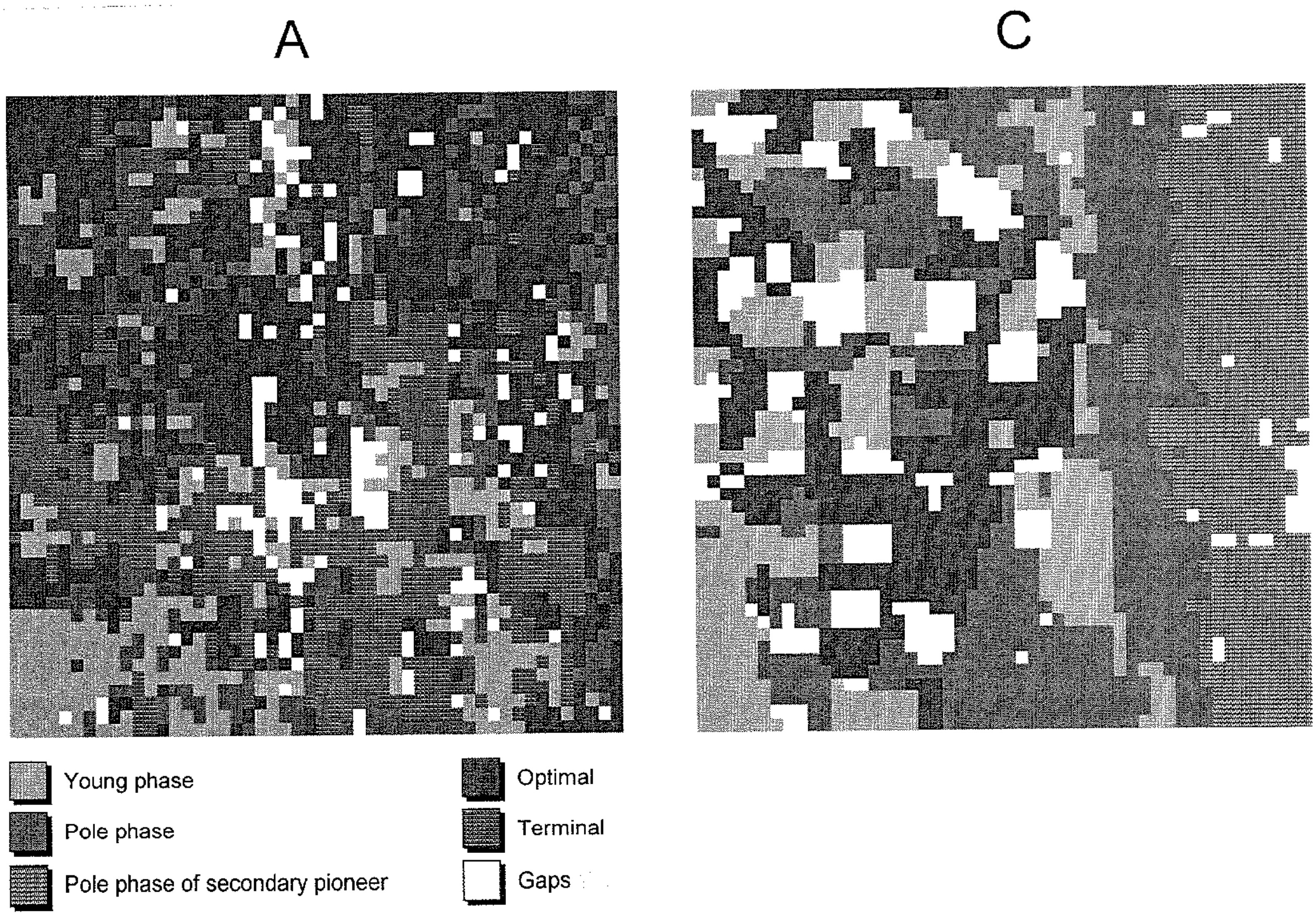

Figure 3.—*Silvatic mosaics representing natural and managed oak-lime-hornbeam forest(letters A and C- the names of plots refer to the map in figure 1).*

Table 1.—*Percentage shares of various developmental phases in three 25-ha plots investigated in the natural (A, B) and managed (C) oak-lime-hornbeam stands in Bialowieza Primeval Forest*

Developmental phase	Study plot		
	A	B	C
Young	16	3	18
Pole	18	19[1]	50[2]
Regeneration	—	10	—
Optimal	40	32	19
Terminal	20	20	—
Gaps	6	15	12

[1]Includes the pre-optimal phase P+.
[2]Includes pioneer secondary stand.

The Minimal Structural Area

The composition of the two 25-ha mosaics representing natural communities of the oak-lime-hornbeam forest in BNP suggests a dynamic equilibrium stage, where a considerable area of diverse, long-lasting optimal phase is accompanied by equal areas of terminal phase with gaps (stand of the past) and three young phases (stand of the future). However, taking into consideration the chaotic character of eco-unit distribution in the plots and their size variability, one must suppose that an area of 25 ha is very close to a community-specific "silvatic unit," or "minimal structural area" defined as "the minimum surface at any one site needed for all architectural growth phases of all locally possible eco-units" (Oldeman 1983, cited after Oldeman 1990, p. 388), "which are perpetually represented by forest self-regulation" (Koop 1981, cited after Oldeman 1990, p. 389).

Disturbance Factors and Mosaic Texture

The texture of the studied natural mosaic indicates the mixed character of "zero events." As expected in natural stands (e.g., Coates and Burton 1997, Lertzman *et al.* 1996), small-scale events, such as the death of a single tree or small groups of trees (caused by biotic or abiotic factors), play an important role in the development of a fine-grained mosaic. However, a wide range of sizes of eco-units showed that the "ideal" model, totally determined by only small-scale phenomena, ascribed by Oldeman (1990) to the conservationists, is not a feature of the actual community. In fact, small-scale phenomena overlap the effects of rare but high-energy events (in our case—local whirlwinds) bearing large eco-units. The observed variety of eco-units in the natural forest secures a wide range of microenvironments suitable for different

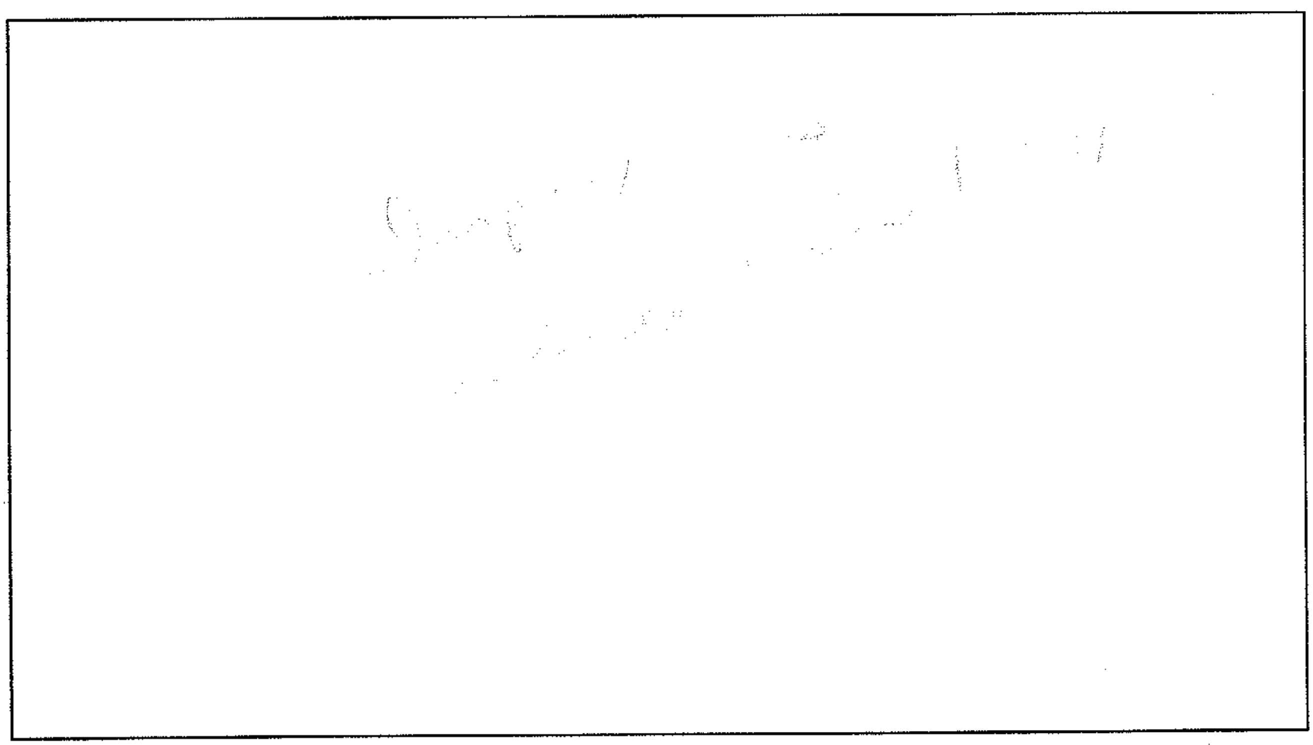

Figure 4.—*Comparison of the mosaic pattern between natural (A and B) and managed (C) stands reveals a dramatic reduction of the fine-grained texture in consequence of the forest management (letters A, B, and C- the names of plots refer to the map in figure 1).*

plant, fungi, and animal species. On the basis of a thorough experimental approach, Coates and Burton (1997, p. 349) stated that "each size of gap has a characteristic combination of light regimes, which are correlated with a number of other microclimate attributes which collectively determine vegetation responses." It must be kept in mind, however, that—as mentioned earlier—gap dynamics remains in a feedback relationship with other features of a community, particularly with tree species composition. Gap dynamics seems to be characteristic of communities in which the tree crown architecture prevents light from penetrating to the ground and inhibits continuous stand renewal beneath the canopy. The model probably does not apply to riverine ash-alder or swamp alder forest communities that lack closed canopies.

When Multifunctional Forestry Jeopardizes Nature Conservation

The studied fragment of the managed forest revealed a clear divergence from the natural pattern found in BNP in terms of mosaic composition and texture, albeit it has been managed according to the current rules of pro-ecological and multifunctional forestry (Anonymous 1997). In practice, pro-ecological forestry means a mere set of techniques and tools realizing an ideal model of multifunctional forest. The main goal of "good forestry" is to diversify the stands, oversimplified due to long-lasting schematic treatment, and to increase the biodiversity standards. An obvious contradiction emerges, however, between the biodiversity protection postulate and the actual effects of multifunctional forestry, when implemented in the remnants of natural forest. There, the components of biodiversity most at risk are the species characteristic of late successional stages, i.e., old growth (Buchholz and Ossowska 1995, Pielou 1995). At a landscape level, old growth is so rare that this is worth serious consideration.

Practical Recommendations

According to the Forest Practices Code of the British Columbia Forest Service (Fenger 1996), two criteria must be met to conserve biodiversity: (1) the old-growth forest should cover at least half the area relative to that occurring naturally, and (2) no more than twice the area in a landscape unit should be forest of less than 40 years compared to that occurring naturally. The retained fragments of old growth should be as large as possible, because patches of old-growth forest smaller than 600 m in diameter do not contain interior forest habitat but consist entirely of edge habitat (Fenger 1996). Applied to the situation of the managed part of the Bialowieza Forest, it indicates a basic tenet of future management: the unquestionable sanctity of all remaining old growth, in order to retain a continuous matrix of late successional stages. Stands must be allowed to transform freely into the terminal phase or gradually renew in small gaps. All the forestry management with logging should be aimed at restoring the natural mosaic pattern. It can be done partially through group cuttings carried out in large fragments of even-aged young or pole phases, thus improving the texture of the mosaic. Future management of the Bialowieza Primeval Forest, besides the structural and dynamic aspects of the forest, should consider the ecological characteristics of particular developmental phases. For instance, by establishing oak plantations, forest management caused considerable changes in soil and field-layer vegetation (Bobiec 1998). The felled-tree openings being reforested immediately do not play the same ecological role as some long-lasting gaps in natural forests. Even old-growth patches left in the CF differ from those in BNP, because of the removal of dying trees and coarse woody debris.

CONCLUSIONS

On the basis of the present material, the following conclusions can be drawn:

1. The silvatic mosaic (as defined by Oldeman 1990), defined by the texture (sizes of eco-units) and relative participation of different developmental phases, is a feature inherent to a given forest community. It develops as an effect of interactions between internal factors, such as tree regeneration, growing, and aging processes, and external factors, such as wind-blows, heavy snow, etc.
2. The mosaic composition of natural fragments of the oak-lime-hornbeam forest in BNP indicates that the silvatic mosaic has reached the equilibrium stage: the optimal (biostatic) phase occupies 34-40 percent of the area, the area of senescent phases is similar to that of the young ones.
3. In Bialowieza, the forestry management of oak-lime-hornbeam forest has led to a sharp discrepancy between the mosaic pattern and composition in protected and exploited parts of the Forest.
4. The idea of multifunctional forestry does not meet the standards of biodiversity conservation on the grounds of 600-km^2 woodlands, where patches of old-growth forest are scarce.
5. To retain a continuous matrix of late successional stages, the unquestionable sanctity of all the remaining old growth must be the basic tenet of any future management of BPF and other ancient woodlands. Any logging should be aimed at restoring of the natural mosaic pattern. It can be done partially through group cuttings carried out in large fragments of even-aged young or pole phase, thus improving the texture of the mosaic and reducing the risk of future large-scale disturbances.
6. The standard methods of forest inventory do not capture the complex nature of the natural forest. The

mosaic approach appears to be an appropriate and efficient tool in the investigation of forest community structure in space. Developed and improved methods, possibly with use of aerial photography, should be basic tools in monitoring forest dynamics and in designing management and conservation measures.

ACKNOWLEDGMENTS

My special thanks are due to Haico van der Burgt, Jos Haga, and Casper Zuyderduyn—forestry students from **'t Vanck,** Helicon Opleidiningen (Velp, The Netherlands)—for their excellent field work. The study was part of the research project 6P04F054 12 financed by the Committee of Scientific Research (KBN). I am grateful to the organizers of this Conference for waiving the participant fee and to the Batory Fund for financing the costs of my trip.

The following people reviewed this manuscript: Richard Busing, Pacific Northwest Research Station, Forestry Sciences Laboratory, Corwallis, Oregon, USA; Rey Offren, Department of Geography, University of Auckland, Auckland, New Zealand; and Berthold Traub, Swiss Federal Institute for Forestry, Snow, and Landscape Research WSL, Bmensdorf, Switzerland

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