1998

CHAPTER 20

ASSESSMENT AND PLANNING FOR FOREST BIODIVERSITY: A EUROPEAN INITIATIVE

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INTRODUCTION

Loss of biological diversity has been recognized as one of the main current threats to the world's forests, and there is a general growing concern for developing new global, regional and national programs for conserving and managing forest biodiversity. According to Wilson (1988), the current global rates of extinction exceed background rates by three to four orders of magnitude. Extinction is caused by a variety of factors. Frankel and Soulé (1981), on the basis of evidence about known extinction, argued that biotic factors rarely cause extinction, especially in continental species, but that habitat destruction, over-exploitation, and the impacts of exotic species are the major causes of modern extinction.

Biological diversity is an irreplaceable value in itself. The diversity of the biosphere creates a genetic bank, crucial for the functioning of ecosystems and to the recovery of ecosystems after disturbances and temporal changes in ecosystem functions as well as changes in environmental factors. Each country that ratified the 'Global Biodiversity Strategy', signed in 1992 in Rio de Janeiro, and the resolutions of the 1990 (Strasbourg) and 1993 (Helsinki) Ministerial Conferences on the Protection of Forests in Europe committed to national monitoring of biodiversity and to preserving the characteristic natural variation.

Among others, the FAO/ECE Meeting of Experts on Global Forest Resources Assessment (Nyyssönen, 1993) emphasized the need for national assessments of forest biodiversity and the necessity of fully integrating biodiversity data with traditional forest inventory practices. While there is a sense of urgency about developing reliable and effective methods for assessing and monitoring forest biodiversity, there is still a lack of applicable tools to monitor the distribution and structure of species variation in temperate and boreal forests – tools that are needed for sound management plans and forest biodiversity conservation programs.

There is no consensus on the best way to measure genetic, species, and ecosystem diversity (Peet, 1974), so it is difficult to state clearly any hypotheses concerning those issues. Samson and Knopf (1994) emphasized that there are no decisive definitions of diversity to guide development of operational approaches for conserving diversity. Under the auspices of the European Forest Institute (EFI) in Joensuu, Finland, a European research project has been launched to identify the parameters, attributes, and variables to be sampled, assessed, and measured in characterizing the biodiversity of various European forest types. Moreover, the project will provide guidelines to national and international institutions for assessing biodiversity through forest resource inventories and indicating measures for preserving biodiversity and improving forest resource management programs. The EFI project will focus on species diversity and ecosystem or community diversity. The discussion below summarizes the background of the EFI project, its research objectives, and the approach chosen.

MONITORING FOREST DIVERSITY: WISHFUL THINKING AND FEASIBILITY

The concept of biodiversity is related to the entirety of all forms of life within a system and covers the entire range of life – from organic molecules to flora and fauna species, plant societies, landscapes, and biomes. If biodiversity is considered not only a static but also a dynamic concept, the genetic variability of species has to be taken into account as well. These three elements of biodiversity – genetic diversity, species diversity, and ecosystem/community diversity – can act in a variety of spatial and temporal dimensions. The observed time interval can range from a few seconds (the life span of a micro-organism) to centuries (the life expectancy of trees) or millennia (evolution). Biodiversity can also be investigated on a local, regional, or global spatial scale. It is therefore essential to define the elements of biodiversity, as well as the spatial and temporal dimensions, to be included in monitoring.

It might be possible to assess the biodiversity of a limited number of forest ecosystems in case studies, but monitoring forest biodiversity on a large scale requires representative, cost-efficient, robust, and sample-based methods. It is doubtful whether the entire spectrum of biodiversity in forest ecosystems can be recorded in regional or national assessment and monitoring programs. In addition to the amount and specificity of the attributes to be assessed, the dynamics of species composition within the vegetation period and succession stage can hardly be recorded. Most often, only a limited number of organisms can be determined. Because of this insufficiency, the term biodiversity should be used to describe an omnibus concept that incorporates the variety of life in all its forms, but should not be used in a quantitative sense. Assessments will cover only sub-systems of forest ecosystems; therefore, the term diversity seems more suitable.

Diversity is a generic term referring to the condition of being different (Gove *et al.*, 1994). A synonym for diversity is variety. According to Pielou (1975), diversity is an equivalent to variance. Variance characterizes the variety of quantitative measures (e.g. tree volumes); diversity characterizes the variety of

qualitative measures (e.g. tree species). Several methods are available to quantify diversity (Pielou, 1975; Magurran, 1988). The objective of all methods is to present multi-dimensional variability such as relative frequencies, spatial patterns, or processes over time in a one-dimensional, ranked order. Among the most commonly used diversity indices are species count, species richness, Shannon index, and Simpson index (Magurran, 1988).

The (not always valid) assumption that diversity decreases with increasing environmental stress has been cited by many authors and has led to a wide use of diversity indices in forest monitoring programs. For example, the UN/ECE Convention on Long-Term Transboundary Air Pollution (Environmental Data Center, 1993) recommended the application of the Shannon index for integrated forest monitoring. However, if the evolution of diversity over time has to be observed, different diversity indices can lead to different results. The Shannon index is very sensitive to changes in species richness, while the Simpson index is mainly influenced by the frequency of the dominant species (Peet, 1974). Köhl and Zingg (1996) applied four diversity indices to the data from six stands, where observations of species, number of stems, and basal area were available for a period of up to 88 years. Inconsistent rates of changes in diversity were obtained depending on the applied measure (number of stems, basal area, or number of species) and the chosen diversity index.

As there are many problems in using methods that measure genetic and species variation, the most promising and most practicable alternative for measuring diversity for the purpose of forest management and land-use planning is to monitor the variation of habitats. As most of the flora and fauna species are fixed to certain habitats and their structural elements (Camp, 1994), the habitat composition of an area reflects its potential species composition. Measuring habitat composition and structure is easy and quick compared to methods based on genetic variation and species richness. Therefore, it is natural to start estimating diversity at the habitat level.

Habitat is the combination of climate, soil, water regime, and vegetation to which a species has adjusted and on which it depends. Habitats create the living conditions for certain additional flora and fauna species on the site, and the ecosystem variation is based on these components. Habitat variation takes place and can be examined on three different scales (Miller, 1978). The smallest scale is the local scale of homogeneous patches (micro-ecosystems). The size of micro-ecosystems is in the range of hectares. Linked patches create a landscape mosaic (meso-ecosystem). A landscape mosaic consists of spatially contiguous patches distinguished by material and energy exchange. They range in size from 10 km^2 to several thousand km^2. In broader scales, landscape mosaics are connected to form larger units (macro-ecosystems). These units of connected mosaics are called regions (Bailey, 1983).

In addition to a preferred habitat at the patch level, some species also require certain key elements in the habitat. Key elements can be, for instance, dead and decayed biomass, big old trees, dense tree groups, stone ruins, springs, spring streams, steeps, or charred wood. At the landscape level, many bird and mammal species require a certain habitat mosaic of a certain scale with a species-specific distribution. Species can also have different habitat requirements depending on the time of the year. In addition to the location of different habitat patches (spatial distribution), variation of the size and shape of the habitat patches (edge effects) are essential to the well-being of some flora and fauna populations. For example, Whitcomb *et al.* (1981) found that forest interior bird species are rare on small (1 to 5 ha) patches and frequent on large (> 70 ha) forests. Fragmentation of habitats causes serious survival problems for certain species. According to Wilcove *et al.* (1986), fragmentation is the principal threat to most species in the temperate zone.

THE NEED TO INTEGRATE FOREST DIVERSITY ISSUES INTO FOREST MANAGEMENT PLANS

The current forest planning procedures in Europe have been developed over a period of more than 200 years. The first planning concepts focused mainly on the timber productive function of forests and were based on area. The area of the forest enterprise (F) was divided into annual cutting areas (F/u) according to the rotation period, u. This system was first employed in the 14th century in the national forest of Nürnberg and the city forest of Erfurt. In the 18th century, felling area/year was determined according to the site class. Since then, forest management planning has undergone many modifications. However, from the very beginning the most important concepts in forest management planning have been sustainability and long-term considerations.

The idea of describing stand dynamics on the basis of permanent observation first emerged in the last century. Gurnaud (1878), working in France, elaborated rules for the application of repeated measurements in estimating increment; this procedure is known as the control method. These rules were first applied in Switzerland by Biolley (1921) in 1890 to the forest of Couvet in the Jura.

Nowadays, forest management planning is no longer restricted to the timber productive function of forests. In most European countries, forest laws stipulate sustained conservation of all forest functions, including biodiversity. Unlike many parts of the world, forests of Central and Southern Europe have to fulfill several functions simultaneously and within the same area. Therefore, integrating biodiversity into forest management planning cannot be restricted to creating preserves, wildlife sanctuaries, or national parks. As neither people nor resource use can be removed from forests, conserving and enhancing forest diversity has to become an integral part of forest management planning. Comprehensive methods have to be provided that simultaneously take into account timber production, other forest products, and biodiversity issues on lands with a variety of owners and users.

THE EUROPEAN INITIATIVE UNDER EFI

In many parts of Europe, the traditional methods of forest management planning have not been developed for planning the conservation of forest biodiversity. There is an obvious gap between the international agreements and practical forestry in maintaining the diversity of forests. As can be seen from many other examples, national institutions and administrative bodies tend to develop their own approaches to solve problems common to various nations, which later on have to be harmonized to come up with comparable figures. To avoid national solo attempts, the European Forest Institute (EFI) in Joensuu, Finland, started a European project that will provide standardized methodologies for diversity assessment and tools for creating management planning strategies based on measures of habitat diversity. Integrating the assessment of habitat diversity into practical management inventories and forest management planning will allow preservation of the natural variation of habitat composition and structural elements or an increase in the variation toward a desired target level.

EFI's research project will consist of five case studies based on common principles and methods that will be modified according to the different environmental factors of five ecoregions – moderate continental needleleaf taiga, western oceanic coniferous and mixed forests, permanently humid western oceanic broadleaf forest, alpine forests, and mixed sclerophyll forests and shrub. These ecoregions cover more than 90 percent of the area of northern, western, middle, and southern Europe. Two representative areas with different socio-economic conditions and land-use history will be selected in each ecoregion.

Every habitat develops several horizontal vegetation layers as a result of forest management, natural disturbances and vegetation succession. One of EFI's research objectives is to identify the factors of physical and community habitats and of certain key elements that can be detected in field inventories and are critical for the survival of species of a certain habitat. The factors of the physical habitat are climate and soil parameters, whereas factors of the community habitat are characteristics of different horizontal layers of vegetation. Based on this, habitat classification systems for different ecoregions will be developed. The systems include all stages of natural forest succession as well as artificially developed habitats that are crucial to diversity. A standardized, common method for measuring the components of the habitat classification system will be suggested.

The consequences of a management regime can only be predicted if the dynamics of different habitats and interactions between habitats are known. Habitat dynamics are initiated and driven by changes in climatic and site conditions and by human impact. Changes in climate can affect forest ecosystems so that they shift from an optimum phase through phases of tree species impoverishment to near disappearance of the forest. Changes in site conditions can have a limiting effect on different tree species and thus affect competition until a single tree species reaches dominance over the other species. Human

CHAPTER 21

ECOLOGICAL MONITORING IN EUROPE AND NORTH AMERICA: BIOSPHERE RESERVE INTEGRATED MONITORING PROGRAMME (BRIM)

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INTRODUCTION

The United National Education and Scientific Committee/Man and the Biosphere (UNESCO/MAB) National Committees of Europe and North America form a sub-network – called EUROMAB – of the larger international MAB cooperative effort. EUROMAB was founded 1987 at its first conference in Berchtesgaden, Germany. Since then, the National Committees have held a conference every two years in order to discuss the further development of the network and its activities.

EUROMAB concentrates on different thematic aspects of ecology, including land-use changes, ecotones, forest ecosystems, the Biosphere Reserve Integrated Monitoring Programme (BRIM), a recently founded working group on societal dimensions, and the Northern Science Network.

BIOSPHERE RESERVE INTEGRATED MONITORING PROGRAMME (BRIM)

Development of BRIM

In 1993, approximately 180 biosphere reserves in 32 countries existed in the EUROMAB region. Over the last quarter of a century, a huge amount of data has been gathered in these biosphere reserves (Schröder *et al.*, 1996). However, the approach to monitoring and research has been sectorial in nature rather than proceeding in a harmonized fashion, emphasizing integration of scientific disciplines. As well, the link between social science and natural science has been insufficient for a true interdisciplinary monitoring program (SRU, 1991). In addition, even though the MAB programme envisioned the biosphere reserves in part as an international information network (see UNESCO, 1984, 1996), data from the reserves and the research and monitoring undertaken within them remain difficult to access.

To increase coordination of the various bio-, geo-, socio-, and climate-monitoring efforts in the biosphere reserves, the 1991 Strasbourg EUROMAB Conference III approved the creation of the Biosphere Reserve Integrated impact can take different forms, but is generally the cause of rapid changes. Clearcuts, afforestation, fertilization, introduction of exotic species, or restrictions to plant only distinct, fast-growing provenances cause severe interferences in forest ecosystems and prevent evolution and natural adaptation processes. The 'optimal' phase of a forest ecosystem is thus created according to human desires.

Natural and human-induced causes of observed trends in biological diversity have to be determined and quantified to permit the consequences of management regimes. Fortunately, relatively comprehensive information about managed forests is available throughout most of Europe. Forest maps have been created for large forest enterprises since the last century, a network of permanent observation plots has been set up during the last 100 years, and forest surveys have a long tradition in monitoring European forests. Combining these data sources and findings from case studies, published research results, and experiments will allow development of a model for predicting the consequences of management regimes with respect to forest diversity. Providing computer-aided optimization techniques for investigating forest management strategies with reference to biodiversity conservation will be the final goal of the project.

Currently six research institutions have joined EFI's research initiative. They are the Finnish Forest Research Institute, Kannus Research Station, Finland; the Swedish University of Agricultural Sciences in Garpenberg, Sweden; the Swiss Federal Institute of Technology (ETH), Zurich, Switzerland; the Federal Institute for Forest, Snow and Landscape Research (WSL) in Birmensdorf, Switzerland; the Instituto Sperimentale per la Selvicoltura of Florence, Italy; and the Center for Agricultural Landscape and Land Use Research (ZALF) in Eberswalde, Germany.

CONCLUSION

It is obvious that in the highly populated areas of Europe, natural habitats have declined and fragmentation of the landscape has increased. Human impacts and changing conditions will affect forest ecosystems. International declarations have addressed these concerns, but there is a substantial lack of international activity to approach these problems and fulfill international commitments as well as a lack of assessment and planning methods for transferring international commitments to the local level.

Assessment of, and planning for, forest biodiversity requires a set of new methods that provide sound information on the current state of forests and their reactions to management activities. Currently, there are no methods to quantify forest biodiversity. The implementation of management concepts is difficult because is not easy to plan for aims that cannot be measured. The project launched by EFI focuses on the classification of key habitats to close the gap between assessment and planning approaches. Still, the project will not answer the question, 'How should the 'optimal' forest, with respect to biodiversity, be structured'?

REFERENCES

Bailey, R. G. (1983). Delineation of ecosystem regions. *Environmental Management*, **7**: 365–73

Biolley, H. E. (1921). *L'aménagement des Forêts par la Méthode Expérimentale et Spécialment la Méthode du Contròle*. Neuchatel, Paris

Camp, O. (1994). Critical elements of forest sustainability. *International Journal of Ecoforestry*, **10**(1): 7–10

Environmental Data Center (1993). *Manual for Integrated Monitoring: Programme Phase 1993–1996*. National Board of Waters and Environment, Helsinki

Frankel, O. H. and Soulé, M. E. (1981). *Conservation and Evolution*. Cambridge University Press, Cambridge

Gove, J. H., Patil, G. P., Swindel, B. F. and Taillie, C. (1994). Ecological diversity and forest management. In Patil, G. P. and Rao, C. R. (eds.) *Environmental Statistics, Handbook of Statistics*, Vol. 12. North Holland, Amsterdam, pp. 409–62

Gurnaud, A. (1878). *Cahier l'Aménagement pour l'Application de la Méthode par Contenance Exposée sur la Forêt des Eperous*. Admis à l'Exposition universelle de Paris en 1878. Troisíeme forme du cahier d'aménagement. Besançon, Paris

Köhl, M. and Zingg, A. (1996). Eignung von Diversitätsindizes bei Langzeituntersuchungen zur Biodiversität in Waldbeständen. *Allg. Forst u. Jagdztg*. **167**(4): 76–85

Magurran, A. E. (1988). *Ecological Diversity and its Measurement*. Croom Helm Ltd., London

Miller, D. H. (1978). The factor of scale: ecosystem, landscape mosaic and region. In Hammond, K. A. (ed.) *Source Book on the Environment*. University of Chicago Press, Chicago, pp. 63–88

Nyyssönen, A. (ed.) (1993). *Proceedings of FAO/ ECE Meeting of Experts on Global Forest Resources Assessment in Cooperation with UNEP and with the Support of FINNIDA (Kotka II)*, Kotka, Finland, 3–7 May 1993. Res. Papers 469. The Finnish Forest Research Institute, Helsinki

Peet, R. K. (1974). The measurement of species diversity. In Johnson, R. F., Frank, P. W. and Michener, C. D. (eds.) *Annual Review of Ecology and Systematics*. Annual Reviews, Inc., Palo Alto, pp. 285–307

Pielou, E. C. (1975). *Ecological Diversity*. J. Wiley and Sons, New York

Samson, F. B. and Knopf, F. L. (1994). Managing biological diversity. *Wildlife Society Bulletin*, **21**: 509–14

Whitcomb, R. F., Lynch, J. F., Klimkiewicz, M. K., Robbins, C. S., Whitcomb, B. L. and Bystrak, D. (1981). Effects of forest fragmentation on avifauna of the eastern deciduous forests. In Burgess, R. L., Sharpe, D. M. and David, M. (eds.) *Forest Island Dynamics in Man-dominated Landscapes*. Springer Verlag, New York, pp. 125–205

Wilcove, D. S., McLellan, C. H. and Dobson, A. P. (1986). Habitat fragmentation in the temperate zone. In Soulé, M. E. (ed.) *Conservation Biology: The Science of Scarcity and Diversity*. Sinauer Associates Inc., Sunderland, MA, pp. 237–56

Wilson, E. O. (1988). The current state of biological diversity. In Wilson, E. O. (ed.) *Biodiversity*. National Academy Press, Washington, DC, pp. 3–18

Article 7 – identification and monitoring

Integrated monitoring in biosphere reserves can assist the contracting parties in meeting the objectives of the Agenda for Scientific and Technological Research, which have been elaborated by the Intergovernmental Committee of the Convention. This ambitious agenda covers a full range of activity, from identifying representative ecosystems and their biodiversity to developing and demonstrating methodologies for the sustainable use of biodiversity. BRIM can facilitate and enhance the inventory of components of biodiversity (particularly those that are threatened), the monitoring of those components, the identification of processes and categories that have or are likely to have significant adverse impacts on biodiversity, and the maintenance and organization of data derived from inventory and monitoring.

Article 8 – *in situ* conservation

Biosphere reserves play an important role in the establishment of systems of protected areas and contribute to the protection of ecosystems, natural habitats, and the maintenance of viable populations of species in natural surroundings. BRIM can assist in furthering this role, especially in the promotion of environmentally sound and sustainable development in areas adjacent to protected places (Ständige Arbeitsgruppe der Biosphärenreservate in Deutschland, 1995).

Article 12 – research and training

Activities in most biosphere reserves include research and training. The direct connection to the international scientific community that the MAB programme – enhanced by BRIM – offers biosphere reserve personnel increases in their access to training and to research results elsewhere.

Articles 17 and 18 – exchange of information and technical and scientific cooperation

Integrated monitoring in biosphere reserves has the potential to open well-established, multi-disciplinary information highways to a broader audience. Regular contacts among biosphere reserves through BRIM can facilitate the exchange of data and technical and scientific methodologies.

OUTLOOK

As noted above, one difficulty in creating integrated monitoring projects is to achieve a truly interdisciplinary approach (Kruse-Graumann *et al.*, 1995). Most monitoring projects are dominated by natural scientists, but the development of

will be the task of the BRIM working group to propose methodologies for assuring integrated monitoring and to catalyze respective pilot projects. A first attempt to include the social science aspects of monitoring in BRIM requested information on permanent plots incorporating research on anthropogenic impacts. Forty-five biosphere reserves reported that to date, they contain permanent plots dedicated to monitoring anthropogenic impacts.

In conclusion, the MAB programmes of Germany and the United States, in cooperation with their MAB colleagues and programs throughout the EUROMAB region, hope that the combined BRIM activities will make a significant contribution to improve the quality and frequency of international cooperation in biodiversity monitoring and research programs.

REFERENCES

EUROMAB (ed.) (1993). *ACCESS: A Directory of Contacts, Environmental Data Bases, and Scientific Infrastructure on 175 Biosphere Reserves in 32 Countries.* USMAB, Springfield, VA

Interim Secretariat for the Convention on Biological Diversity (ed.) (1994). *Convention on Biological Diversity: Text and Annexes.* Interim Secretariat for the Convention on Biological Diversity, Chatelaine

Kerner, H. F., Spandau, L. and Köppel, J. G. (eds.) (1991). *Methoden zur angewandten Ökosystemforschung: Werkstattbericht MAB Mitteilungen 35.1 and 35.2.* German MAB National Committee, Bonn

Kruse-Graumann, L., *et al.* (eds.) (1995). *Proceedings of the EUROMAB Workshop Societal Dimensions of Biosphere Reserves: Biosphere Reserves for the People*, 23–25 January 1995, Königswinter. MAB Mitteilungen 41. German MAB National Committee, Bonn

Schönthaler, K., Kerner, H. F., Köppel, J. and Spandau, L. (1994). *Konzeption für eine Ökosystemare Umweltbeobachtung: Pilotprojekt für Biosphärenreservate.* Ufoplan Nr. 10104040/08 Vols. 1 and 2. Umweltbundesamt, Berlin

Schröder, W., Fränzle, O., Keune, H. and Mandry, P. (eds.) (1996). *Global Monitoring of Terrestrial Ecosystems.* Ernst & Son, Berlin

SRU (Council of Experts for Environmental Questions) (1991). *Allgemeine ökologische Umweltbeobachtung: Sondergutachten.* Metzler-Poeschel, Stuttgart

Ständige Arbeitsgruppe der Biosphärenreservate in Deutschland (eds.) (1995). *Biosphärenreservate in Deutschland: Leitlinien für Schutz, Pflege und Entwicklung.* Springer, Berlin

UNESCO (1984). Action plan for biosphere reserves. *Nature and Resources*, **20**(4): 11–22

UNESCO (ed.) (1996). *Biosphere Reserves: The Seville Strategy and the Statutory Framework of the World Network.* UNESCO, Paris

WBGU (German Advisory Council on Global Change) (1993). *World in Transition: Basic Structure of Global People–Environment Interactions.* Economica, Bonn

WBGU (German Advisory Council on Global Change) (1994). *World in Transition: The Threat to Soils.* Economica, Bonn

WBGU (German Advisory Council on Global Change) (1996). *World in Transition:*

Monitoring Programme (BRIM). It is overseen by a working group that meets at irregular intervals and reports to the EUROMAB Conference.

The activities of BRIM should help overcome the current shortcomings of the international network and set the stage for long-term cooperation and integrated environmental monitoring and research (Kerner *et al.*, 1991; Schönthaler *et al.*, 1994).

ACCESS

The first step must be to elaborate an inventory of the potential of the biosphere reserve network. On the basis of the 1987 UNESCO survey of the international biosphere reserve network, USMAB conducted an inquiry into the research and monitoring activities of the individual biosphere reserves that covered topics such as infrastructure and accessibility and also garnered the addresses and names of officials in the reserves. The resulting publication, known as ACCESS (EUROMAB, 1993), supplies the basic information for an open network and has been widely distributed.

Parallel to this activity, USMAB began developing a standardized protocol for monitoring flora and fauna in biosphere reserves in the EUROMAB region. The protocol has been tested and improved over several years, and part of it, MAB Fauna, was being readied for application.

ACCESS 1996

Once the ACCESS directory was under preparation, it became obvious that the publication was just the first step in creating a hierarchically structured system for making information available. Consequently, the German MAB National Committee agreed to undertake a second inquiry to document more of the details of the monitoring and research activities conducted in biosphere reserves. Because monitoring and research usually take place on permanent plots, a detailed questionnaire was sent to all EUROMAB biosphere reserves and the respective National Committees. The questionnaire was directed at discovering which biosphere reserves have permanent plots, what type of plots are maintained, and which topics are investigated at the plots.

The results of this survey will be published by USMAB in its capacity as the Secretariat for the EUROMAB BRIM Programme. The publication, titled ACCESS 1996: A Directory of Permanent Plots Which Monitor Flora, Fauna, Soil, Hydrology, Geology, Climate, and Anthropogenic Changes at 132 Biosphere Reserves in 27 Countries, should be available by the time this proceedings document is released. Like its predecessor, ACCESS 1996 will be published in paper/soft cover format as well as on the Internet at various web sites and locations. Readers can electronically access this new directory at http://WWW.UNESCO.ORG/MAB/The MABNet.htm/.

ACCESS 1996 will also contain a series of summary tables and charts depicting the biogeographic distribution of the various types of permanent plots by biome, using the UNESCO Udvary classification system. These tables will indicate not only the current coverage, or representative nature, of the biosphere reserves, but also will hint at one of the future tasks of the MAB Programme: to improve the coverage of the network and develop a system for indicating the representative nature of the ecosystems within biosphere reserves.

ACCESS 1996 will follow the format of the original ACCESS directory in identifying each biosphere reserve's administrative entity, latitude and longitude coordinates, and elevation. The publication will also summarize information concerning the permanent plots maintained at each biosphere reserve, including research objectives, management of data acquisition, data availability, and plot type and spatial distribution, and indicate whether the plots are situated in terrestrial, aquatic, or marine environments. The total number of plots will be listed along with the year each was established. To facilitate contact with the data base of each permanent plot at each biosphere reserve, ACCESS 1996 will provide the name of a contact person who is responsible for administration and coordination of the monitoring and research program and the telephone number and, where available, the Fax number and Internet/E-mail address of the contact. If the biosphere reserve maintains a home page on the World Wide Web, ACCESS 1996 will list the Uniform Resource Locator (URL) address.

Summary tables in the document will provide a quick reference by country, biosphere reserve, type of plots (by topic), their functional objectives, status of computerization of data, and their distribution within the biosphere reserve. Detailed summaries will be provided for permanent plots dedicated to flora, fauna, hydrology, anthropogenic impact, climate, soil, and geology.

Note that the Climate Convention calls for monitoring and research. In many of the biosphere reserves of the European region, monitoring of climate-relevant parameters is underway (WBGU, 1993, 1994, 1996). Access 1996 will provide an overview of more than 98 biosphere reserves in which monitoring or research dedicated to issues related to climate is occurring in permanent plots.

APPLYING BRIM: AN EXAMPLE

BRIM can assist parties to the Convention on Biological Diversity in fulfilling some of the requirements of the Convention (Interim Secretariat for the Convention on Biological Diversity, 1994), as described below.

Article 5 – cooperation

BRIM provides the link among biosphere reserves, each of which is under national sovereignty, and facilitates cooperation among the contracting parties by providing space.

actually be structural when considering the habitat of species dependent on the lichens. Different factors are likely to influence the diversity of these two groups (Huston, 1994), a consideration for researchers in developing and carrying out monitoring programs.

Many studies of species diversity can be related to different spatial scales through point, α-, β-, γ- and ε-diversity (Whittaker, 1977) – which are essentially equivalent to micro-habitat diversity, within-habitat diversity, between-habitat diversity, landscape diversity, and regional diversity (see also MacArthur, 1965). These equivalences are expressed for clarification only: it is possible to apply them at a variety of different scales (Allen and Starr, 1982; O'Neill *et al.*, 1986). Of the types just noted, α- and β-diversity tend to be the most widely used (Southwood, 1978; Magurran, 1988). Pattern diversity (Palmer, 1990; Zobel *et al.*, 1993) also needs to be considered, with the basic assumption being that this is the variation attributable to species interactions as opposed to environmental gradients.

In practice, several on-going programs have adopted a fairly coarse approach to assessing ecosystem and species diversity. For example, Radcliffe *et al.* (1994) primarily considered only vertebrates, specifically excluding vascular plant diversity and discounting fungi and insects on the basis that there was insufficient information available about them. Such an approach probably reflects the potential interest in species diversity; there is considerably more public concern about the presence of bears than a micro-lepidopteran (see below).

The value of long-term monitoring has been demonstrated sufficiently often to preclude the need for any further justification (Strayer *et al.*, 1986; Likens, 1989; Peterken, 1993b). Long-term monitoring of various aspects of biodiversity has a substantial history, and considerable data are available. However, much of this information is fragmented and site-specific, making interpretation difficult. This paper describes a program in Switzerland that is currently in its initial stages. It is an interdisciplinary program associated particularly with assessing the effects of air pollution and climatic change on forest ecosystems. The basic project has been described by Innes (1994), and the details of the criteria used in the selection of the monitoring plots are given in Innes (1995). Biodiversity is included as one of a series of ecosystem characteristics that need to be included in any assessment of ecosystem change.

METHODS FOR ASSESSING BIODIVERSITY BASED ON TAXONOMY

Species diversity has been the subject of many investigations. Traditional approaches have generally considered diversity as consisting of two components – the variety and the relative abundance of species. These are assessed for specific groups and/or functional types and can either be measured separately or combined into some form of index. Assessments of variety are relatively easy

area (i.e. species density). This is different from species richness, which is the number of species that occur within a given number of individuals or biomass (Kempton, 1979).

A number of indices have been devised that take into account both the number of species and their relative abundance. Further information on numerical measures of α-diversity is given by Magurran (1988) and Krebs (1989). These and other measures of α-diversity are purely numerical and, as to be expected, involve the loss of information when they are calculated. For example, the indices do not take into account species composition, and a spruce forest would have the same index value as a beech forest provided that the numbers and relative abundance of the species were the same. While much effort has been expended on comparing the different indices, such studies have contributed little to the general mechanisms underlying species diversity (Huston, 1994). In addition, the value of statistics dealing with overall diversity within an ecosystem is of questionable ecological relevance, since they reveal nothing of the processes occurring in the system or of the relative functions of the organisms in it.

To assess the different scales of diversity within an area, a much more integrated approach is required that includes not only species abundances but also their functions, sizes, spatial distribution, and other information (see for example, the dominance–diversity curves of Whittaker, 1965, 1975, and the standardized methods for assessing amphibians presented in Heyer *et al.*, 1994). Consequently, in recent years, a range of methods has been used to assess biodiversity. In particular, attention has focused on indicator species and functional groups, whether as 'keystone species' (Paine, 1966), indicators of particular environmental conditions (Kremen, 1992), or indicators of guilds (Root, 1967) that are believed to respond to environmental change in a similar fashion. Noss (1990) recognizes several other indicator types in addition to the above, including 'umbrellas' (species with large-area requirements that, if protected, will also protect a variety of species with smaller area requirements), 'flagships' (popular, charismatic species that can attract the attention of the public), and 'vulnerables' (species that are viewed as being at risk). The indicator approach has a number of problems (Verner, 1984; O'Neill *et al.*, 1986; Block *et al.*, 1987; Landres *et al.*, 1988), but these can sometimes be overcome if sufficient care is taken with indicator identification (Pearson, 1994).

Assessments of indicators are based not only on presence or absence, but also on population dynamics. Very often, indicators are believed to be endangered species. Recent developments in the United States have concentrated on the preservation of forest habitat for the northern spotted owl (*Strix occidentalis* subsp. *caurina*) (Thomas *et al.*, 1990) and the red-cockaded woodpecker (*Picoides borealis*). By providing 'old-growth' habitats for these two species, together with all the necessary ecosystem structures to enable a transfer of individuals between forest areas, the maintenance of populations of many other species is believed to be ensured. A wide range of potential indicator species

CHAPTER 22

ASSESSMENT OF BIODIVERSITY IN ECOSYSTEM MONITORING PLOTS WITH PARTICULAR REFERENCE TO SWITZERLAND

John L. Innes, Walter Keller and Ruedi Boesch

INTRODUCTION

Biodiversity, as defined in Europe and under the Convention for Biological Diversity, is 'the variability among living organisms from all sources, including *inter alia* terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species, and of ecosystems. Biological diversity encompasses not only species but also ecological structures, functions and processes'.

Under this definition, biodiversity is more of a concept than a measurable phenomenon. Consequently, most studies have concentrated on those measurable aspects of biodiversity such as the species diversity of particular groups that can be determined, and there are as yet no holistic studies covering the complete species diversity of an area. This deficiency may not be significant from an ecological point of view because the number of species present in an area is probably less important than the viability of the ecosystem functions in that area (Goodman, 1975, Pielou 1977). For example, while boreal forests have lower numbers of species than tropical forests, this does not impair their biological significance (if such a phenomenon can be defined). In the context of forest ecosystems, it would be possible to increase the biological diversity of a natural area by replacing part of the natural vegetation with introduced species, but doing so clearly does not represent an improvement in biodiversity.

Current ecological and political concern is focused on losses of biodiversity and on ways in which these losses can be halted or reversed. Thus, monitoring changes in biodiversity is seen by many as a priority for research.

The available literature indicates that it is possible to assess the biological variation of particular groups of organisms (e.g. amphibians, birds, or higher plants). A fundamental division exists here between structural and interstitial species. According to Huston (1994), structural species are those species that create or provide the physical structure of the environment. Interstitial species are those that are dependent on the structural species. In relation to forests, the structural species are often considered to be the trees, but they may also include some shrub and herb species. However, the concept is scale-dependent, and species that might normally be considered as interstitial, such as lichens, may although it is frequently assumed that results from one geographical region can be readily transferred to another, this is not always the case. European bird species seem to be much more eclectic in their habitat requirements than those in North America (Järvinen and Väisänen, 1980; Hansson; 1994) as an example, and the relationships between patch size and the occurrence of species typical of the forest interior that have been developed in North America are seemingly inapplicable in Europe, although some aspects of stand structure may be (Tellería *et al.*, 1992). Even a species such as the black woodpecker (*Dryocopus martius*) that may be considered typical of European 'old-growth' forests can occur in a wide range of different forest types, provided that there are enough sufficiently large trees for nesting, and will forage on open ground. In such studies, it is important to separate different guilds and analyze them separately. When this is done, relationships may become apparent that were not so when the overall species diversity was considered (Hansen *et al.*, 1994).

Another problem concerns the differential use of habitat types. Referring to European forest bird species, while some have very narrow requirements, a number seem to be dependent on the presence of a mosaic of different structural (successional) stages. These include the woodlark (*Lullula arborea*), nightjar (*Caprimulgus europaeus*), wryneck (*Jynx torquila*), and green woodpecker (*Picus viridis*)(Avery and Leslie, 1990; Bowden, 1990; Simberloff, 1995). Such a mosaic has been recognized in forests for many years (Cooper, 1913), and it tends to be accentuated by forest management. However, in Europe, there has been a trend toward decreasing use of forest resources and a general aging of the tree population (Kauppi *et al.*, 1992), suggesting that the balance between early and late-successional habitat stages is changing. This is typical of the type of phenomenon that needs to be resolved through careful monitoring.

There are various ways in which the data from studies of vertical and horizontal structure can be analyzed. The majority of the techniques used to relate plant communities to environmental indicators are of relevance here (Ter Braak, 1987; Wildi and Orlóci, 1990; Debinski and Brussard, 1994) as are a number of other methods used in quantitative plant ecology (see Digby and Kempton, 1987). Considerable care is needed with the derivation and interpretation of multivariate indices because they are often difficult to relate to any actual phenomenon (Peters, 1991).

A variety of measures of β-diversity are available. For data related to species presence–absence data, these include β_W (Whittaker, 1960); β_C (Cody, 1975); β_R, β_I, and β_E (Routledge, 1977); and β_T (Wilson and Schmida, 1984). These are all variable in their relative efficiency and, as with species diversity indices, the choice of which index (or which range of indices) to use is strongly dependent on the objectives of the study. Wilson and Schmida (1984) emphasize that any evaluation of the performance of these indices should take into account a number of factors, including the turnover of species between different habitats, the requirement that the indices are additive, the need for independence from the

best of these, given the above requirements and in relation to analyses of variation across environmental gradients, was β_T. This can be expressed by:

$$\beta_T = \frac{g(H) = l(H)}{2\alpha}$$

where g is the gain and l the loss of species along a gradient H, and α is the average number of species found within each habitat or community.

Assessment methods derived from landscape ecology

Landscape ecology offers considerable potential for the assessment of biodiversity. Many of the techniques in use are quite old, having been developed in geography, but the use of modern technology such as geographic information systems has greatly speeded up the type of analysis that can be done (Kienast *et al.*, 1994). The basic elements of landscape ecology, namely patches, edges and corridors, can be readily quantified and monitored over time. Difficulties may arise when attempts are made to analyze the ecological significance of these units. The importance of horizontal patchiness in explaining species diversity is well known (Roth, 1976; Wiens *et al.*, 1987; Gerell, 1988), although it is dependent on how the patches are defined. In addition, the recognized relationship between patch size and diversity (Gleason, 1922, and many studies since) adds a complicating factor to any interpretation of patchiness, as does the degree of isolation of individual patch types (Lynch and Whigham, 1984; Askins *et al.*, 1987) and the history of individual patches (Lovejoy *et al.*, 1983, 1986; Hermy, 1994; Rescia *et al.*, 1994). Explanations for supposed relationships between patch sizes, fragmentation and species diversity are frequently given but these are often unsupported by empirical studies or rely heavily on quite site-specific case studies (Huston, 1994; Wiens, 1995). In particular, the use of mobile groups of organisms (e.g. birds) in the study of patch diversity is often complicated by interactions among individuals from different patches, invalidating many of the theories and suppositions associated with avian metapopulation dynamics (Harrison, 1991; Simberloff, 1995).

Other groups may be much less mobile and therefore more suitable for study. Many invertebrates are more habitat-specific than birds and also tend to interact less with neighboring populations (Thomas, 1995). However, the links between habitat and population dynamics are unclear; population extinctions have been recorded at the same time as increases in adult food plant availability. It is the immature stages of many invertebrates that appear to be extremely specific in their habitat requirements, whereas surveys are often made of the adult abundance (Thomas, 1995).

Edges are also known as an important factor affecting diversity, particularly in avian communities, and there is a substantial literature covering this area.

be made. However, it is clear that a number of different indicators will be required. The danger exists that these indicators will in the future prove less useful than originally thought, but the status of ecological knowledge today is such that the level of risk appears acceptable. By encompassing a sufficient number of indicators, a sufficiently comprehensive picture may be possible.

Pearson (1994) has suggested that the choice of indicators should be based the following requirements:

(1) the indicators are taxonomically well-known and stable,

(2) their biology and general life history is well-understood,

(3) their populations are readily surveyed and manipulated,

(4) higher taxa occupy a breadth of habitats and a broad geographical range,

(5) there is a specialization of each population within a narrow habitat,

(6) the patterns observed in the indicator taxon are reflected in other related and unrelated taxa, and

(7) the indicators are of potential economic importance.

The priority ranking of these criteria depends on whether the indicators are being used for environmental monitoring or for biological inventories. No one indicator can reflect all values; thus, a combination appropriate to the scale of the study should be chosen (Noss, 1990).

Surrogates for species diversity in forests

The investigation of the structural and functional diversity of forests has received considerable attention over the past 30 years. Many of the principles have developed from the perceived need to maintain a number of different successional stages within the landscape (Franklin, 1988), and the assessment of structural diversity has become a goal in itself. This perhaps reflects the view that structure includes not only the spatial and temporal abundance of species, but also resource allocation; niche relations; species-area; food webs; body-size relations; foraging techniques; age distribution; vertical, horizontal, and temporal distributions; and morphology (McIntosh, 1995). The surrogate approach is based on the supposition that a more complex habitat will support a greater variety of species (MacArthur *et al.*, 1962), and this appears to be supported by empirical observations (Johnston and Odum, 1956; MacArthur and MacArthur, 1961; Recher, 1969; Karr and Roth, 1971; Lovejoy, 1972; Moss, 1978; Urban and Smith, 1989). However, exceptions occur (Orians, 1969; Ralph, 1985; Hansen *et al.*, 1994), and vertical complexity does not necessarily provide an explanation for variations in animal species richness (Flather *et al.*, 1992). A large literature base details niche separation within habitats, and the quantification of the structural elements having a relationship with niche dimensions are reasonably

well-known for some species groups (Cody, 1974; Verner, 1984; Szaro, 1987). The process has been formalized through the development of resource matrices (Colwell and Futuyma, 1971). Methods for summarizing these into indices are provided by Levins (1968), Hurlbert (1978) and Smith (1982), among others, assuming that the derivation of indices has a value.

At its coarsest level, the use of structural diversity as a surrogate for species diversity involves the development of habitat affinity tables, which can be expanded to include affinity tables for different stages of habitat development and different habitat structures. Within Europe, this approach is aided by the substantial body of information that is available for many species, particularly vertebrates and higher plants. However, for vertebrates, much of this information is related to relatively large scales (e.g. forest type), and detailed information on the precise habitat preferences of individual species is often only available for rare and endangered species, particularly where conservation interests have spurred research into precise habitat requirements (e.g. for the capercaillie, *Tetrao urogallus*) (Leclercq, 1987; Rolstad and Wegge, 1987; Angelstam, 1992; Storch, 1993a, 1993b, 1994). In addition, the temporary use of habitats (e.g. during dispersal) needs to be taken into account (Hanski, 1991; Wiens *et al.*, 1993). Even less is known about the requirements of invertebrates, with only limited information being available for most groups. Given that the greatest diversity in forest ecosystems normally occurs within the invertebrates – in a wood in Cambridgeshire, England, Steele and Welch (1973) recorded that invertebrates represented at least 76% of the fauna – the lack of information on most faunal and several floral groups represents a significant limitation. It is extremely unlikely that the autoecological requirements of all species within an area will ever be known. As a result, autoecological studies of habitat requirements have fallen out of favor among ecologists (Simberloff, 1995).

Within habitats, several methods have been developed (Elton and Miller, 1954; Bunce and Shaw, 1973), ranging from traditional assessments of stand structure (e.g. size distribution) and vertical zonation (Davis and Richards, 1933–34; Cyr, 1977) to much more detailed assessments of the dead wood in forests (Hunter, 1990; Ratcliffe, 1993) or the vertical structure of the habitat (Short, 1982, 1988; Streeter *et al.*, 1983). The majority of this work has been developed within the North American context, where standing dead wood and fallen stems are believed to form an important part of the forest ecosystem (Samuelsson *et al.*, 1994). A major difficulty with the approach has been the relationship between these structural indicators and the actual species diversity at a site (Schamberger, 1988). For example, the presence of dead wood alone is of little relevance as an indicator and, in some cases, the species diversity of some groups may be independent of the presence of dead wood (Hansen *et al.*, 1994).

The majority of studies that have been undertaken to date are relatively local (of necessity) and it is unclear to what extent the results obtained from one area can be applied to another. This becomes clear when the ecological functions of dead wood in different regions are compared (Harmon *et al.*, 1986). In addition,

Table 22.3 Observed tree species distributions compared to predicted occurrences from the phytosociological tables of Frehner (1963) and Kuoch (1954). Values for the plots are given as percentages of the trees present. Predicted values refer to the percentage of original field plots that held a given species; superscripts indicate abundance (Braun–Blanquet classification scheme for a 250 to 400-m^2 plot: r = one or two individuals; + = < 10 individuals; 1 = > 10 individuals, < 5% of surface area; 2 = 6 to 25% surface area; 3 = 26 to 50% surface area)

Tree species	*Othmarsingen*			*Alptal*		
	Plot 1	*Plot 2*	*Predicted*	*Plot 1*	*Plot 2*	*Predicted*
Picea abies	10	27	100^{2-3}	71	94	100^{2-3}
Abies alba	3	0	88^{2-3}	12	5	100^{3}
Fagus sylvatica	70	72	100^{2-3}	0	0	94^{+-1}
Quercus robur	1	1	32^{+-1}	0	0	0
Quercus petraea	5	0.4	64^{+-1}	0	0	0
Carpinus betulus	4	0	64^{+-1}	0	0	0
Tilia cordata	4	0	8^{+}	0	0	0
Sambucus nigra	3	0	68^{+-1}	0	0	0
Acer pseudoplatanus	0	0	28^{+-1}	0.4	0	31^{r}
Fraxinus excelsior	0	0	8^{r-+}	0.4	0	36^{r}
Alnus incana	0	0	0	17	1	25^{r}

Othmarsingen, the natural vegetation type would be Galio odarati-Fagetum typicum, typical variation, and the *Carex pilosa* variation, following Frehner (1963). At Alptal, it would be Equiseto-Abietetum, following Kuoch (1954). The typical tree species for Othmarsingen is *Fagus sylvatica*, and the influence of forestry practices is revealed by the presence of *Picea abies* and *Abies alba*. At Alptal, forestry practices are responsible for the absence of *F. sylvatica*, the dominance of *P. abies*, and the presence of *A. alba* in the dominant and co-dominant canopy layers. Further information on the use of this classification scheme can be found in Ellenberg (1988).

Use of forest structure as a surrogate

A basic tool used in the assessment of vertical stand structure is hemispherical photography. Photographs are taken on a fixed grid throughout the plot, and the images are subsequently electronically scanned. This provides a variety of information, including estimates of leaf area (in broad-leaved stands), estimates of the light penetration at ground level, and a quantitative assessment of vertical stand structure. As the coordinates of the photography points are known to the nearest cm, the assessments can be repeated over time. All other measurements are also geo-referenced, making it possible to establish a link between, for example, leaf area at a point and throughfall chemistry.

Quantitative assessments of specific vertical strata have been recommended by Short (1982, 1988). These are rather limited, and in the Swiss program,

Table 22.4 Structural indicators used for the assessment of biodiversity (order of indicators has no significance)

Stem density, basal area, and average dbh of trees:
  total, by species, by size class
Stem density of shrubs:
  total, by species
Stem density, basal area, and average dbh of seedlings:
  total, by species
Density of snags:
  total, 10 to 24.9 cm dbh, >25.0 cm dbh, by species
Decay class of snags
Percent canopy closure:
  total, by species
Height to bottom and top of main crown canopy
Height of identifiable layers within the canopy
Average height of shrub layer
Percent of ground surface coverage:
  by species, rock or bare soil, coarse woody debris (including decay class), litter
Potential natural vegetation
Litter depth
Epiphyte diversity:
  on deciduous species, on coniferous species, number of species, abundance
Leaf area:
  Total, by species

more detailed above-ground stratification is used (Table 22.4). The basic model still needs to be tested in Switzerland using, for example, avian guilds. In particular, the utilization of defined habitats needs to be assessed through detailed field work involving the target species/functional groups and the subsequent data analyzed using, for example, Bonferroni-Z tests (Neu *et al.*, 1974).

Several stand characteristics are taken directly from maps made of the plots. The maps are generated from low-level aerial photography combined with ground surveys and include crown positions and dimensions, vegetation types, snags, coarse woody debris and other features. The maps are supplemented with a list of stand characteristics that are routinely assessed as part of the integrated program (Table 22.4). The choice of stand indicators reflects past studies of forest structure (Busing and White, 1993; Kruse and Porter, 1994). Assessments of the potential redundancy in the list is part of an on-going research project associated with the monitoring program. Many of these assessments are made as measurements related to studies of phenomena (such as stand growth and regeneration) other than biodiversity.

Several structural characteristics of the plots are also of interest for subject areas (such as silviculture) other than biodiversity. The main problem is determining the area over which such assessments should be made because many aspects of species diversity require an area larger than 2 ha. Some of the measures are extended to a 30-ha area, or even to the entire catchment, and the is discontinuous, and grazing occurs in both open areas and in the forest. Annual precipitation is 2,200 mm, 40% of which falls as snow. The mean annual temperature is 5 °C. The area was largely cleared from the fourteenth to the nineteenth century, but has since been partially reforested. Hydrological monitoring began in 1968 to assess water quantity and quality, and a meteorological station was installed in 1982. Monitoring and research activities were increased in the period from 1985 to 1989 when the site became one of three intensively researched forest ecosystems in Switzerland (Schüpbach, 1991). Since 1989, a number of research activities have been undertaken, resulting in a considerable amount of data on ecological processes operating within the catchment.

Species inventories

Most of the considerable work carried out on the diversity of site and vegetation types in Switzerland has concentrated on the higher plants (see, for example, Ellenberg and Klötzli, 1972, for a detailed description of the different forest types present in Switzerland). Much less is known about other species groups, although there have been several studies of endangered or declining species such as the Scops owl (*Otus scops*) (Arlettaz *et al.*, 1991).

The limitations associated with the use of diversity indices for species groups alone can be illustrated by tree data from the Long-Term Forest Ecosystem Research Programme in Switzerland. Data are available for two sites, Othmarsingen in the canton Aargau and Alptal in the canton Schwyz, each with two plots having been assessed. The data refer to the numbers of trees with a diameter at breast height greater than 5 cm. At the two sites, all trees within a 2-ha area were assessed, with the data for each ha being reported separately. The basic data are presented in Table 22.1. In Table 22.2, the various indices for the four sites are shown. The number of tree species varied between the sites, but this alone is a poor index of the diversity of the site. The highest values for the Shannon (H) and the Simpson ($1-D$) indices and the lowest value of the Berger–Parker index (d) were recorded in the plot with the greatest number of species. However, one of the Alptal plots had very similar values, reflecting the mixed nature of the stand. Although these indices are of interest, all the information on the structure (size distribution) of the stand is lost.

These limitations are not new. They have been recognized for a considerable time (Hurlbert 1971; Peet, 1974; Krebs, 1989; Spellerberg, 1991). Each index has specific advantages and disadvantages (Magurran, 1988), with some (e.g. log series α, log normal λ, the Q statistic, and the Margalef index) having much better discriminating abilities than others. It is therefore rather surprising that particular indices (dominance/evenness), known to have poor discriminating abilities (the Berger–Parker index, Shannon evenness, and Brillouin evenness) continue to be used on their own. Instead, the use of several diversity indices, combining one or more richness indices, an evenness index, and assessments of

Table 22.1 Tree species and social class of trees in four 1-ha monitoring plots (D = dominant; Cod = codominant; Subd = subdominent; Supp = suppressed)

Tree species	*# stems*	*D*	*Cod*	*Subd*	*Supp*
Othmarsingen 1					
Picea abies	20	2	–	2	16
Abies alba	6	1	–	2	3
Fagus sylvatica	147	64	27	24	32
Quercus robur	2	–	2	–	–
Quercus petraea	11	3	7	1	–
Carpinus betulus	8	–	3	5	–
Tilia cordata	8	6	2	–	–
Sambucus nigra	7	–	–	1	6
Othmarsingen 2					
Picea abies	63	–	–	5	58
Fagus sylvatica	168	79	50	8	31
Quercus robur	3	1	2	–	–
Quercus petraea	1	–	1	–	–
Alptal 1					
Picea abies	168	70	74	22	2
Abies alba	28	10	8	8	2
Acer pseudoplatanus	1	–	1	–	–
Fraxinus excelsior	1	1	–	–	–
Alnus incana	40	5	33	2	–
Alptal 2					
Picea abies	336	136	135	45	20
Abies alba	18	9	5	3	1
Alnus incana	4	2	–	2	–

Table 22.2 Various measures of diversity for the tree layer in two 1-ha plots at each of two Swiss sites (H = Shannon index; d = Berger–Parker index; D = Simpson index)

Site	*# species*	*H*	*d*	*1-D*
Othmarsingen 1	8	1.14	0.70	0.49
Othmarsingen 2	4	0.67	0.71	0.42
Alptal 1	5	1.01	0.71	0.46
Alptal 2	3	0.26	0.94	0.12

the species abundance distribution, appears to have considerable value (Magurran, 1988).

The tree species distributions shown in Table 22.1 indicate what is currently present. This reflects the influence of selective forestry and provides no indication of the extent to which the forest stand has been changed. In Table 22.3, the proportions of each species and the proportions that would be expected (as derived from the reference plots for the respective forest types) are given. At

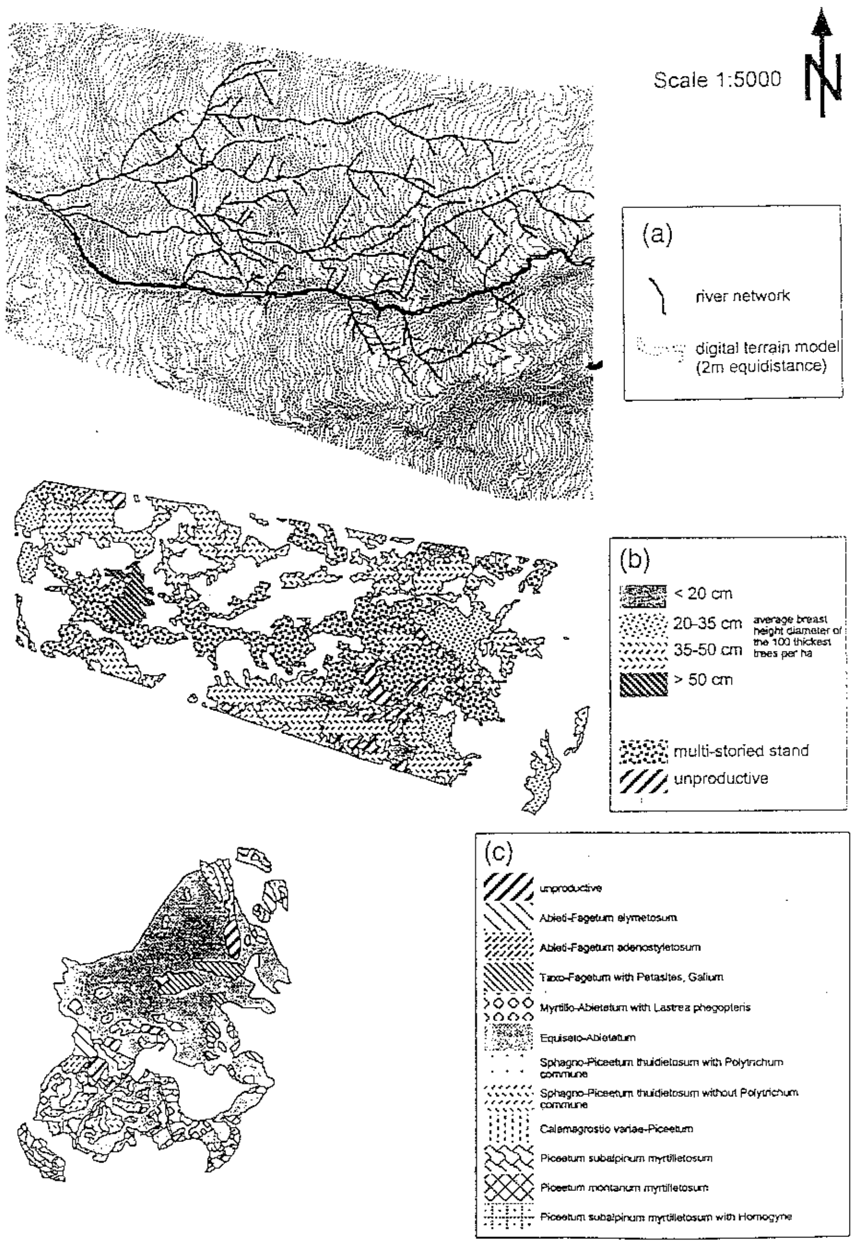

Figure 22.1 (a) Digital terrain model and hydrological map for the Erlentobel catchment in Alptal (b) Stand map for the catchment. Six classes of forest stand are recognized, based on the average dbh of the thickest 100 trees/ha. Unmarked areas represent meadows (c) Potential natural vegetation for a part of the Erlentobel catchment. The blank areas are improved meadows where the PNV is no longer discernable. The classification follows

how landscape heterogeneity may change under different scenarios and enable the quantitative assessment of landscape heterogeneity on successive occasions.

Modeling is particularly useful for assessing the potential effects of a change in environment on the biodiversity of an area. Such changes are normally driven by external forcing factors, such as climate or stand management practices. Modeling is likely to be a key factor in any attempt to assess whether the aims of biodiversity conservation are being achieved within Swiss forests.

Two parallel lines are currently being developed. One set of models is based on gap-phase dynamics and looks at the development of individual species under changing environmental conditions (Kräuchi, 1994). The other model (FORCYTE) is driven by nutrient dynamics and looks at long-term changes in nutrition and biomass, given particular starting points and management regimes. Both model types are being calibrated with data from the monitoring plots so that site-specific scenarios can be developed and tested later.

CONCLUSIONS

A variety of measures are available to assess biodiversity in forests. A critical factor is how biodiversity is defined; this will strongly influence how the assessments are approached. In addition, the purpose of the assessments is important as different methods will be used if biodiversity is being assessed or if aspects of biodiversity are being assessed as a surrogate for other processes. It is very important to look at biodiversity at a variety of scales. At the finest scale, it involves the diversity of genetic material. Methods exist to assess this, but it also important to consider the flow of genetic material. For example, with animals, it is important to consider within the theme of biodiversity the ability of animals to move from one area of habitat to another. In this respect, the degree of fragmentation of the landscape provides a measure of the genetic flow capabilities, although the nature and ecological significance of fragmentation needs to be evaluated carefully for each species under study (Wiens, 1995).

Species inventories and assessments of the relative abundance of species provide useful measures of a particular aspect of biodiversity. It is extremely unlikely that any exhaustive lists of all species present in each forest area will ever be compiled. At present, no such list exists for any forest in Switzerland. A recurrent problem with such lists will be to establish a baseline. What is the normal abundance of particular species? The Ellenberg–Klötzli classification system for forest vegetation does not help in this respect, although the empirical information upon which it is based could be used as a baseline against which future changes can be measured. The baseline can be checked against other historical data, but explanations for historical variations in species abundance are generally unavailable.

Structural diversity within and between stands provides a partial surrogate for the inventory of some of the more difficult species groups such as the determination of which other measures should be extended spatially is the subject of on-going research. A link between the structural parameters and the species diversity of specific groups has not yet been made, and this is also a subject of research.

Long-term process monitoring

As it is impossible to measure all processes within a forest ecosystem, decisions are needed as to which processes to monitor. The processes can be broadly divided into abiotic and biotic, although clearly there is an interface between the two. Generally, the abiotic factors (climate, pollution, soil chemistry, etc.) drive the biotic processes, and some degree of concentration on the abiotic processes therefore seems appropriate. Table 22.5 lists the abiotic processes that are being monitored within the Swiss forest monitoring program.

Table 22.5 Abiotic processes assessed in the monitoring plots (some assessments not made in all plots)

Within the forest plot	*Outside the forest*
Meteorology:	
Air temperature	Air temperature
Air humidity	Air humidity
Wind speed	Wind speed
UV-B radiation	
Photosynthetically active radiation	Photosynthetically active radiation
Precipitation	Precipitation
	Soil temperature (2 depths)
	Soil humidity (2 depths)
	Throughfall
	Stemflow
	Soil moisture availability
Nutrient flux:	
Precipitation chemistry	Throughfall chemistry
Stream chemistry	Stemflow chemistry
	Soil-water chemistry
	Litter chemistry
	Heavy metal deposition
Atmospheric Pollution	O_3, SO_2, NO_x, CO_2
Pedological changes: Soils are sampled in detail every 10 years. Chemical, physical, and mineralogical analyses are undertaken by horizon and by fixed depths	
Nutritional status: Nutritional status of the main tree species is determined every two years. The analyses cover N, S, P, Ca, Mg, K, Na, Zn, Mn, Fe, Cu, F, Cl, Cd, Pb, Al, and B	

In considering ecosystem processes, it is important to remember that the processes may not have a direct relationship to species diversity. This is a fundamental point that must be taken into account if the broader definition of biodiversity is accepted. Many biotic processes within the ecosystem (e.g. primary production) may be more directly influenced by environmental factors than the species present. Indeed, some processes, such as certain types of chemical fractionation within the soil, may be entirely abiotic.

A variety of biotic processes are included in the routine assessments. These include regeneration, mortality, net primary production, litter production, litter decomposition, and live biomass accumulation. Methods are currently being sought to extend these measurements to include gross photosynthesis, leaf respiration, and decomposer respiration. As with many of the structural aspects of diversity, these process measurements represent an end in themselves. As an example, there is considerable concern over the possible effects of increased nitrogen deposition in the plots. While experimental research is required to fully answer this, the assessment and monitoring of processes involving nitrogen will generate hypotheses and also enable some hypotheses – generated, for example, by modeling – to be assessed.

Landscape ecology

Within Switzerland, the first stage in such an assessment is the preparation of detailed maps of the site and vegetation types. This has already been undertaken by some cantons (Schmider *et al.*, 1993), but for many parts of Switzerland, the best maps available are the national topographical maps. Reviews of the methods available can be found in Burrough (1986) and Turner and Gardner (1991).

The process can be illustrated by a preliminary analysis that has been taken at one of the intensive monitoring plots in the Swiss program. The basic underlay is the digital terrain model and hydrology for the site (Figure 22.1a). This is supplemented by a stand map derived from aerial photography (Figure 22.1b) and a map of the potential natural vegetation (Ellenberg and Klötzli, 1972; Keller *et al.*, 1986) gained by intensive ground mapping (Figure 22.1c). Other detailed information available but not shown here relates to geology, geomorphology and soils. These preliminary data were expanded during the 1995 field season and will be used for the development of a structural diversity data base for the Alptal site. Other sites will be included in the future.

Modeling

Modeling forms a critical part of the assessment of biodiversity. The models may be simple assessments of diversity, or they may be complex models of ecosystem development under current or changing environmental conditions as, for example, developed for Derborence (Valais) and Zürichberg (Zürich) by Kräuchi (1994). In relation to biodiversity, modeling can provide predictions of

Ellenberg, H. and Klötzli, F. (1972). Waldgesellscaften und Waldstandorte der Schweiz. *Mitt. Eidg. Anst. forstl. Versuchsw.*, **48**: 587–930

Elton, C. S. and Miller, R. S. (1954). The ecological survey of animal communities: with a practical system of classifying habitats by structural characteristics. *Journal of Ecology*, **42**: 460–96

Flather, C. H., Brady, S. J. and Inkley, D. B. (1992). Regional habitat appraisals of wildlife communities: a landscape-level evaluation of a resource planning model using avian distribution data. *Landscape Ecology*, **7**: 137–47

Franklin, J. F. (1988). Structural and functional diversity in temperate forests. In Wilson, E.O. (ed.) *Biodiversity*. National Academy Press, Washington, DC, pp. 166–75

Franklin, J. F., Cromack, K., Denison, W., McKee, A. W., Maser, C., Sedell, J., Swanson, F. and Juday, G. (1981). *Ecological Characteristics of Old-growth Douglas-fir Forests. General Technical Report PNW-118.* USDA Forest Service, Pacific Northwest Forest and Range Experimental Station, Portland, OR

Frehner, H. K. (1963). Waldgesellschaften im westlichen Aargauer Mittelland. *Beitr. Geobot. Landesaufn. Schweiz.*, **44**

Gardner, R. H. and O'Neill, R. V. (1991). Pattern, process, and predictability: The use of neutral models for landscape analysis. In. Turner, M. G. and Gardner, R. H. (eds.) *Quantitative Methods in Landscape Ecology: The Analysis and Interpretation of Landscape Heterogeneity*. Springer Verlag, New York, pp. 289–307

Gerell, R. (1988). Faunal diversity and vegetation structure of some deciduous forests in South Sweden. *Holarctic Ecology*, **11**: 87–95

Geuse, P., Bauchau, V. and Le Boulenge, E. (1985). Distribution and population dynamics of bank voles and wood mice in a patchy woodland habitat in central Belgium. *Acta Zoologica Fennica*, **173**: 65–8

Gleason, H. A. (1922). On the relation of species and area. *Ecology*, 3: 158–62

Goodman, D. (1975). The theory of diversity-stability relationships in ecology. *Quarterly Reviews in Biology*, **50**: 237–66

Greatorex-Davies, J. N. (1991). Woodland edge management for invertebrates. In Ferris-Kaan, R. (ed.) *Edge Management in Woodlands*. Forestry Commission Occasional Paper 28. Forestry Commission, Edinburgh, pp. 25–30

Gulinck, H., Walpot, O. and Janssens, P. (1993). Landscape structural analysis of central Belgium using SPOT data. In Haines-Young, R., Green, D. R., Cousins, and S. H. (eds.) *Landscape Ecology and GIS*. Taylor and Francis, London, pp. 129–39

Haggett, P., Cliff, A. D. and Frey, A. (1977). *Locational Methods*. Edward Arnold, London

Hansen, A. J., Vega, R. M., McKee, A. W. and Moldenke, A. (1994). Ecological processes linking forest structure and avian diversity in western Oregon. In Boyle, T. J. B. and Boyle, C. E. B. (eds.) *Biodiversity, Temperate Ecosystems, and Global Change*. Springer Verlag, Berlin, pp. 217–45

Hanski, I. (1991). Single-species metapopulation dynamics: Concepts, models and observations. *Biological Journal of the Linnean Society*, **42**: 17–38

Hansson, L. (1993). Bird numbers across edges between mature conifer forest and clearcuts in central Sweden. *Ornis Scandinavica*, **14**: 97–103

Hansson, L. (1994). Vertebrate distributions relative to clear-cut edges in a boreal forest landscape. *Landscape Ecology*, **9**: 105–15

Harmon, M. E., Franklin, J. F., Swanson, F. J., Sollins, P., Gregory, S. V., Lattin, J. D., Anderson, N. H., Cline, S. P., Aumen, N. G., Sedell, J. R., Lienkaemper, G. W., Cromack, K. and Cummins, K. W. (1986). Ecology of coarse woody debris in

Harrison, S. (1991). Local extinction in a metapopulation context: An empirical evaluation. *Biological Journal of the Linnean Society*, **42**: 73–88

Haslett, J.R. (1994). Community structure and the fractal dimensions of mountain habitats. *Journal of Theoretical Biology*, **167**: 407–11

Hermy, M. (1994). Effects of former land use on plant species diversity and pattern in European deciduous woodlands. In Boyle, T. J. B. and Boyle, C. E. B. (eds.) *Biodiversity, Temperate Ecosystems and Global Change*. Springer Verlag, Berlin, pp. 123–44

Heyer, W. R., Donnelly, M. A., McDiarmid, R. W., Hayek, L. C. and Foster, M. S. (eds.) (1994). *Measuring and Monitoring Biological Diversity. Standard Methods for Amphibians.* Smithsonian Institution Press, Washington, DC

Hobbs, R. J. (1992). The role of corridors in conservation: Solution or bandwagon? *Trends in Ecology and Evolutution*, **7**: 389–92

Hunter, M. L. (1990). *Wildlife, Forests and Forestry: Principles of Managing for Biological Diversity.* Prentice-Hall, Englewood, NJ

Hurlbert, S. H. (1971). The nonconcept of species diversity: a critique and alternative parameters. *Ecology*, **52**: 577–86

Hurlbert, S. H. (1978). The measurement of niche overlap and some relatives. *Ecology*, **59**: 67–77

Huston, M. A. (1994). *Biological Diversity: The Coexistence of Species on Changing Landscapes.* Cambridge University Press, Cambridge

Innes, J. L. (1994). Design of an intensive monitoring system for Swiss forests. In Beniston, M. (ed.) *Mountain Environments in Changing Climates*. Routledge, London, pp. 281–98

Innes, J. L. (1995). Theoretical and practical criteria for the selection of ecosystem monitoring plots in Swiss forests. *Environmental Monitoring and Assessment*, **36**: 271–94

Isaaks, E. H. and Srivastava, R. M. (1989). *An Introduction to Applied Geostatistics.* Oxford University Press, New York

Järvinen, O. and Väisänen, R. A. (1980). Quantitative biogeography of Finnish land birds as compared with regionality in other taxa. *Annales Zoologica Fennica*, **17**: 67–85

Johnston, D. W. and Odum, E. P. (1956). Breeding bird populations in relation to plant succession on the piedmont of Georgia. *Ecology*, **37**: 50–62

Karr, J. R. and Roth, R. R. (1971). Vegetation structure and avian diversity in several new world areas. *American Naturalist*, **105**: 423–35

Kauppi, P. E., Mielikäinen, K., and Kuusela, K. (1992). Biomass and carbon budget of European forests, 1971 to 1990. *Science*, **256**: 70–4

Keller, W., Gadola, C. and Cereghetti, E. (1986). *Standortskarten als Grundlagen der Planung*. Report 286, Swiss Federal Institute of Forestry Research. Eidgenössische Anstalt für das forstliche Versuchswesen, Birmensdorf

Kempton, R. A. (1979). Structure of species abundance and measurement of diversity. *Biometrics*, **35**: 307–22

Kienast, F., Brzeziecki, B. and Wildi, O. (1994). Computergestützte simulation der räumlichen verbreitung naturnaher waldgesellschaften in der Schweiz. *Schweiz. Z. Forstwes.*, **145**: 293–309

Kräuchi, N. (1994). Modelling forest succession as influenced by a changing environment.

decomposers and is also an important aspect of
assessed in and of itself (Franklin, 1988). Development work is still underway in this area, and some refinement of the methods is necessary. A major issue is likely to be the extent to which specific habitat structures, including the structural species composition, can be used to predict species richness. This is still a major issue of debate in ecology (McIntosh, 1995).

Landscape heterogeneity provides the highest level of interpretation within Switzerland. Here, techniques such as remote sensing may be the most applicable. Data can now be stored and readily analyzed using geographic information systems, and the data can be spatially related to other environmental data collected within the area.

There are many other problems with the assessment of biodiversity. In the program described in this paper, a variety of different aspects of biodiversity are assessed. Such an approach is considered essential if useful data, rather than species lists, are to be generated. Past experience of forest monitoring in Switzerland (Innes, 1994) has indicated that it is possible to become heavily involved with parameters that later turn out to have rather limited value and that are difficult or impossible to evaluate. Although the definition of the concept of biodiversity remains rather broad, there is sufficient experience within ecology to know which variables are of importance in ecosystems. Using the framework of Franklin *et al.* (1981), these variables should cover composition, structure and function. Ignoring any will result in the possibility that major changes in forest ecosystems are missed.

ACKNOWLEDGMENTS

We are grateful to M. Kaennel for help with the literature search and to E. Wyder for digitizing the information shown in Figure 22.1c.

REFERENCES

Allen, T. F. H. and Starr, T. B. (1982). *Hierarchy. Perspectives for Ecological Complexity.* University of Chicago Press, Chicago, IL

Angelstam, P. (1992). Conservation of communities: the importance of edges, surroundings and landscape mosaic structure. In Hansson, L. (ed.) *Ecological Principles of Nature Conservation.* Elsevier, London, pp. 9–70

Arlettaz, R., Fournier, J., Juillard, M., Lugan, A., Rossel, D. and Sierro, A. (1991). Origines du déclin de la population relictuelle du Hibou petit-duc, *Otus scops*, dans les Alpes valaisannes (sud-ouest de la Suisse): une approche empirique. In Juillard, M. (ed.) *Rapaces Nocturnes.* Actes du 30e Colloque interrégional d'ornithologie Porrentruy, Switzerland, pp. 15–30

Arnold, G. W. (1983). The influence of ditch and hedgerow structure, length of hedgerows and area of woodland and garden on bird numbers on farmland. *Journal of Applied Ecology*, **20**: 731–50

Askins, R. A., Philbrick, M. J. and Sugeno, D. S. (1987). Relationship between the

Conservation, 39: 129–52

Avery, M. and Leslie, R. (1990). *Birds and Forestry.* T. & A. D. Poyser, London

Besag, J. and Gleaves, J. T. (1973). On the detection of spatial pattern in plant communities. *Bulletin of the International Statistical Institute*, **45**: 153–8

Bierregaard, R. O., Lovejoy, T. E., Kapos, V., dos Santos, A. A. and Hutchings, R. W. (1992). The biological dynamics of tropical rainforest fragments. *BioScience*, **42**: 859–66

Block, W. M., Brennan, L. A. and Gutierrez, R. J. (1987). Evaluation of guild-indicator species for use in resource management. *Environmental Management*, **11**: 265–69

Bowden, C. G. R. (1990). Selection of foraging habitats by woodlarks (*Lullula arborea*) nesting in pine plantations. *Journal of Applied Ecology*, **27**: 410–19

Bunce, R. G. H. and Shaw, M. W. (1973). A standardized procedure for ecological survey. *Journal of Environmental Management*, **1**: 239–85

Burrough, P. A. (1986). *Principles of Geographic Information Systems for Land Resources Assessment.* Clarendon Press, Oxford

Busing, R. T. and White, P. S. (1993). Effects of area on old-growth forest attributes: implications for the equilibrium landscape concept. *Landscape Ecology*, **8**: 119–26

Byth, K. and Ripley, B. D. (1980). On sampling spatial patterns by distance methods. *Biometrics*, **36**: 279–84

Carter, C. I. (1991). Ride orientation and invertebrate activity. In Ferris-Kaan, R. (ed.) *Edge Management in Woodlands.* Forestry Commission Occasional Paper 28. Forestry Commission, Edinburgh, pp 17–21

Cody, M. L. (1974). *Competition and the structure of bird communities.* Monographs in Population Biology 7. Princeton University Press, Princeton

Cody, M. L. (1975). Towards a theory of continental species diversity bird distributions over Mediterranean habitat gradients. In Cody, M. L. and Diamond, J. M. (eds.) *Ecology and Evolution of Communities.* Harvard University Press, Cambridge, MA, pp. 214–57

Colwell, R. K. and Futuyma, D. J. (1971). On the measurement of niche breadth and overlap. *Ecology*, **52**: 567–76

Cooper, W. S. (1913). The climax forest of Isle Royale, Lake Superior and its development. *Botanical Gazette*, **15**: 1–44, 115–40, 189–235

Cyr, A. (1977). A method of describing habitat structure and its use in bird population studies. *Pol. Ecol. Studies*, **3**: 41–52

Davis, T. A. W. and Richards, P. W. (1933–4). The vegetation of Moraballi Creek, British Guiana, an ecological study of a limited area of Tropical Rain Forest. Parts I and II. *Journal of Ecolology*, **21**: 350–84 and **22**: 106–55

Debinski, D. M. and Brussard, P. F. (1994). Using biodiversity data to assess species-habitat relationships in Glacier National Park, Montana. *Ecological Applications*, **4**: 833–43

Digby, P. G. N. and Kempton, R. A. (1987). *Multivariate Analysis of Ecological Communities.* Chapman and Hall, London

Downey, I., Heywood, I., Kless, P., Pauknerova, E. and Petch, J. (1990). GIS for landscape management, Zdarske Vrchy, Czechoslovakia. In Conference Proceedings: *GIS for the 1990s.* Ottawa, Ontario, pp. 1528–38

Ellenberg, H. (1988). *Vegetation Ecology of Central Europe.* Cambridge University Press, Cambridge

Schamberger, M. (1988). Monitoring wildlife habitat: a critique of approaches. *Stat. J. U.N. Econ. Comm. Eur.*, **5**: 303–13
Schmider, P., Küper, M., Tschander, B. and Käser, B. (1993). *Die Waldstandorte im Kanton Zürich*. Verlag der Fachvereine an den schweizerischen Hochschulen und Techniken, Zürich
Schüpbach, E. (ed.) (1991). *Meteorologie und Luftchemie in Waldbeständen*. Verlag der Fachvereine, Zürich
Short, H. L. (1982). Development and use of a habitat gradient model to evaluate wildlife habitat. *Transactions of the North American Wildlife Natural Resources Conference*, **47**: 57–72
Short, H. L. (1988). A habitat structure model for natural resource management. *Journal of Environmental Management*, **27**: 289–305
Simberloff, D. (1995). Habitat fragmentation and population extinction of birds. *Ibis*, **137**: S105–S111
Smith, E. P. (1982). Niche breadth, resource availability, and inference. *Ecology*, **63**: 1675–81
Southwood, T. R. E. (1978). *Ecological Methods*. Chapman and Hall, London
Spellerberg, I. F. (1991). *Monitoring Ecological Change*. Cambridge University Press, Cambridge
Steele, R. C. and Welch, R. C. (eds.) (1973). *Monks Wood: A Nature Reserve Record*. Natural Environment Research Council, Huntingdon
Storch, I. (1993a). Patterns and strategies of winter habitat selection in alpine capercaillie. *Ecography*, **16**: 351–59
Storch, I. (1993b). Habitat selection by capercaillie in summer and autumn: is bilberry important? *Oecologia*, **95**: 257–65
Storch, I. (1994). Habitat and survival of capercaillie *Tetraourogallus* nests and broods in the Bavarian Alps. *Biological Conservation*, **70**: 237–43
Strayer, D., Glitzenstein, J. S. and Jones, C. G. (1986). *Long-Term Ecological Studies: An Illustrated Account of their Design, Operation, and Importance to Ecology*. Occasional Publications 2. Institute of Ecosystem Studies, New York
Streeter, R. G., Chalk, D. E., Thomas, C. H. and Krohn, W. B. (1983). National appraisals for wildlife habitat: from inventory to management. In Bell, J. F. and Atterbury, T. (eds.) *Renewable Resource Inventories for Monitoring Changes and Trends*. Oregon State University Press, Portland, OR, pp. 764–677
Szaro, R. C. (1987). Guild management: an evaluation of avian guilds as a predictive tool. *Environmental Management*, **10**: 681–88
Tellería, J. L., Santos, T., Sánchez, A. and Galarza, A. (1992). Habitat structure predicts bird diversity distribution in Iberian forests better than climate. *Bird Study*, **39**: 63–8
Ter Braak, C. J. J. (1987). The analysis of vegetation–environment relationships by canonical correspondence analysis. *Vegetatio*, **69**: 69–77
Thimonier, A., Dupouey, J. L., Bost, F. and Becker, M. (1994). Simultaneous eutrophication and acidification of a forest ecosystem in North-East France. *New Phytologist*, **126**: 533–9
Thomas, J. A. (1995). Why small cold-blooded insects pose different conservation problems to birds in modern landscapes. *Ibis*, **137**: S112-S119
Thomas, J. W., Forsman, E. D., Lint, J. B., Meslow, E. C., Noon, B. R. and Verner, J. (1990). *A Conservation Strategy for the Northern Spotted Owl*. US Government Printing Office, Portland, OR

Turner, M. G. and Gardner, R. H. (eds.) (1991). *Quantitative Methods in Landscape Ecology: The Analysis and Interpretation of Landscape Heterogeneity*. Springer Verlag, New York
Urban, D. L. and Smith, T. M. (1989). Microhabitat pattern and the structure of forest bird communities. *American Naturalist*, **133**: 811–29
Van der Zande, A. N., ter Keurs, W. J. and van der Weijden, W. J. (1980). The impact of roads on the densities of four bird species in an open field habitat: Evidence of a long distance effect. *Biological Conservation*, **18**: 299–321
Verner, J. (1984). The guild concept applied to management of bird populations. *Environmental Management*, **8**: 1–13
Warren, M. S. (1985). The influence of shade on butterfly numbers in woodland rides, with special reference to the wood white, *Leptidea sinapis*. *Biological Conservation*, **33**: 147–64
Warren, M. S. (1991). Woodland edge management for butterflies. In Ferris-Kaan, R. (ed.) *Edge Management in Woodlands*. Forestry Commission Occasional Paper 28. Forestry Commission, Edinburgh, pp. 22–4
Whittaker, R. H. (1960). Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs*, **30**: 279–338
Whittaker, R. H. (1965). Dominance and diversity in land plant communities. *Science*, **147**: 250–60
Whittaker, R. H. (1975). *Communities and Ecosystems*. Macmillan, New York
Whittaker, R. H. (1977). Evolution of species diversity in land communities. In Hecht, M. K., Steere, W. C. and Wallace, B. (eds.) *Evolutionary Biology* Vol. 10. Plenum, New York, pp. 1–67
Wiens, J. A. (1995). Habitat fragmentation: island vs. landscape perspectives on bird conservation. *Ibis*, **137**: S97–S104
Wiens, J. A., Rotenberry, J. T. and Van Horne, B. (1987). Habitat occupancy patterns on North American shrub-steppe birds: the effects of spatial scale. *Oikos*, **48**: 132-47
Wiens, J. A., Stenseth, N. C., Van Horne, B. and Ims, R. A. (1993). Ecological mechanisms and landscape ecology. *Oikos*, **66**: 369-80
Wildi, O. and Orlóci, L. (1990). *Numerical Exploration of Community Patterns*. SPB Academic Publishing, The Hague
Wilson, M. V. and Schmida, A. (1984). Measuring beta diversity with presence–absence data. *Journal of Ecology*, **72**: 1055-64
Zobel, K., Zobel, M. and Peet, R. K. (1993). Change in pattern diversity during secondary succession in Estonian forests. *Journal of Vegetation Sciences*, **4**: 489–98

Krebs, C. J. (1989). *Ecological Methodology.* Harper and Row, New York
Kremen, C. (1992). Assessing the indicator properties of species assemblages for natural areas monitoring. *Ecological Applications*, **2**: 203–17
Krummel, J. R., Gardner, R. H., Sugihara, G. and O'Neill, R. V. (1987). Landscape patterns in a disturbed environment. *Oikos*, **48**: 321–84
Kruse, R. L. and Porter, W. F. (1994). Modeling changes in habitat conditions in northern hardwoods forests of the Adirondack Mountains of New York. *Forest Ecology and Management*, **70**: 99–112
Kuoch, R. (1954). Wälder der Schweizer Alpen im Verbreitungsgebiet der Weisstanne. *Mitt. Eidg. Anst. Forstl. Versuchswes.*, **30**: 133–260
Landres, P. B., Verner, J. and Thomas, J. W. (1988). Ecological uses of vertebrate indicator species: a critique. *Conservation Biology*, **2**: 316–28
Leclercq, B. (1987). Influence de quelques pratiques sylvicoles sur la qualité des biotopes à Grand Tétras (*Tetrao urogallus*) dans le massif du Jura. *Acta Œcologia*, **8**: 237–46
Leibundgut, H. (1985). *Der Wald in der Kulturlandschaft: Bedeutung, Funktion und Wirkungen des Waldes auf die Umwelt des Menschen.* Paul Haupt, Bern
Levins, R. (1968). *Evolution in Changing Environments: Some Theoretical Explorations.* Princeton University Press, Princeton, NJ
Likens, G. E. (ed.) (1989). *Long-term Studies in Ecology.* Springer, New York
Lovejoy, T. E. (1972). Bird species diversity and composition in Amazonian rain forests. *American Zoologist*, **12**: 711–20
Lovejoy, T. E., Bierregaard, R. O., Rankin, J. M. and Schubert, H. O. R. (1983). Ecological dynamics of tropical forest fragments. In Sutton, S. L., Whitmore, T. and Chadwick, A. C. (eds.) *Tropical Rainforest: Ecology and Management.* Blackwell Scientific, Oxford, pp. 377–84
Lovejoy, T. E., Bierregaard, R. O., Rylands, A. B., Malcolm, J. R., Quintela, C. E., Harper, L. H., Brown, K. S., Powell, A. H., Powell, G. V. N., Schubart, H. O. R. and Hays, M. B. (1986). Edge and other effects of isolation on Amazon forest fragments. In Soulé, M. E. (ed.) *Conservation Biology: The Science of Scarcity and Diversity.* Sinauer Associates, Sunderland, MA, pp. 257–85
Lynch, J. F. and Whigham, D. F. (1984). Effects of forest fragmentation on breeding bird communities in Maryland, USA. *Biological Conservation*, **28**: 287-324
MacArthur, R. H. (1965). Patterns of species diversity. *Biological Reviews*, **40**: 510–33
MacArthur, R. H. and MacArthur, J. W. (1961). On bird species diversity. *Ecology*, **42**: 594–98
MacArthur, R. H., MacArthur, J. W. and Preer, J. (1962). On bird species diversity. II. Prediction of bird census from habitat measurements. *American Naturalist*, **96**: 167–74
McIntosh, R. P. (1995). H. A. Gleason's 'individualistic concept' and theory of animal communities: a continuing controversy. *Biological Reviews*, **70**: 317–57
Magurran, A. E. (1988). *Ecological Diversity and its Measurement.* Croom Helm, London
Mayle, B. A. and Gurnell, J. (1991). Edge management and small mammals. In Ferris-Kaan, R. (ed.) *Edge Management in Woodlands.* Forestry Commission Occasional Paper 28. Forestry Commission, Edinburgh, pp. 42–8
Mazurkiewicz, M. and Rajska-Jurgiel, E. (1987). Numbers, species composition and residency of a rodent community in field-forest ecotones. *Acta Theriologica*, **32**: 413–32
Moss, D. (1978). Diversity of woodland songbird populations. *Journal of Animal Ecology*, **47**: 521–27

Neu, C. W., Byers, C. R. and Peek, J. M. (1974). A technique for analysis of utilization-availability data. *Journal of Wildlife Management*, **38**: 541–45
Noss, R. F. (1990). Indicators for monitoring biodiversity: A hierarchical approach. *Conservation Biology*, **4**: 355–64
O'Neill, R. V., DeAngelis, D. L., Waide, J. B. and Allen, T. F. H. (1986). *A Hierarchical Concept of Ecosystems.* Monographs in Population Biology 23. Princeton University Press, Princeton, NJ
Orians, G. H. (1969). The numbers of bird species in some tropical forests. *Ecology*, **50**: 783–801
Palmer, M. W. (1990). Spatial scale and patterns of vegetation, flora and species richness in hardwood forests of the North Carolina piedmont. *Coenoses*, **5**: 89–96
Paine, R. T. (1966). Food web complexity and species diversity. *American Naturalist*, **100**: 65–75
Pearson, D. L. (1994). Selecting indicator taxa for the quantitative assessment of biodiversity. *Philosophical Transactions of the Royal Society of London*, series B, **345**: 75–9
Peet, R. (1974). The measurement of species diversity. *Annual Review of Ecology and Systematica*, **5**: 285–302
Peterken, G. F. (1993a). *Woodland Conservation and Management.* Chapman and Hall, London
Peterken, G. F. (1993b). Long-term studies in forest nature reserves. In Broekmeyer, M. E. A., Vos, W. and Koop, H. (eds.) *Proceedings of the Symposium on European Forest Preserves.* Pudoc, Wageningen, pp. 35–48
Peters, R. H. (1991). *A Critique for Ecology.* Cambridge University Press, Cambridge
Pielou, E. C. (1977). *Mathematical Ecology.* John Wiley and Sons, New York
Radcliffe, G., Bancroft, B., Porter, G. and Cadrin, C. (1994). *Biodiversity of the Prince Rupert Forest Region.* Ministry of Forests, Victoria, British Columbia
Ratcliffe, P. R. (1993). *Biodiversity: Britain's Forests.* The Forestry Authority, Edinburgh
Ralph, C. J. (1985). Habitat association patterns of forest and steppe birds of northern Patagonia, Argentina. *The Condor*, **87**: 471–83
Recher, H. F. (1969). Bird species diversity and habitat diversity in Australia and North America. *American Naturalist*, **103**: 75–80
Rescia, A. J., Schmitz, M. F., Martín de Agar, P., de Pablo, C. L., Atauri, J. A. and Pineda, F. D. (1994). Influence of landscape complexity and land management on woody plant diversity in northern Spain. *Journal of Vegetation Sciences*, **5**: 505–16
Ripley, B. D. (1988). *Statistical Inference for Spatial Processes.* Cambridge University Press, Cambridge
Rolstad, J. and Wegge, P. (1987). Distribution and size of Capercaillie leks in relation to old forest fragmentation. *Oecologia*, **72**: 389–94
Root, R. B. (1967). The niche exploitation pattern of the blue-gray gnatcatcher. *Ecological Monographs*, **37**: 317–50
Roth, R. R. (1976). Spatial heterogeneity and bird species diversity. *Ecology*, **57**: 773–82
Routledge, R. D. (1977). On Whittaker's components of diversity. *Ecology*, **58**: 1120–27
Rudnicky, T. C. and Hunter, M. L. (1993). Reversing the fragmentation perspective: effects of clearcut size on bird species richness in Maine. *Ecological Applications*, **3**: 357-66
Samuelsson, J., Gustafsson, L. and Ingelög, T. (1994). *Dying and Dead Trees: A Review of Their Importance for Biodiversity.* Swedish Threatened Species Unit, Uppsala