BIODIVERSITY CHALLENGES TO FOREST SCIENTISTS

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BOYLE, T.J.B. 1992. Biodiversity challenges to forest scientists. The major challenges facing forest scientists in dealing with biodiversity can be considered in terms of five subject headings: how do the level and distribution of biodiversity affect ecosystem functioning; how do we measure biodiversity; how do we value it; how can we identify key areas for conservation; and how can we promote solutions to these challenges internationally? Many of the issues within each subject area are strongly inter-linked, particular two common themes, the need to study ecosystem processes, and the need to pay careful attention to problems of scale.

Key words: Biodiversity - forest science - measurement - economics - protected areas ecosystem functioning - scale - pattern

BOYLE, T.J.B. 1992. Cabaran-cabaran biodiversiti kepada saintis. Cabaran utama yang dihadapi oleh saintis-saintis perhutanan apabila berurusan dengan biodiversiti dapat digolongkan kepada 5 tajuk perkara: bagaimana peringkat dan taburan biodiversiti mempengaruhi fungsi ekosistem: bagaimana biodiversiti di ukur, bagaimana kita menilainya, bagaiamana kita boleh mengenalpasti kawasan utama untuk pemeliharaan dan bagaimana kita boleh menggalakkan penyelesaian kepada cabaran-cabaran ini diperingkat antarabangsa. Banyak daripada isu-isu didalam setiap bidang utama ini berhubung kait terutama sekali oleh dua tema yang biasa , keperluan mengkaji proses-proses ekosistem dan keperluan memberi perhatian kepada masalah-masalah ukuran.

Introduction

Forests constitute the most diverse ecosystem on earth. It has been estimated that more than 50% of all species are found in tropical rainforests which cover only 7% of the earth's surface (Myers 1988). Tropical dry forests have similar levels of species diversity (Jansen 1988), and even in relatively species -poor temperate and boreal regions, forests are still home to a disproportionate number of species (*e.g.*, Boyle 1992)

In the past few years a large number of international policy initiatives, most of them including the involvement of foresters, have provided valuable analyses of the actions required to manage and conserve biodiversity. Such initiatives include the report of the world Commission on Environment and Development (the "Brundtland Commission"), published in 1987; various products of the 1992 United Nations Conference on the Environment and Development (UNCED); the "Caracas Declaration" resulting from the 4th World Congress on National Parks and Protected Areas in 1992; and innumerable national reports and strategies. Three documents containing particular recommendations for forestry and having global applicability are briefly reviewed below

Caring for the earth

The World Conservation Union (IUCN), in partnership with the United Nations Enviroment Programme (UNEP) and the World Wide Fund for Nature (WWF), has published *Caring for the Earth: A Strategy for Sustainable Living* (World Conservation Union *et al.* 1991). The document constitutes a development of the World Conservation Strategy, published by the same agencies in 1980 (World Conservation Union *et al.* 1980). Chapter 14 deals with forest lands, and lists 10 "Actions Items" that include the need to:

- establish a permanent estate of natural and modified forest... and manage it to meet the needs of all sectors of society; identify all sectors that benefit from the forests, define the benefits, establish objectives for sustaining them, and state how the objectives are to be achieved;
- establish a comprehensive system of protected natural forests;
- increase national capacity to manage forests sustainably; adopt environmental policies that protect ecological services and biodiversity;
- expand efforts to conserve forest genetic resources;
- create a market for forest products from sustainably managed source and use wood more efficiently; promote the application of internationally acceptable criteria for sustainability of management; and
- increase the capacities of lower-income countries to manage forests sustainably and improve international cooperation in forest conservation and sustainable development.

Here, indeed, are some major challenges to foresters, each having an impact on biodiversity: conservation, a balance between natural and modified forests, assuring the sustainability of all benefits, and increased international cooperation.

Global biodiversity strategy

The World Resources Institute (WRI), in partnership with IUCN and UNEP, has also produced *The Global Biodiversity Strategy* (World Resources Institute *et al.* 1991), following a number of consultative meetings with government, industry and nongovernmental organizations around the world. The strategy is obviously closely related to *Caring for the Earth*, with two of the three partners also responsible for the latter document. However, whereas *Caring for the Earth* deals with all aspects of sustainable living, the *Global Biodiversity Strategy* covers specially the conservation of biodiversity. The Strategy notes that among the fundamental causes of biodiversity loss are the steadily narrowing spectrum of traded products, economic systems and policies that fail to value the environment and its resources, deficiencies in knowledge and its application, and legal and institutional systems that promote unsustainable exploitation. Many of the Strategy's 85 actions relate to forests and forestry. Some of the more prominent ones are to:

- establish an early warning network to monitor potential threats;
- abandon forestry practices that encourage resource degradation;
- strictly regulate transfer of species and genetic resources and their release into the wild;

- reduce pressure on fragile ecosystems by using land already under cultivation more efficiently;
- incorporate conservation of biodiversity into the management of all forests;
- use flagship species to increase support for conservation;
- fill major gaps in the protection of genetic resources;
- undertake national biodiversity inventories; and
- promote basic and applied research on biodiversity conservation.

Clearly, many of the themes contained in the *Caring for the Earth* action items are repeated in the *Global Biodiversity Strategy* : greater conservation efforts, sustainable practices, and increased research.

A research agenda for biodiversity

The International Union of Biological Sciences (IUBS), the Scientific Committee on Problems of the Environment (SCOPE) and the United Nations Educational, Scientific and Cultural Organization (UNESCO) have jointly launched *From Genes* to Ecosystems: A Research Agenda for Biodiversity (Solbrig 1991b). The Research Agenda contains a discussion of various scientific hypotheses that require testing, and also a list of recommendations related to monitoring. It includes the hypotheses that:

- genetic diversity has no effect on ecosystem funtion;
- habitat fragmentation has no effect on genetic diversity of the fragmented populations;
- no aspect of life history has any influence on the probability of extinction;
- keystone species are essential for maintaining species richness in communities under all environmental conditions;
- local species diversity is determined by local environmental properties and processes...communities with the same degree of spatial heterogeneity and ... dynamic equilibrium between opposing processes... should exhibit the same level of species diversity;
- spatial heterogeneity of the regional landscape has no effect on the number of functional types or coexisting species in a local community;
- the local disturbance regime has no effect on the number of functional types in a community;
- removal and addition of species that produce changes in spatial configuration of landscape elements will have no significant effect on ecosystem, functional properties over a range of time and space scales; and
- removal and addition of ecosystem components that produce changes in spatial configuration of landscape elements will have no significant effect on the disturbance response behaviour of an ecosystem over a range of time and space scales.

The recommendations related to monitoring include the preparation, within five years, of a count of all described species; the establishment of a global network

of systematists; a workshop on techniques to estimate species richness; and use of existing remote sensing technology to assist in monitoring.

The activities described in the *Research Agenda* are of special relevance to forest scientists, in contrast to those in *Caring for the Earth* and *The Global Biodiversity Strategy*, which apply to forest managers also. A common thread runs through all three documents, however: the need for conservation, application of sustainable practices, and technology cooperation. If forest scientists can provide answers to the hypotheses posed in the IUBS/UNESCO/SCOPE *Research Agenda*, it will allow forest managers to undertake those actions proposed in the first two documents.

The challenges to the forest scientists can therefore be considered under the headings:

- how the level and distribution of biodiversity affect ecosystem functioning;
- how do we measure biodiversity;
- how do we value it;
- how can we identify key areas for conservation; and
- how can we promote progress in meeting the challenges in all of the world's forests?

How do the level and distribution of biodiversity affect ecosystem functioning?

It is clear that biological diversity affects ecosystem functioning and the efficiency with which ecosystems perform their ecological services. There are innumerable examples where a drastic reduction in ecosystem diversity, usually as a result of human activities, has caused a reduction in ecosystem functions. In the field of forestry, a classic case is the loss of primary productivity in high-intensity German monospecies plantations (Norton & Ulanowicz 1992). Yet it is equally clear that high diversity does not necessarily confer a high degree of resiliency on the ecosystem. Some of the most diverse ecosystems, tropical forests, are highly susceptible to long-term damage following human disturbances such as timber harvest or land clearance for shifting agriculture. In contrast, the low-diversity boreal forests usually regenerate quickly following the same type of disturbance. Indeed, it has been hypothesized that environmental stability is the cause of high diversity (Sanders 1986), which would imply that high-diversity ecosystems are not well adapted to environmental fluctuations.

Thus, it appears that for any ecosystem there must be a level of biodiversity required for its functioning, but also a level above which diversity cannot be maintained because there are limitations of environmental stochasticity. It is this relationship that is unclear, and has led Solbrig (1991a) to conclude:

"One hundred years of research in genetics, systematics, evolution, and ecology have produced a large body of data that points to the importance of diversity for proper function of organisms and ecosystems, but we still lack a comprehensive rigorous theory of Biodiversity." Such a "comprehensive rigorous theory" will need to address not only the quantitative aspects of numbers and relative abundance, but also the qualitative aspect of representation of species (or alleles at the genetic level). As Lovejoy (1988) points out, we do not understand the role of most species in any ecosystem, especially the rare species, largely as the result of the their rarity. We recognize the concept of "keystone species" and for some ecosystems we can name some organisms that appear to perform keystone functions. However, insofar as every individual of every species interacts with other individuals of the same and other species, the concept of keystone species is of limited value. Rather than a bipartite classification of species into keystone and non-keystone, a continuous gradient of species based on their significance to ecosystem functioning should be recognized.

A more complete understanding of ecosystem functioning and the role of individual species is required in order to assess the consequences of removal from, or addition to ecosystems of individual species. Additions very often take the form of exotic species that are introduced deliberately to increase the productivity of some component of the system, or as an accidental consequence of ignorance or negligence. Similarly, removals may be deliberate, or the accidental result of other activities. A classic example of the disastrous consequences of an accidental addition of a species is the introduction of white pine blister rust (Cronartium ribicola) to North America from Europe (Boyce 1938). This disease has decimated eastern white pine (Pinus strobus) in Newfoundland, and has severely affected the status of both eastern and western white pine (P. monticola) throughout North America. Experiences with the plantation culture of Brazil nut (Bertholletia excelsa) provide examples of the results of both deliberate and accidental removal. Modification of the natural forest to provide better opportunities for planting of Brazil nut resulted in the deliberate removal of associated plant species, and the consequent accidental removal of species of Apidae that are the primary pollinators of Brazil nut (Brune 1990). A more thorough understanding of the ecosystem would have saved the considerable expense of failed plantations.

Conceptual models are devised to simplify complex systems, and identification of keystone species substitutes for what would appear to be an impossibly idealistic objective of classifying each species for its relative significance to ecosystem functioning. However, one theory of ecosystem functioning proposes that ecosystems have properties - the so-called "emergent properties" - that are greater than the sum of the properties of their constituent species (Solbrig & Nicolis 1991). Although the validity of this theory is debated, it nevertheless serves to remind us that ecosystems can be viewed in more than one way. Instead of functions of individual species, the action and interaction of processes provide an alternative approach to the analysis of ecosystem function. Ecosystem integrity requires the maintenance of ecosystem processes, and insofar as these processes are dependent on the diversity of the system, the study and monitoring of processes may prove to be more productive than an "autecological" species-based approach.

Namkoong (1992) argued for a process-oriented approach by proposing that the goal for management of natural ecosystems should be maintenance of ecological integrity, and conservation of biodiversity should be seen as a means of attaining that goal, or as an indicator, rather than as the goal itself. Norton and Ulanowicz (1992) used "dimensional analysis" to identify the critical processes associated with loss of productivity in German plantation forests. Lande (1988) also stressed the importance of considering processes in designing conservation strategies. In reveiving recovery plans for two endangered bird species in America, Lande postulated that strategies based on demographic processes would have a far greater chance of success than the existing strategies based on the population genetics of the two species.

Another factor that must be incorporated into any theory of biodiversity is its distribution. Biodiversity is arranged in distinct spatial patterns at all levels. The distribution of genetic diversity is often found to be non-random (*e.g.* Linhart *et al.*, 1981). Species distribution is also usually associated with discrete patches of habitat. Although on a broad scale the distribution of habitat is clearly related to environmental variables, the significance of small-scale patterns and non-random distribution of genetic diversity is not well understood (Lovejoy 1988). Human manipulations typically tend to simplify or eliminate spatial patterns. Natural mixed forests are often replaced by plantations of a single (or a few) species. The genetic diversity of these plantations may be random, over-dispersed, highly structured, or in the extreme case of monoclonal plantations, absent. The risks associated with reduction in biodiversity are well known from past experience and ecological theory, but policy guidelines governing pattern and distribution are generally more concerned with convenience than with any ecological principles.

Increasingly, theories derived in fields of science such as mechanics and engineering are being modified and adapted for use in ecology. One such theory governing the movement of particles through a matrix, "percolation theory" (Stauffer 1985), predicts that if there exists a critical set of sites through which energy or material flows (the "backbone"), the loss of other sites will have no significant effect, whereas the loss of backbone sites would have far greater consequences (Gardner & Turner 1991). In recent years landscape ecologists have devoted considerable effort to the development of "neutral models" of the distribution of landscape units, with which actual distribution can then be compared (*e.g.*, Gustafson & Parker 1992). Percolation theory is of obvious relevance to maintenance of ecosystem processes, and infers that maintenance of a critical frequency of landscape units, requiring the conservation of "keystone habitat patches" may be as significant as the identification and conservation of keystone species.

As well as being distributed in a spatial pattern, biodiversity is organized in a hierarchical fashion, from individual genes to landscapes, the so-called "functional" or "control hierarchy" (Solbrig 1991a). Different levels within the hierarchy vary in their spatial and temporal scales, with genetic processes occurring on much finer temporal and spatial scales than processes at community or higher levels. It is the interaction of processes at different temporal scales that results in the spatial patterns discussed above (White 1979, Bartell & Brenkert 1991). Therefore, the study of any system must include a consideration of scale, and conservation efforts

should be based on the same considerations. Lord and Norton (1990) discuss the importance of scale in determining the effects of habitat fragmentation, and distinguish between "geographical", coarse-grained fragmentation, typical of forest clearance patterns, and "structural," fine-grained fragmentation, as may result from invasions of alien species. They point out that finer-scale fragmentation is more likely to affect intrinsic ecosystem function, and that at any given scale the impact on individual species is related to how that species utilizes the habitat (*e.g.*, "generalist" versus "specialist" species). Both management and conservation of biodiversity should focus on the scale corresponding with the most critical processes, as described in the previously quoted example of dimensional analysis given by Norton and Ulanowicz (1992).

How do we measure biodiversity?

The problem of measuring biodiversity encompasses two questions: What statistical procedures can be used and, on an operational level, what data can be collected?

The simplest statistical assessment involves counts, but although counts have the advantage of simplicity, they fail to reflect the frequency of different types. Indices that account for both number and frequency are therefore more useful indicators of diversity. Two such indices are Shannon's index and Simpson's index (Patil & Taillie 1982, Swindel *et al.* 1991).

Pielou (1977) proposed three conditions that should be satisfied by a measure of diversity. These were that:

- the index should be maximized, for a given number of species (alleles, ecosystems), when the numbers of individuals of each species are equal;
- with equal numbers of individuals for each species, a system with more species should have a larger index; and
- if a community can be classified into subclasses, the index should be additive over the subclasses.
- Patil and Taillie (1982) added a fourth condition:
- as rarer species become more abundant at the expense of more common species, the index should increase.

Simpson's index does not satisfy the third condition, whereas Shannon's index satisfies all four. The mathematical characteristics of the two indices also differ. Simpson's index is more sensitive to changes in common species, whereas Shannon's index is affected by changes in rare species (Peet 1974). Because indices reflect both numbers and frequency, the contribution of each to a given index value is not apparent. Additional information can be gained from the calculation of "evenness," in representation of the units being studied. More complex methods for comparison of diversity in different communities have also been developed (Swindel *et al.* 1987).

Patil and Taillie (1982) quantified diversity of a community as its average "rarity", and derived a general relationship between rarity and a "diversity index"

 (Δ_{β}) which, when β assumes particular values, can be equated with simple counts, with Shannon's index, or with Simpson's index. When the magnitude of Δ_{β} over all possible values of β is compared for two communities, their relative diversity can be determined with no loss of information.

The problem with all these quantitave methods is that they take no account of the qualitative aspects of diversity. If one species in a community is replaced by another species *at the same frequency*, the various measures described above will indicate no change in diversity. However, as implied by the discussion in the previous section, the community or ecosystem will have changed because the new species will not perform the same functions as the original species. The changed community will now be more similar (or less similar) to other communities in the landscape, so community diversity will have changed. In other words, the scale of measurement is important. If the community is considered in isolation, diversity will indeed not have changed as a result of this species substitution, but on a larger scale, the total diversity will have changed. This problem is not resolved simply by including a measure of beta diversity such as those proposed by Whittaker (1972) and Christensen and Peet (1984). Those measures reflect the reoccurrence of individual species, rather than the diversity of ecosystem based on their relative properties.

The measurement of ecosystem diversity within a landscape again encounters the problems related to pattern and shape. Most methods of estimating spatial statistics, such as autocorrelation, require classification of types through procedures such as ordination (Turner *et al.* 1991). However, image textural measures (originally derived for engineering applications), which do not require *a priori* classification, have recently been used to quantify the spatial arrangement of landscapes (Musick & Grover 1991).

Turning to the question of operational procedures for data collection, it is obviously impractical to collect data on the number and frequency of all species in an ecosystem (even more so the number and frequency of all alleles at all loci for every species). Problems derive both from methodology, in terms of species identification, sampling methods, and scale, and from the sheer quantity of data that must be collected, often from very remote sites.

Compromises must be made in order to obtain sufficiently precise estimates from an acceptable expenditure of resources. The compromises may take the form of recording only certain groups of organisms, such as vascular plants, all plants, breeding birds, mammals, vertebrates, certain classes of invertebrates, or combinations of such groupings. Such an approach has been used in many parts of the world, and identifying taxa that may be useful indicators in different ecosystems poses a major challenge to systematists and ecologists.

Alternatively, the compromise may consist of an indirect approach through a measure of some other form of diversity. For example, it is well known that structural diversity is related to species diversity (Franklin 1988). Estimating structural diversity in a community may therefore provide an acceptable assessment of species diversity. The calculation of leaf area index at different heights in the canopy of the community is a simple measure of at least part of structural diversity

(although it does not account for the contribution of such features as fallen trees, and standing snags). MacArthur and MacArthur (1961) calculated "foliage height diversity" for various sites in the eastern United States and Panama, and found a strong relationship with bird species diversity, though not necessarily with total plant diversity. Their foliage height diversity consisted of a very simple estimate of leaf area at different heights. Refinements of their approach through use of modern technology and statistical methods, for example by quantifying not only the amount of foliage down a height profile, but also the spatial arrangement of foliage at each height, may improve the relationship between such profiles and species diversity of groups other than birds.

How do we value biodiversity?

The value of biodiversity is a topic that has received widespread attention (*e.g.*, Norton 1988, Randall 1988,1991, McNeely & Dobias 1991, Ehrlich & Ehrlich 1992, Perrings *et al.* (1992). Total value can be broken down into its components in a number of ways. Perrings *et al.* (1992) recognize two categories of value, namely "use value" and "non-use value". Use value, which corresponds with Norton's (1988) "commodity value" can be futher subdivided into "direct economic" and "indirect economic" values (Ehrlich & Ehrlich 1992), or alternatively "current use" and "expected future use" value (Randall 1988). Non-use value is made up of "aesthetic value" (Ehrlich & Erhlich 1992), or "amenity value" (Norton 1988), "existence value" (Randall 1988), also termed "ethical value" (Ehrlich & Ehrlich 1992), and "moral value" (Norton 1988).

Quantification of use value is well covered by existing market economics theory. However, when dealing with natural resources, Randall's (1988) expected future use component of use value may be very difficult to assess. The recent discovery of significant medicinal properties of an extractive from the bark of the previously commercially insignificant Pacific yew (*Taxus brevifolia*) emphasizes the difficulty of placing an accurate value on biodiversity. Estimation of non-use value is much more difficult, and is not easily handled by current economics theory. As noted by Perrings *et al.* (1992), the market value of biodiversity does not reflect the change in human welfare resulting from its loss, in other words the market value does not approach the social value of biodiversity. It is interesting to note that the existence value allocated by Thais to one of their National Parks due solely to the presence of wild elephants (over and above the tourist value) amounted to about \$6 million, as indicated by an economic survey (Dixon & Sherman 1991).

A major problem with valuing biodiversity is that many of the benefits are nonquantifiable in monetary terms. For example, the maintenance of functioning ecosystems and the enhancement of ability to adapt to future climate change are two facets of conserving biodiversity for which a value cannot easily be calculated (Cleland & Scott 1990, Probst & Crow 1991). Value is usually allocated to individual components of ecosystems, most often to species. The maintenance of ecosystem functions depends on interactions among species, in other words the value of an individual species arises only from the presence of other species and its interactions with them. This prompted Perrings *et al.* (1992) to conclude that some of the challenges that must be faced in more accurately assigning a value to biodiversity include measurement of the impact of disturbances and the effects of changing population sizes, or of removing species; and the development of system-level indicators.

How can we identify key areas for conservation?

The World Commission on Development and the Environment proposed that the extent of protected areas throughout the world should be trebled (World Commisison on Development and the Environment 1987). Similar targets have been proposed by IUCN,UNEP and WWF (World Conservation Union *et al.* 1991), and the Caracas Declaration of the 4th World Congress on National Parks and Protected Areas. Whatever may constitute an appropriate target, there is no question that additional areas of land need to be protected, in order to protect the welfare of present and future generations at a time of increasing human pressure on natural resources. It is only sensible to try to ensure that the areas protected are those which will provide the greatest future value of all ecosystem services per unit area. The challenge lies in developing suitable procedures for identifying such areas.

In the absence of reliable information on future value of natural resources, as discussed in the previous section, the logical approach is to protect areas of high diversity and areas that contain particularly rare, or unique resources. Such an approach has often been used, for example, by Hopper and Burgman (1983), Moran and Hopper (1983), and Sampson *et al.* (1988) for various species of eucalypts. These authors used morphological and allozyme data from discrete populations of eucalypt species to quantify the distinctness of the sampled populations and to identify those which differed substantially from populations already within protected areas. Although such an approach is useful for species of known or potential commercial value, it is practicable only for a small fraction of all species. In any case, the conclusion reached for different species would soon result in conflicting recommendations and an unrealistically large area being proposed for protection.

An alternative approach is the application of gap analysis (Davis *et al.* 1990, Scott *et al.* 1991), as illustrated by an example from Newfoundland, Canada. Pristine forest habitat was identified as being forest areas greater than $10 \ km^2$, and located more than a certain distance from the nearest road. The area of pristine forest in Newfoundland was mapped and, using Geographical Information Systems technology, related to existing "ecoregions" in the province (Taylor *et al.* 1991). Those areas of pristine forest located in ecoregions having a low percentage of forest already protected were identified as candidates for protection. In an effort to avoid conflict with other potential users, the locations of candidate areas were compared with maps of mineral distribution, areas of value for hydro-electric development, and areas already scheduled for timber harvesting. Candidate areas that, as far as possible, did not meet any of these alternative-use criteria were then proposed for protection.

The missing link in this example from Newfoundland is the lack of reliable estimates of the relative diversity of different ecoregions (or their subdivisions, "ecodistricts"). Such estimates could be used to allocate priority among candidate areas that met all other criteria, if specific information on individual candidate areas is not available. Information on relative diversity could also be used to make recommendations on areas that did not meet all criteria. For example, an area of pristine forest in high-diversity ecoregion might be recommended for protection even if the potential mineral value was quite high, whereas a similar area in a lowprotection ecoregion would only be recommended if the mineral value were much lower or nil.

Other aspects that must be considered in the identification of protected areas are the size, shape, and distribution of the areas. These issues have received much attention (e.g., Shafer 1990), particularly in relation to island biogeography theory and species-area relationships. Evidence for the applicability of this theory to fragmentation of terrestrial ecosystems is equivocal (see Simberloff & Abele 1976), and MacArthur and Wilson (1967) specifically warned against this extension of a theory derived for equilibrium conditions on oceanic islands. Nevertheless, certain conclusions on reserve size and shape can be made. Large reserves will conserve more biodiversity than small reserves, and it is better to minimize the length of boundry per unit area (leading to more circular, rather than elongated reserves), and to reduce the distances among reserves. On the other hand, a larger number of small reserves can sample a wider range of diversity in an heterogeneous environment, and for species with small area requirements, this strategy may be more effective (Diamond 1980). In a world of conflicting interests, where compromises must be made, the problem lies in how much, and in relation to which feature of the reserve, to compromise.

The conservation strategy for the northern spotted owl (*Strix occidentalis*) in the Pacific Northwest of the United States recommended the establishment of a network of conservation areas, averaging 25, 000 *ha*, and separated by no more than 20 *km* (Wood 1991). However, the strategy has come under criticism, and Lande (1988) has postulated that because it is founded on population genetics, it is likely to lead to the extinction of the owl, because viable populations may not be maintained. Lande argued that the demographics of the species should provide the basis for the strategy, since maintenance of demographic processes is much more critical to the short- and medium-term survival of a species than population genetic factors, beyond a minimum threshold.

How can progress on forest biodiversity issues be promoted internationally?

International cooperation is often taken to mean information exchange and technology cooperation, and indeed these are important issues. However, cooperation can refer also to information acquisition, through the comparative study of ecosystems in different regions. Dealing first with the more traditional applications of the term, mechanisms for information exchange are already well developed. In the field of forest science, the International Union of Forest Research Organizations (IUFRO) is the most appropriate body to fulfill the function, and the study of biodiversity will benefit from greater involvement of IUFRO in the subject. Opportunities for technology cooperation are largely controlled by national governments. However, in the current international political climate which has given rise to so many initiatives such as those listed in the Introduction, opportunities for technology cooperation in the field of biodiversity are particularly promising. As government officials are not able to determine suitable projects for such cooperation themselves, forest scientists must take the initiative and vigorously pursue the opportunities that exist.

The various regions of the world differ substantially in the status of, and pressures on, forest biodiversity. Tropical regions are known, in general, to have much greater levels of diversity than temperate and boreal regions. Also, the impact of human activities is quite different in the "North" from that in the "South". Soule (1991) considered six stresses on biodiversity at genetic, species, community and ecosystem levels. He suggested that in lower income countries, exotic species, habitat fragmentation, over exploitation, and habitat loss were the main threats occuring, especially at the genetic and species levels. In contrast, in higher-income countries, exotic species, pollution, climate change, and habitat fragmentation were the main factors, with risks to whole ecosystems as well as to genes and species. Despite these differences, there are many similarities in the proposed solutions around the world. For example, recommendations for action on conserving biodiversity in Bangladesh (Huq 1991), Indonesia (Indonesian Forestry Community 1990), and the United States (Goklany 1992) all focus on better and more sustainable management of natural resources.

This similarity of proposed solutions presents a challenge to forest scientists, namely to establish to what extent the underlying processes that maintain biodiversity are similar in both tropical and temperate zones. The environmental stability theory of Sanders (1968) suggests that temperate diversity might approach the level of tropical diversity, but for the greater incidence and magnitude of environmental disturbances in temperate regions. Far more ecological information is available from temperate regions, and in the absence of specific information on the tropics, temperate zone management systems have often been proposed for the tropics. There is now some evidence (*e.g.* Hamrick & Loveless 1989) that, in terms of populations genetics, tropical tree species show greater similarities to temperate species than was expected. This implies that, without information on the population genetics of a particular species, the application of management strategies based on the genetic patterns found in temperate species may be acceptable. Further work is required to establish whether the critical processes that regulate ecosystem functions are similar in tropical and temperate ecosystems.

Conclusion

In this discussion of the five subject areas that pose particular challenges to forest scientists, some common themes have often been repeated, and serve to link

concepts in each area. The two most notable common themes are the importance of studying ecosystem processes, and the importance of scale.

A process-oriented approach to the study of biodiversity is logical when it is considered that the role of individual organisms or species is determined by their functions. Not all biodiversity can be conserved, and not all needs to be conserved because there is some functional redundancy in ecological systems and the possiblility exists for some functional substitution (Westman 1990). Only by studying processes can the limits of ecosystem functioning be estimated. This is consistent with Namkoong's (1992) recommendation that conservation of biodiversity should be a mechanism rather than a goal, and Gee's (1992) comment that biodiversity is a system rather than a list. Only through a thorough understanding of ecosystem processes, and the degree to which they are similar in tropical and temperate zones, can international criteria for sustainable forest management, called for in *Caring for the Earth* and in the UNCED "Forest Principles" truly receive widespread acceptance.

It is inevitable that for a concept as broad and diffuse as biodiversity, scale should be one of its most significant attributes. The functional hierarchy for biodiversity ranges from genes and the very rapid, localized molecular genetic processes, to the extremely slow geological process associated with landscapes. It therefore becomes very important to identify the most appropriate intermediate scale at which the spatial extent and rate of processes have the greatest impact on ecosystem functioning. It may indeed be found that the real differences of biodiversity between the tropical and temperate zones are simp ult of the different scales at which critical processes occur.

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References

BARTELL, S.M. & BRENKERT, A.L. 1991. A spatial-temporal model of nitrogen dynamics in a deciduous forest watershed. Pp. 379-398 in Turner, M.C. & Gardner, R.H. (Eds.) Quantitative Methods in Landscape Ecology. Ecological Studies. Volume 82. Springer-Verlag, New York.

BOYCE, J.S. 1938: Forest Pathology. McGraw-Hill, New York.

- BOYLE, T.J.B. 1992. Biodiversity of Canadian forests: current status and future challenges. *The Forestry Chronicle* 68: 444-453.
- BRUNE, A. 1990. Reproductive biology and tropical plantation forestry. Pp. 349-354 in Bawa, K.S.
 & Hadley, M. (Eds.) *Reproductive Ecology of Tropical Forest Plants*. Man & The Biosphere Series.
 Volume 7. UNESCO, Paris, and Pathenon Publishing, Carnforth, United Kingdom.
- CHRISTENSEN, N.L. & PEET, R.K. 1984. Measures of natural diversity. Pp. 43-56 in Cooley, J.L.
 & Cooley, J.H. (Eds.) Natural Diversity in Forest Ecosystems: Proceedings of the Workshop. Institute of Ecology, University of Georgia, Athens, Georgia.
- CLELAND, D.T. & SCOTT, R.E. 1990. The U.S. Forest Service perspective on managing for biodiversity on federal lands. *Michigan Academician* 22: 355-363.

- DAVIS, F.W., STOMS, D.M., ESTES, J.E. SCEPAN, J. & SCOTT, J.M. 1990. An information systems approach to the preservation of biological diversity. *International Journal of Geographical Information Systems* 4: 55-78.
- DIAMOND, J.M. 1980. Patchy distribution of tropical birds. Pp. 57-74 in Soulé, M.E. & Wilcox, B.A. (Eds.) Consevation Biology: An Evolutionary-Ecological Perspective. Sinauer Associates, Sunderland, Massachusetts.
- DIXON, J.A. & SHERMAN, P.B. 1991. Economics of protected areas. Ambio 20: 68-74.
- EHRLICH, P.R. & EHRLICH, A.H. 1992. The value of biodiversity. Ambio 21: 219-226.
- FRANKLIN, J.F. 1988. Structural and functional diversity in temperate forests. Pp.166-175 in Wilson, E.O. (Ed.) *Biodiversity*. National Academy Press, Washington, DC.
- GARDNER, R.H. & TURNER, M.G. 1991. Future directions in quantitative landscape ecology. Pp. 519-526 in Turner, M. G. & Gardner, R.H. (Eds.) *Quantitative Methods in Landscape Ecology*. Ecological Studies .Volume 82. Springer-Verlag, New York.
- GEE,H. 1992. The objective case for conservation. Nature 357: 639.
- GOKLANY,I. 1992. America's Biodiversity Strategy: Actions to Conserve Species and Habitats. United States Department of the Interior and United States Department of Agriculture, Washington, DC.
- GUSTAFSON, E.J. & PARKER.G.R. 1992. Relationships between land cover proportion and indices of landscape spatial pattern. *Landscape Ecology*, 7: 101-110.
- HAMRICK, J.L. & LOVELESS, M.D. 1989. The genetic structure of tropical tree populations: Associations with reproductive biology. Pp.129-146 in Bock, J.H. & Linhart, Y.B. (Eds.) The Evolutionary Biology of Plants. Westview Press, Boulder, Colorado.
- HOPPER, S.D.& BURGMAN, M.A. 1983. Cladistic and phenetic analyses of phylogenetic relationship among populations of *Eucalyptus caesia*. Australian Journal of Botany 31: 35-49.
- HUQ, S. 1991. Biodiversity in Bangladesh. Bangladesh Environmental Newsletter 2: 4-5.
- INDONESIAN FORESTRY COMMUNITY. 1990. Indonesia: tropical forests forever. *Journal of Forestry* 88(9): 26-31.
- JANSEN, D.H. 1988. Tropical dry forests: the most endangered major tropical ecosystem. Pp. 130-137 in Wilson, E.0. (Ed.) *Biodiversity*. National Academy Press, Washington, DC.
- LANDE, R. 1988. Genetics and demography in biological conservation. Science 241: 1455-1460.
- LINHART, Y.B., MITTON, J.B., STURGEON, K.B. & DAVIS, M.L. 1981. An analysis of genetic architecture in populations of ponderosa pine. Pp. 53-59 in Conkle, M.T. (Ed.) Proceedings Symposium on Isozymes of North American Forest Trees and Forest Insects. July ,1979. Berkeley, CA. US Department of Argiculture, Forest Service, General Technical Report PSW-48.
- LORD, J.M. & NORTON, D.A. 1990. Scale and the spatial concept of fragmentation. *Conservation Biology* 4: 197-202.
- LOVEJOY, T.E. 1988. Diverse considerations. Pp. 421-427 in Wilson, E.O. (Ed.) *Biodiversity*. National Academy Press, Washington, DC.
- MACARTHUR, R.H. & MACARTHUR, J.W. 1961. On bird species diversity. Ecology 42: 594-598.
- MACARTHUR, R.H. & WILSON, E.O. 1967. *The Theory of Island Biogeography*. Princeton University Press, Princeton, New Jersey.
- MCNEELY, J.A. & DOBIAS, R.J. 1991. Economic incentives for conserving biological diversity in Thailand. *Ambio* 20: 86-90.
- MORAN, G.F. & HOPPER, S.D. 1983. Genetic diversity and the insular population structure of the rare granite rock species *Eucalyptus caesia* Benth. *Australian Journal of Botany* 31: 161-172.
- MUSICK, H.B. & GROVER, H.D. 1991. Image textural measures as indices of landscape pattern. Pp. 77-104 in Turner, M.G. & Gardner, R.H. (Eds.) *Quantitative Methods in Landscape Ecology*. Ecological Studies .Volume 82. Springer-Verlag, New York.
- MYERS, N. 1988. Tropical forests and their species: going, going...? Pp. 28-35 in Wilson, E.O.(Ed.). *Biodiversity*. National Academy Press, Washington, DC.
- NAMKOONG, G. 1992. Creating policy on genetic diversity. In Szaro, R. (Ed.) *Biodiversity in Managed* Landscapes: Theory and Practice. Oxford University Press, Oxford, United Kingdom. (In press).
- NORTON, B. 1988. Commodity, amenity, and morality: the limits of quantification in valuing biodiversity. Pp. 200-205 in Wilson, E.O. (Ed.) *Biodiversity*. National Academy Press, Washington, DC.

- NORTON, B. G. & ULANOWICZ, R.E. 1992. Scale and biodiversity policy: a hierarchical approach. *Ambio* 21: 244-249.
- PATIL, G.P. & TAILLIE, C. 1982. Diversity as a concept and its measurement. *Journal of the American Statistical Association* 77: 548-561.
- PEET, R. K. 1974. The measurement of species diversity. Annual Review of Systematics and Ecology 5: 285-307.

PIELOU, E.C. 1977. Mathematical Ecology. John Wiley & Sons, Toronto, Ontario.

- PERRINGS, C., FOLKE, C. & MALER, K. G. 1992. The ecology and economics of biodiversity loss: the research agenda. *Ambio* 21: 201-211.
- PROBST, J. R. & CROW, T. R. 1991. Integrating biological diversity and resource management. Journal of Forestry 89(2): 12-17.
- RANDALL, A. 1988. What mainstream economists have to say about the value of biodiversity. Pp. 217-223 in Wilson, E.O. (Ed.) *Biodiversity*. National Academy Press, Washington, DC.
- RANDALL, A. 1991. The value of biodiversity. Ambio 20: 64-74.
- SAMPSON, J.F., HOPPER, S.D. & JAMES, S.H. 1988, Genetic diversity and the conservation of *Eucalyptus crucis* Maiden. *Australian Journal of Botany* 36: 447-460.
- SANDERS, H.L. 1968. Marine benthic diversity: A comparative study. *American Naturalist* 102: 243-282.
- SCOTT, J. M., CSUTI, B., SMITH, K., ESTES, J. E. & CAICCO, S. 1991. Gap analysis of species richness and vegetation cover: an integrated biodiversity conservation strategy. Pp. 282-297 in Kohm, K.A. (Ed.) Balancing on the Brink of Extintion: the Endangered Species Act and Lessons for the Future. Island Press, Washington, DC.
- SHAFER, C.L. 1990. Nature Reserves: Island Theory and Conservation Practice. Smithsonian Institution Press, Washington, DC.
- SIMBERLOFF, D.S. & ABELE, L.G. 1976. Island biogeography theory and conservation practice. *Science* 191: 285-286.
- SOLBRIG O.T. 1991a. Biodiversity: scientific issues and collaborative proposals. Man & The Biosphere Digest 9. UNESCO, Paris.
- SOLBRIG, O.T. (Ed.). 1991b. From Genes to Ecosystems: a Research Agenda for Biodiversity. International Union of Biological Sciences, Paris.
- SOLBRIG, O.T. & NICOLIS, G. 1991. Biology and complexity. Pp. 1-6 in Solbrig, O.T. & Nicolis, G. (Eds.) Perspectives in Biological Complexity. International Union of Biological Sciences, Paris.
- SOULE, M.E. 1991. Conservation: tactics for a constant crisis. Science 253: 744-753.
- STAUFFER, D. 1985. Introduction to Percolation Theory. Taylor & Francis, London.
- SWINDEL, B.F., CONDE, L.F. & SMITH, J.E. 1987. Index-free diversity orderings: concept, measurement and observed response to clear-cutting and site preparation. *Forest Ecology* and Management 20: 195-208.
- SWINDEL, B.F., SMITH, J.E. & ABT, R.C. 1991. Methodology for predicting species diversity in managed forests. *Forest Ecology and Management* 40: 75-85.
- TAYLOR, C., LAMBERT, E. & FREUNDSCHUH, S. 1991. A Geographical Information Systems Approach to Protected Areas Planning for the Island of Newfoundland. Contract Report, Forestry Canada, St. John's, NF. (Unpublished).
- TURNER, S.J., O'NEILL, R.V., CONLEY, W., CONLEY, M.R. & HUMPHRIES, H.C. 1991. Pattern and scale: statistics for landscape ecology. Pp. 17-50 in Turner, M.G. & Gardner, R.H. (Eds.) *Quantitative Methods in Landscape Ecology*. Ecological Studies .Volume 82. Springer-Verlag, New York.
- WESTMAN, W.E. 1990. Managing for diversity: unresolved science and policy questions. *Bioscience* 40: 26-33.
- WHITE, P.S. 1979. Pattern, process, and natural disturbance in vegetation. *The Botanical Review* 45: 229-299.
- WHITTAKER, R.H. 1972. Evolution and measurement of species diversity. Taxon 21: 213-251.

WOOD, G.W. 1991. Owl conservation strategy flawed. Journal of Forestry 89(2): 39-42.

WORLD COMMISSION ON ENVIRONMENT AND DEVELOPMENT (WCED). 1987. Our Common Future. Oxford University Press, Oxford, United Kingdom.

- WORLD CONSERVATION UNION, UNITED NATIONS ENVIRONMENT PROGRAMME AND WORLD-WIDE FUND FOR NATURE. 1980. World Conservation Strategy. World Conservation Union, Gland, Switzerland.
- WORLD CONSERVATION UNION, UNITED NATIONS ENVIRONMENT PROGRAMME AND WORLD-WIDE FUND FOR NATURE. 1991. Caring for the Earth: a Strategy for Sustainable Living. World Conservation Union, Gland Switzerland.
- WORLD RESOURCES INSTITUTE, WORLD CONSERVATION UNION AND UNITED NATIONS ENVIRONMENT PROGRAMME. 1991. The Global Biodiversity Strategy. World Resources Institute, Washington, DC.