

The phenomenon of biodiversity in conservation biology

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‘Biodiversity’ has become a popular term in conservation biology. We review the history of the term. It has several historical origins from ecology, genetics and evolutionary biology. The term ‘biodiversity’ refers to the fact that heterogeneity at different ecological levels is a fundamental property of natural systems. The term itself is abstract and descriptively complex, i.e., several alternative criteria can be used to operationalize the term. Consequently, the term is context-specific when used in conservation and management. The term ‘biodiversity’ should be used cautiously and carefully in management, and it is desirable to try to combine multiple-scale and multiple-level approaches simultaneously. Idiosyncrasies of particular systems and environments should be recognized and it seems unlikely that ‘biodiversity’ could be measured using a simple, single index.

1. Introduction: ‘biodiversity’ — a new discourse

‘Biodiversity’ is a growth industry in conservation biology. This is shown by the increase in the use of the term in titles and abstracts of scientific papers (Fig. 1), and in the increasing flow of books that have the term ‘biodiversity’ in one form or another in their title. Some authors try to give a rigorous definition to the term, but often it is employed just as a loose synonym for ‘life on

the earth’ (World Conservation Monitoring Centre 1992).

‘Biodiversity’ is also infiltrating administrative language, particularly after the UN conference on the environment and development held in Rio de Janeiro in June 1992 (United Nations Environment Programme 1992). The conference declared preservation of biodiversity as a major element in ‘sustainable development’, and, what will influence the use of the term even more, ‘biodiversity’ was acknowledged as a new type of natural resource, providing raw material for productive activities ranging from plant and animal breeding and genetic engineering to medical

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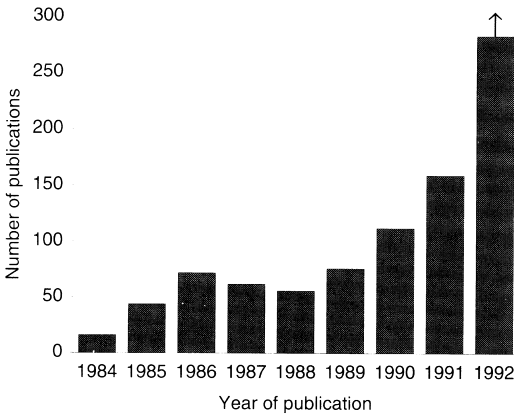


Fig. 1. The occurrence of terms 'biodiversity' and 'biological diversity' in titles and/or abstracts of scientific journals. The figure for 1992 is an underestimate, the probable amount of publications may well be twice that shown. Source of data: Cambridge Life Sciences Collection (up to 3/1993).

industries. 'Biodiversity' is appearing as a resource to be systematically surveyed and prospected (Reid et al. 1993), much as geological resources were surveyed and prospected in the 19th century.

This is an important achievement. There is no justification for being cynical about the increasing use of 'biodiversity' in different contexts. The worry about the fate of biological diversity of the earth is certainly warranted (e.g. Wilson 1988, 1992), and thus the change in the public attitude toward biodiversity is certainly positive. Overviews of biodiversity issues abound (Solbrig 1991a, 1992, World Conservation Monitoring Centre 1992, ICBP 1992). However, it is important to recognize that the term has changed meaning since it was originally launched in conservation discussions in the 1980s.

In a word, 'biodiversity' has given rise to a new 'discourse'; by the term discourse we refer to a discussion that defines and redefines meanings and significances (Foucault 1972, Bove 1990, Rouse 1991). The meaning of 'biodiversity' is the phenomenon the term is supposed to stand for. The significance of 'biodiversity' is the total argument given in support of the urgency of biodiversity preservation.

The origin of the discourse on biodiversity is in ecology, evolutionary biology and conserva-

tion, but the focus of the discourse has shifted and the framework has widened rapidly in a very short time. The same term can be used with widely different meanings which creates potential for confusion. The problem is not primarily terminological, to be solved by adjudicating on linguistic usage. The problem originates in the fact that concern for 'biodiversity' relates to several different realms of human practice and, consequently, the issue of biodiversity can in actual fact be defined in different contexts. Thus, the problems are genuinely conceptual. We chart the structure of this problem area in Fig. 2.

Although there is no point in dreaming of general agreement on, or even rules for, biodiversity terminology, conceptual rigor is necessary within specified contexts. In this paper we focus on the conservation discourse on biodiversity. However, we stress that our domain of ecological and conservation (or biological) context is but one alternative. Since the conservation concern of biodiversity draws essentially upon biological arguments, we aim at clarifying the biological background of the discourse. In several areas and especially in management, conservation of 'biodiversity' includes a large cross-sectional area linking fields like environmental economy and environmental law with the concept, but these are beyond the scope of this paper.

The questions we ask relate to ecological theory (What are the reasons for the belief that 'diversity' is an important feature of nature?), to conceptual history (How and why was the concept conceived?), to methodological issues (How to develop operationalizable approaches in biodiversity research?), and to conservation practice (How to develop research of practical relevance?). But there is confusion concerning the meaning of the term 'biodiversity' even within the biological context. Thus, our first task is to explain, why the concept of 'biodiversity' is difficult to define unambiguously even within biology.

2. Elements of biological diversity

The origin of the word 'biodiversity' is quite recent. As far as we know the term was first used in its present literary form in the title of the book

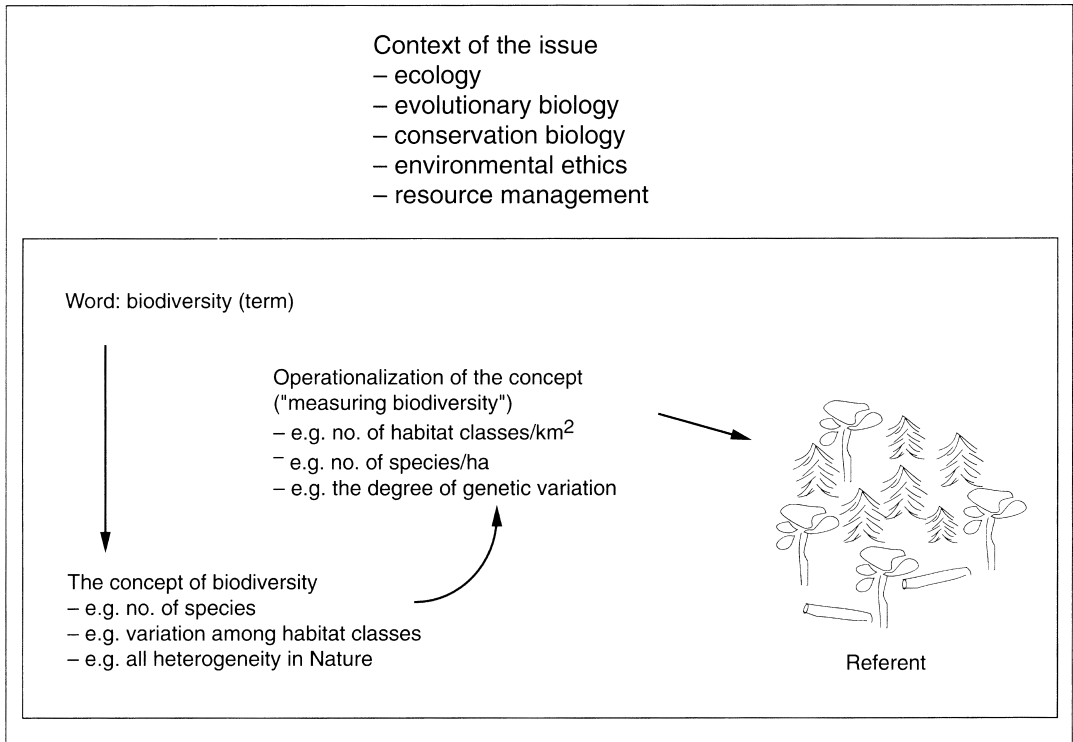


Fig. 2. The formation of 'biodiversity' under different contexts. Depending on the context the meaning of 'biodiversity' may be quite different and this urges to use clear specifications of the term whenever it is used. (Modified after Kouki 1993)

edited by E.O. Wilson in 1988. The book was based on a symposium held in 1986. Before that, a more lengthy term 'biological diversity' was used to elucidate the concept.

The difficulties in defining 'biodiversity' originate from the general character of the term: it is a descriptive, but simultaneously an abstract and descriptively complex term. The term is primarily descriptive, because it summarizes a universal, phenomenological observation about nature: natural entities appear 'diverse'. Interpretation of this generalization, either by explaining why biological entities are diverse, or by explicating the ultimate significance of this diversity for life on the earth, is an entirely different matter. Thus, the first necessity is to draw a distinction between patterns of biodiversity, and explanations of those patterns, or assessments of their significance.

However, this is complicated because 'biodiversity' is an abstract concept. The criteria used

in describing 'diversity' require independent justification; this point is elaborated below. It follows that the 'diversity' derived under any set of criteria has no immediately obvious relationship to ecological functions. The assumed significance of a particular type of 'diversity' must be congruent with the criteria used when it was derived.

Furthermore, the concept is descriptively complex (Wimsatt 1974). Wimsatt adopted the notion of 'descriptive complexity' to characterize systems that can be divided into parts using alternative criteria, and the result looks different depending on which one is adopted. 'Biodiversity' accords with this characterization. As we discuss below, alternative units can be used in describing 'diversity' (Fig. 2), and the boundaries of patterns perceived using alternative units do not necessarily coincide.

Descriptively 'diversity' equals 'variability' or 'heterogeneity'. These are fundamental characteristics of biological systems, and the argu-

ment can be defended, from non-linear thermodynamics, that internal heterogeneity is a general necessary condition for the existence of life (Brooks & Wiley 1986, Weber et al. 1988). However, living structures do not appear as an amorphous ‘heterogeneity’, but their heterogeneity has structure that can be envisaged as a hierarchy of levels (Pattee 1973, Allen & Starr 1992, Salthe 1985, O’Neill et al. 1986, Solbrig 1991a). Heterogeneity exists within each level of biological hierarchy, and this further reduces the transparency of the significance of any particular type of heterogeneity.

In the context of biodiversity a relevant set of levels of heterogeneity are: heterogeneity within organisms, within populations, within communities and ecosystems, and within biomes and the biosphere. As a general rule entities within each level are heterogeneous. This heterogeneity is thought to be an essential part of the internal dynamics of system(s) distinguished on that level. Thus, molecular heterogeneity is essential for the dynamics of the genome and of physiology within organisms. Individual variability within populations is essential for population viability. Functional properties of communities and ecosystems depend on the variety of the populations present (and for this statement it is immaterial whether ‘communities’ are considered stochastic assemblages or tightly packed super organisms). Finally, biomes and the biosphere are patchworks of different communities and ecosystems.

Biological hierarchies can be constructed in different ways, from different theoretical perspectives, none of which is necessarily “better” than the others: major criteria are structural, functional and genealogical (evolutionary) (Salthe 1985, Grene 1987). The structural hierarchy outlined above is readily visible to human observers, but it may be epiphenomenal to underlying functions and to genealogy. In other words, although the phenomenon of ‘diversity’ is readily visible according to structural criteria (molecules in the genome look different, individuals within a population look different, populations within a community look different, etc.), the significance of ‘diversity’ probably lies behind this phenomenology. Indeed, the significance of biological diversity is commonly explained either in terms of function or evolution (e.g. Solbrig 1991b).

This is tied to two general, metaphoric arguments:

- A) In the context of function, diversity is viewed as providing buffers against unexpected perturbations and disturbances; this is based on the *resilience metaphor*.
- B) In the context of genealogy, diversity is viewed as providing raw material for adaptive change and evolution; this is based on the *selection metaphor*.

The general arguments on which these claims are based need not be repeated here. Instead, a methodological problem shared by both metaphors needs emphasis: neither ‘resilience’ nor ‘selection’ is scale-free. An individual, a population, or a community maybe ‘resilient’, but this is based on very different mechanisms (Holling 1973, Levins 1974, Puccia & Levins 1985, Levin 1992). Similarly, ‘selection’ can occur within each one of these levels but in quite different ways (Lewontin 1970, Salthe 1985, Buss 197). The entities on different levels of biological hierarchy have different ontological status. They differ from each other concerning their “entity-ness”, that is, the character of the processes which determine their recognition. More generally, the delimitation of ecological ‘entities’ is necessarily relative, because the distinction between ‘external’ and ‘internal’ is relative (Levins 1973, Allen & Starr 1982). This is what makes ‘resilience’ and ‘selection’ level- and scale-dependent.

3. Which diversity is relevant in conservation?

In a biological context ‘biodiversity’ refers to a scale-dependent mixture of heterogeneities which are essential for the functional integrity and historical adaptiveness of biological systems. Thus, the next task is to specify the focus of the conservation concern of biodiversity in this mixture of biological heterogeneities. It seems to us that the conservation focus is defined using criteria that stem “from the outside”, from the human concern, for example, from the goal to maintain the planet earth habitable for human beings, or to preserve the beauty — as human beings recognize it — of variable nature. Without this concern there would

be no need to adopt 'biodiversity' as an umbrella term but it would be more profitable to concentrate on various aspects of biological heterogeneity one at a time, using a different name for each one of them.

All phenomena of biological diversity are not equally important for conservation. For instance, the heterogeneity of immunological reactions within individual birds is critical in bird biology, but bird individuals are of conservation concern only in exceptional cases, when population viability depends on the survival of single individuals. There is a difference between humans and other animals in the ethical attitude adopted toward individuals, resulting from the human perspective. Thus, the human concern "truncates" the range of biologically essential heterogeneity that is important in the conservation discourse on 'biodiversity'. The smallest scales, processes within individuals, are basic for life, but not of concern within the 'biodiversity' discourse because they continue to function as long as there are organisms. On the other hand, on larger scales phenomena that may not differ very much from what has happened on the earth before, for instance extinctions and the impoverishment of ecological systems on the biome/ biogeographic level, are of great concern.

Thus far we have focused on units that belong to the biological hierarchy. These units, however, have also 'external' boundary conditions, determined by geophysical processes and physical and chemical properties of the environment. Heterogeneity of 'external' boundary conditions is also an important phenomenological feature of nature, and it is perfectly sensible to evaluate also the 'diversity' of boundary conditions. An essential issue only is that boundary conditions and biological units be not mixed with each other.

A useful terminology for clarifying this distinction was suggested by Margalef (1979), who distinguished between external 'structure' and ecological 'pattern'. Austin et al. (1984) analyzed the nature of external factors influencing vegetation patterns and discussed methods for studying such interactions. A fruitful generic term for describing external boundary conditions that influence the dynamics and behaviour of biological units 'within' is the environmental forcing func-

tion (Huntley & Webb 1988, Delourt & Delcourt 1991). This is another umbrella term that can include, for instance, physical factors such as climate and moisture regime, disturbances such as wildfires or tidal waves, and spatial configurations of the environment such as insularity and isolation of single habitat patches or habitat archipelagoes. The relative significance of these alternative factors varies greatly in different environments; for instance, temperature is generally the critical 'forcing function' at high latitudes, and moisture closer to the equator. 'Diversity' of, for instance, disturbance regimes contributes greatly to the heterogeneity of ecological systems. The algae communities on sites exposed to wave action are very different from those in sheltered bays, even though the distances in metres are negligible. This conclusion can be extended back in time: boundary conditions of the past are detectable in present patterns of ecological diversity (Hunter et al. 1988).

The overall conclusion seems inevitable that even within the conservation discourse, 'biodiversity' is not a well-defined concept, it does not refer to any well-defined set of phenomena and their theoretical interpretation. Rather, 'biodiversity' covers a whole range of manifestations of biological heterogeneity that can be investigated independently of each other.

4. Origin of the conservation concern

The conservation discourse on biodiversity originated with notion of a 'diversity crisis', which came about gradually during the 1970s with increasing awareness of an extinction wave that was threatening as a consequence of human population growth and increasing intensity of environmental modification (Myers 1979, Ehrlich & Ehrlich 1981). The general prediction derived from island biogeography that the number of species inhabiting any environmental type such as the tropical rainforest will decline monotonously with a decrease in area of the environmental type was also important. The relationship was assumed to be approximately linear when a logarithmic transformation was used on area, or both area and species number (e.g. Connor & McCoy 1979). Erwin (1988) showed that even

the non-transformed species-individuals (or species-area) relationship in the tropics seems to be linear. This gave an impression that — in the tropics — species extinctions are occurring linearly to the proportion of area lost. Prior to these studies, natural history data on human-caused extinctions particularly on birds had been collected (e.g., Greenway 1967), but the new approach seemed to allow mechanistic predictions of extinction rates without needing to care about natural history details.

The threat of an imminent extinction wave proffered interest in the mechanisms of extinction, and in population viability; this approach drew upon both population genetics and population ecology (Soulé & Wilcox 1980, Frankel & Soulé 1981, Soulé 1987).

The next stage was a growing interest in the consequences of extinctions, for instance, what are the effects on functional integrity of ecosystems; this was a common thread in articles in Soulé (1986). Emphasis was also directed to changes in boundary conditions of ecosystems, particularly changes in habitat configurations generically called ‘fragmentation’ (Burgess & Sharpe 1981, Harris 1984, Wilcove et al. 1986, Saunders et al. 1987, 1991, Haila et al. 1993b), and on the importance for conservation of active management of habitats and environmental types (Spellerberg et al. 1991, Saunders et al. 1993)

The historical origins of the conservation discourse are thus heterogeneous and somewhat idiosyncratic. The role of biogeographic theory has been particularly controversial from early on (Simberloff & Abele 1976, Higgs 1981, Margules et al. 1982). Another important controversy centred on the relationship of diversity to community stability; we return to this issue below. One can suspect that some confusion in the ‘conservation discourse on biodiversity’ is due to a tension between acknowledging the urgency of the issue and identifying weak links in the arguments. The biodiversity crisis may seem so urgent that doubt concerning the validity of any single argument used is taken as an assault on the issue. This is quite manifestly the case with conservation applications derived from island biogeography and the ‘single-large-or-several-small’ reserves debate (Diamond 1975, Diamond & May 1981, Simberloff & Abele 1976, Simberloff 1986,

Järvinen 1982) — however, a consensus seems to be emerging that on an abstract level ‘SLOSS’ is simply a non-question. Qualifications are needed as to what the ‘area’ considered actually consists of, what the relevant species are, and how the ecological systems considered work.

There are, however, other, theoretically much more challenging problems which we merely list here:

- 1) Is it possible to use surrogates, for instance critical species, or particular species groups (e.g., Pearson & Cassola 1992) in assessing biological diversity?
- 2) What are the minimum thresholds of diversity before ecological systems lose their functional integrity or evolutionary adaptability? This is the question of redundancy (Walker 1992) — ‘diversity’, being a synonym for ‘heterogeneity’, is by definition redundant, but is there a lower limit to diversity (see also Lawton & Brown 1993)?
- 3) How do different human modifications of the environment actually influence ecological diversity? The problem is to adequately characterize such environmental changes that bring forth threats to ‘biodiversity’. Human-induced changes have often been characterized too typologically. Fragmentation is the case in point. For instance, inferences about bird community impoverishment in small forest patches based on mere presence/absence data are often unjustified because the probability that a species is present in a patch is a function of regional abundance (Helliwell 1976, Haila & Järvinen 1981) — nevertheless, conceptual and methodological biases in fragmentation studies have tended to hide this simple mechanical relationship from sight (Haila et al. 1993a)

It seems clear that much research and theoretical clarification is still needed on how human activities actually ‘change nature’. The problem is that nature changes by herself, and recording mere change is not particularly interesting — what matters is the relationship between human-induced and natural change (Haila & Levins 1992). Salthe (1985) made some interesting suggestions as to how human activities may interfere with between-level interactions in the ecological hierarchy: for

instance, changes in populations are caused by either changes in values of reproductive parameters — ‘initiating conditions’ — or changes in the environment — ‘boundary conditions’ (see e.g. Lawton 1993). These effects go usually together, particularly when human activities change the ‘environmental forcing functions’ important in a particular system, for instance, disturbance regime (Huntley & Webb 1988). A vast literature is available, for instance, on how ecological systems have changed as a consequence of efficient suppression of wildfires.

Human activities have also increased biological diversity in many regions in the world. In the boreal zone, for instance, this has been through creation of new habitats which are dominated by alien species (Hämäläinen 1983). In Central Europe it has been estimated that human influence increased the overall floristic diversity until early this century (Sukopp 1972, Kornas 1983). Human influence is not necessarily, always and everywhere negative from the point of biodiversity. This, however, should not be apology for ruthless exploitation and despoliation of nature. The conservation discourse on biodiversity focuses primarily on ‘natural’ diversity patterns, but it is impossible to completely exclude human historical influence. A general idea is needed about how human-induced disturbance regimes relate to natural ones (Peet et al. 1983, Behre 1988).

5. Operationalizing diversity in conservation

A major methodological complication following from the discussions above is that it is not at all obvious how to keep separate different scales and criteria when ‘biodiversity’ is evaluated. Measurements made using standard units probably ‘measure’ vastly different phenomena depending on what are the objects of measurement (Fig. 2). This is almost a truism (Rosen 1977, Wiens 1989, Haila 1992, Levin 1992). The only remedy is to make all considerations explicitly context specific, and explicitly scaled. In this section we review briefly some ecological research traditions that have dealt with biological diversity, some of them long pre-dating the ‘conservation discourse on biodiversity’, and draw

methodological outlines that can be applied in conservation research.

5.1. Species diversity

The interest in collecting quantitative data from natural communities and populations originated in the late 19th century (McIntosh 1985, Haila 1992), and this soon gave rise to questions concerning variation in the number of species in different types of samples and in different sized areas. Such descriptive patterns in the statistical variation in species richness were studied from the early 1920s onwards (Fisher et al. 1943, Preston 1960, Williams 1964).

In MacArthurian ecology this was connected with strong assumptions about forces structuring communities (MacArthur 1965) — thus, MacArthur’s notion of ‘diversity’ was burdened by theoretical assumptions and thus differed from the earlier ones (Kingsland 1985, Haila 1992).

This proffered a new de-construction of the notion of species diversity: Hurlbert (1971) showed that ‘species diversity’ is not a universally interesting concept but makes sense only in particular, well-defined contexts. May (1975) reviewed the evidence showing that most patterns in sample species richness reflect statistical characteristics of the abundance variation of different populations. This stimulated such operationalizations of species diversity that standardize for sample size, rarefaction (Simberloff 1978).

The positive legacy of this tradition is the availability of some useful, operationalizable measures of species richness and its variation; particularly Whittaker’s (1977) spatially explicit distinction between within site (alpha-), between site (beta-), and regional (gamma-) diversities (Fig. 3) is useful because it incorporates the question of scaling (although it needs to be emphasized that the ‘scales’ are not in nature but in the calculations: the particular decision on scaling in every case needs to be justified on independent grounds).

5.2. Genetic diversity

Genetic variability of populations is generally considered important for population viability (e.g.

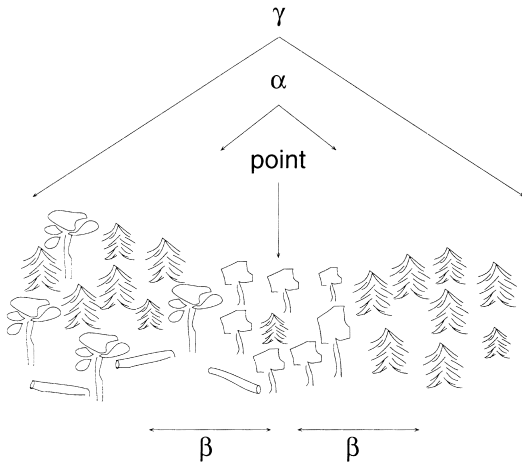


Fig. 3. Spatially different components of diversity. Each component of diversity may further be divided on species groups (e.g. plants, insects, birds) or on ecological hierarchy levels (genes, species, ecosystems). (Modified after Kouki 1993)

Soulé 1986, 1987). These ideas relate to the selection metaphor. It is thought that genetic variability is necessary for populations to survive environmental bottlenecks. While this may generally be the rule there are also some possible exceptions (Walter 1991).

One difficulty in the research of genetic diversity is that adequate methods to summarize the vast natural variability in genomes are largely lacking. The recent rapid methods based directly on DNA structure have somewhat alleviated this difficulty (Solbrig 1991b), because the overall variation of the whole genetic material within an individual can now be assessed. The previous methods — like analyses of protein polymorphism — concentrated largely on the variation in a few specific loci within the genome of an organism. However, the problem of determining the significance of the variation that is detected remains, since the functioning of the whole DNA content of the cell is unknown. The significance of genetic variation is well established in population genetics theory, but empirical demonstrations from nature are lacking (Caughley 1994).

Also the global patterns of genetic diversity are poorly known. The data available shows that there are huge differences in the DNA contents of different animal and plant groups. Also the

genetic relatedness of species in different groups is highly variable (World Conservation Monitoring Centre 1992). This implies that general patterns — as decreasing species diversity from tropical to polar regions — might be less likely to be found in genetic diversity. Overall, the patterns — both local, regional and geographical — of genetic diversity still remain an open yet a challenging problem.

5.3. The significance of species diversity

In the first half of this century ecologists, beginning with Elton (1927) tended to assume instinctively that diversity enhances community stability (Goodman 1975). However, May (1973) showed mathematically that this is unlikely to be the case, and Levins (1974) demonstrated that it depends on the structure of the system whether feedback loops are stabilizing or destabilizing. Later these conclusions were corroborated in empirical studies which demonstrated that diversity in natural communities is higher in moderately disturbed than in stable communities (Connell 1978, Sousa 1980, Paine & Levin 1981).

The concept of 'community' adopted in the diversity–stability controversy is questionable. Whittaker (1967) demonstrated that plant distributions along environmental gradients are seldom divisible into neat communities and promulgated 'gradient analysis' as a proper approach (Austin 1985, 1986).

Currently it seems impossible to assess whether species diversity is important for stabilization or destabilization of community dynamics or functioning. What ought to be stressed is that by definition no two species are equal. The extent to which this inequality affects a community depends on how different the species are functionally. This is an area that most probably is important, for instance, in aquatic systems and soils (Levin 1989, 1992, Paul 1989, Steele 1991), but empirical data are largely missing. Relevant questions can be formulated, but they have hardly been addressed empirically.

Some special cases of functional inequality are naturally known. For example, in the tropics some fruit-bearing plants may be extremely important as resources for several other species

although these plants may be quite uncommon (Soulé 1986). In the boreal regions, some small mammal-fungal relationship may be equally important (Maser et al. 1978).

Ecological research has largely dealt with either the most numerous species in the community or the rarest. Yet if the numbers of individuals and species in the intermediate abundance groups are combined, they typically make up a majority of the community. Consequently, these moderately common species may play a crucial role in cycling both nutrients and energy through the whole system. These species deserve more attention.

5.4. The significance of environmental heterogeneity

Research on environmental heterogeneity is closely related to the previous topic, but it scales at least one level up to the heterogeneity of boundary conditions, or 'environmental forcing functions', and landscape structures. This heterogeneity relates to population dynamics through processes such as immigration and extinction, and to distribution patterns through the performance of individual species along environmental gradients (Austin et al. 1984, 1990).

In large parts of the boreal region, for instance, both environmental heterogeneity and environmental dynamics have changed as a consequence of intensive forest management (e.g., Hansson 1992, Angelstam & Holmer 1993). Forestry has brought about at least three differences in the basic structure of boreal coniferous forests: (1) fragmentation of old-growth forests has increased, i.e. patches are smaller and more distant from each other, (2) deciduous component of tree community has diminished, and (3) the amount of dead but still standing trees in the forests has decreased, possibly from 10–12 m³/ha to 0–2 m³/ha (Linder & Östlund 1992). In the dynamics there seem to be at least two differences: (1) fires modify forests less often (Zackrisson 1977), and (2) rotation times of forest development are shorter to maintain high net production of timber (e.g. Hunter 1990, Kuusela 1990).

These changes affect populations both qualitatively and quantitatively. By the former we

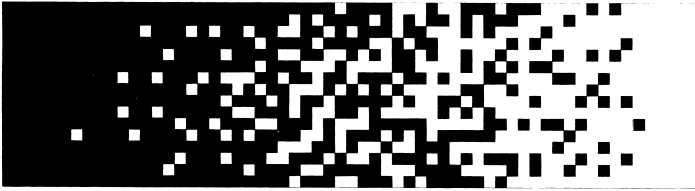
mean that certain forest environments have become rare and thus it is impossible for species requiring these environments to survive. By quantitative effects we mean that spatial configuration of populations are affected. These changes split populations into several smaller ones that are connected through occasional migration, i.e., into 'metapopulations' (Levins 1969, Gilpin & Hanski 1991) which have received a lot of attention recently. In a metapopulation, the regional occurrence of the species depends on balance between local extinctions and colonizations (Hanski & Gilpin 1991). Thus, management policies derived solely from the present distribution of species may be misleading. This is also a research area where population genetics and ecology merge.

Heterogeneity of the 'boundary conditions' and heterogeneity of ecological systems merge together for instance through 'mosaic phenomena' emphasized by Whittaker & Levin (1977). This term refers to small-scale successional cycles following for instance the death of single plant individuals. Such cycles vary depending on the character of the local environment (e.g. Kuuluvainen 1994, Syrjänen et al. 1994), dubbed 'microsite' by Whittaker & Levin (1977).

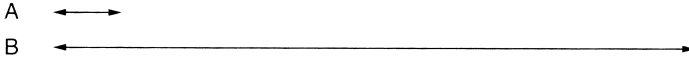
Landscape features are, however, difficult to manage. The problem is, methodologically, that the basic unit is not unambiguous, as it is unambiguous in species diversity (conditionally upon accepted taxonomy). In regions where the flora and fauna are poorly known, biogeographic and landscape patterns may appear as a useful, and practically only possible surrogate for evaluating diversity (Noss 1983). However, the problem always remains that decisions on the number of types considered, and on the representativeness of these types of the local biota, must be validated with actual ecological data (Margules et al. 1988, Belbin 1993). Furthermore, any measure used to describe heterogeneity is scale-dependent, as we show in Fig. 4. Such measures can possibly be useful with regard to named species whose ecology is well known, but as general indicators of environmental heterogeneity they are of doubtful value.

We see two alternative approaches to create and manage environmental heterogeneity in forests. First, to try to mimic 'natural' dynamics as

Configuration of environment:



Scale of measurement:



Diversity across landscape:

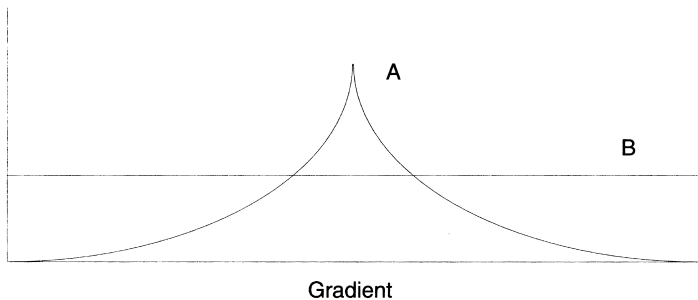


Fig. 4. Scale-dependency of environmental diversity measurement. The true landscape pattern is shown on the top of the figure. Higher resolution of spatial measurement units (A) leads to a quite different diversity pattern across a landscape than a lower resolution measurement (B). (Modified after Kouki 1993)

well as possible. Here the basic questions relate to regeneration processes of forests. For example, what are relative importance of large-scale and small-scale regeneration processes in different forest types (e.g. Angelstam & Holmer 1993, Mladenoff et al. 1993, Kuuluvainen 1994, Syrjänen et al. 1994). This implies that history is incorporated into interpretation of diversity variation, and the descriptive/explanatory schemes (Haila & Levins 1992). Second, to investigate population dynamics and especially spatial population dynamics of a set of species with different ecological characteristics and infer what the forests should look for the maintenance of viable populations of these species. This is a more time- and resource-consuming task. However, both approaches need to be used in practice. We ought to understand the ecological processes which lead to population declines and eventually to extinctions (Caughley 1994), and these cannot be inferred from forest dynamics alone.

5.5. Traditional nature protection and biodiversity: do they differ?

Traditionally nature protection has aimed at preserving target species and landscapes. The focus has thus been on particular systems considered, for example, beautiful, vulnerable or of particular scenic significance (Götmark & Nilsson 1992). As we discussed previously, 'biodiversity' can be specified in several different ways and these specifications may be different from the original context of nature conservation. The problems lie both in the structure and dynamics of the systems that are aimed to conserve. Natural variation in ecological systems is considerable even without the impact of man. Thus we need to ask what and how large is this natural variation to get an insight on which human-induced disturbances actually are detrimental to species and ecosystems. Furthermore, natural systems have their own internal dynamics so that the observed pattern — or heterogeneity — does not remain constant over time.

Protection of biodiversity may lead to quite different management policies than previously applied depending on what aspects are emphasized. For example, if the main purpose is to maintain ecological integrity and functioning of an ecosystem, at the species level this will most likely put emphasis on the species that are very abundant, or moderately abundant, rather than on the rare species. The reason is that most of these species have the greatest influence on energy and matter flows in ecosystems. On the other hand, if the aim of the biodiversity protection is to protect as many species and environmental types as possible, the main emphasis will be first at the rarest types, because these are likely to disappear first. In management policies the two aims outlined are naturally not mutually exclusive, but their essential difference should nevertheless be recognized.

This again emphasizes the context-specificity of the biodiversity discourse. We feel especially suspicious about attempts to “measure biodiversity”. Usually the aim seems to be to find a single index on which to base management decisions. However, given the large variation in the natural dynamics different ecological systems this seems impossible (see also Väisänen & Heliövaara 1994). Globally it seems possible to identify hot-spots of diversity, i.e. areas that contain large numbers of endemic, rare or vulnerable species. Locally we should, however, pay more attention to population processes of single species and/or peculiarities of the systems to be protected. Under these circumstances a single measure of biodiversity seems useless. In other words, results of ‘biodiversity’ evaluations are likely to remain criteria-specific, and context-specific.

6. Conclusions

‘Biodiversity’ is not a concept but a term (an ‘umbrella term’), and every particular description of ‘diversity’ is fuzzy. Great terminological variation cannot be avoided and it is, consequently, always necessary to specify the context. This can be fruitfully done by distinguishing different ‘discourses’ which create the background for defining the meaning of the term. Conservation discourse is one among them; others in-

clude, for instance, ‘economic discourse’ on the economic value of biodiversity, ‘management discourse’ on the methods and means of maintaining biodiversity in human-modified environments, or ‘ethical discourse’ on the relevance of biodiversity to the human relationship with nature. These different ‘discourses’ are naturally interdependent. Biological arguments that underline the importance of biological diversity for maintaining the earth habitable for human beings have validity in the other fields as well, but the distinctions are also important because the terms used may have different meanings.

The issue of biodiversity is much broader than merely the question of extinctions and endangered species. This is an important conclusion for avoiding confusion in policy and management activities. Ultimately, the key to ‘biodiversity’ is heterogeneity which is a necessary characteristic of ecological systems, but this gives no shorthand for conservation and management decisions which must always be based on explicitly defined criteria.

The new emphasis that biological diversity is valuable also as a resource is an important starting-point for getting the issue generally acknowledged. However, the integration of biodiversity preservation into management practices is a more demanding task than adding new variables to profit calculations. The specific ecological features of the systems exploited should be recognized and incorporated into management practices. This calls for close co-operation between fundamental research and applied management, and motivation and mobilization of local people into undertaking demanding practical tasks. For instance, reintroducing native vegetation to degraded agricultural lands requires co-operation of farmers on the scale of natural units such as catchments which hardly ever coincide with boundaries of individual farms. More than merely economic motivation is required for success in such tasks. Several articles in Saunders et al. (1993) discuss the experience gained in revegetation efforts in the Western Australian wheatbelt.

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