Updated version 14 April 2000

Technical Report No. 1

BEAR

Indicators for forest Biodiversity in Europe

Indicators of biodiversity: recent approaches and some general suggestions

Lennart Hansson
Department of Conservation Biology SLU
Box 7002, SE-750 07 UPPSALA, Sweden
e-mail: Lennart.Hansson@nvb.slu.se

Background and early development

Biodiversity has been defined as all variation on the genetic, species and ecosystem levels, in agreement with the Rio Convention. Diversity on the landscape level ('gamma-diversity') may also have important effects on lower levels (e.g. Noss 1990, Hansson et al. 1995) and may be a determinant of large parts of regional diversity. It would be completely impossible to try to monitor all this potential variability and, indeed, only certain aspects of the biological variability may in the long run be important to retain: Invading species are usually considered undesirable. Local human disturbance can increase species richness. However, we still do not know which species are actually necessary for normal ecosystem functioning (Lawton 1994). Thus, there are two general problems in biodiversity management: 1) Which is the important (or representative, or 'valued') biodiversity for a certain system or region and 2) How in a fairly simple way make sure that that variability is retained.

The first problem has to be solved first. There has indeed been some recent progress in understanding the effects of varying biodiversity on ecosystem patterns and processes (e.g., Naeem et al. 1994, Grime 1997, Jones et al. 1997). The extinction risk of endangered herbivores has been related to the level of plant biodiversity (Ritchie 1999). And the ethical arguments for preserving biodiversity are stressed repeatedly.

The second problem is related to a selection of ecological indicators. An indicator may be a species, a structure, a process or some other feature of a biological system, the occurrence of which insures the maintenance or restoration of the most important aspects of biodiversity for that system. Diversity is often equated with species richness, although this is not in agreement with the Rio Convention. Some authors have instead stressed the importance of ecological mechanisms (Noss 1990) and keystone species (or 'drivers' instead of 'passengers' in the ecological systems, Walker 1992). The concept of 'biotic integrity' (Angermaier and Karr 1994) covers biological diversity but also includes the ability of an ecosystem to function and maintain itself, including its native biodiversity. Certain indicator systems have already been developed with this biotic integrity particularly in mind.

The interest in indicators has a long history within ecology. The earliest use was probably to manually demarcate various plant associations within phytosociology. Such a function is still retained in more recent and advanced methodology in that discipline, e.g. in the TWINSPAN (Two-Way INdicator Species Analysis, however see Dufrene and Legendre 1997 for recent criticism) statistical program to separate various vegetation units in a tangled mosaic. Indicators have been common in ecotoxicology, e.g. as laboratory systems to demonstrate possible toxic effects of environmental contaminants. Certain fish species have often been used in this context, the miners′ canary is a noteworthy example. Lichens have for long been known to be severely negatively affected by pollutants in the air. This relationship has been exploited for field monitoring of pollution, using several lichen species as indicators (Hawksworth and Rose1976, Skye 1979).

Indicators have also been used to demonstrate general population trends, e.g. the declining brown hare for wildlife generally in the European agricultural landscapes. Particularly in the US, one species has been selected as an indicator for a whole guild or even an ecosystem ('Management Indicator Species' as the bald eagle or the Florida panther, e.g. Severinghaus 1981, Verner 1984). However, this approach has met with limited success (e.g. DeGraaf and Chadwick 1984, Landres et al. 1988). Finally, indicators have already been used in conservation biology, as umbrella species (Launer and Murphy 1994, usually large species with wide areal requirements, presumed to also cover the requirements of other species, e.g. tigers) or flagships (Noss 1990, large appealing species attracting interest to their ecosystem, e.g. pandas). Problems with these various approaches have been discussed and evaluated by Landres et al. (1988).

Policy indicators

The subsequent discussion about possible indicators of biodiversity has developed in different directions. Some authors have argued for indicators for policy-making and others have tried to develop indicators for practical use in management and monitoring. At policy-making, indicators may be used to compare different localities, regions or countries regarding the biodiversity, or care of biodiversity. Such indicators can also be used to set priorities for land use and for conservation projects. Reid et al. (1983) presented a list of 22 such indicators for genetic diversity (also for domesticated species), species diversity and community diversity. These indicators consisted, e.g., of number or percent of species threatened by extinction, number of endemic species, number of species with decreasing populations, percentage of area in strictly protected reserves and present crop area related to that area thirty years earlier. Most of these statistics are fairly readily available from official sources. They are usually only applicable on a regional level. They can hardly be used to survey the development or recovery of a separate threatened ecosystem, reserve or forest stand. Such problems require management indicators and mainly that latter type of indicators will be treated below.

Criteria and indicators proposed in the 'Helsinki-Process' for protection of biodiversity of Europan forests (Loiskekoski et al. 1994) may be considered mainly as policy indicators. They evidently need to be supplemented with management indicators.

Single species vs community indicators

Some earlier use of particular indicator species as a monitoring device has met with severe criticism: in ecotoxicology toxic effects on laboratory specimens may not mean anything to natural populations due to compensatory survival (e.g. Cairns 1986), and neither to whole communities due to overwhelming competition or predation effects. Likewise, in conservation single species may simply not cover the vulnerability of any extensive system due to complex niche diversification. Different species may also be limited in different ways, e.g. by specific food resources, by predation or by social factors. There may even be negative correlations between abundances of indicator species and certain other species if there is strong interspecific competition between them. An example of the limitation of a separate species is the spotted owl that has got the rank of an indicator species but does not indicate all the needs of sympatric threatened amphibians (Harrison and Fahrig 1995).

A solution to the problems with single conservation indicator species appears to be a limited group of species better covering the environmental variability of concern (Landres et al. 1988, Wilcove 1990). Birds as a group have been advocated as such wide-spectrum indicators (Järvinen and Väisänen 1979), containing residents, short distance and long-distance migrants, short- and long-lived species, granivores and insectivores, etc. Conventional diversity indices utilised in community ecology (e.g. species richness and the Shannon-Wiener or Simpson indices) were supposed to be useful for comparisons. However, even in such cases problems may arise: The species richness of birds associated with lakes and wetlands has generally increased but this increase is mainly due to eutrophication or pollution. Certain bird communities of Baltic islands demonstrated a decrease in Shannon-Wiener index when protected (Väisänen and Järvinen 1977); however, the actual reason was an disproportionate increase in the herring gull while all other species also increased but less so.

Statistical indicators

Much recent work has centred around statistical indicators, i.e. single species or species groups that are strongly correlated with total species richness or with species richness within certain taxa. This approach thus neglects important aspects in the original definition of biodiversity. Williams and Gaston (1994) proposed the use of the diversity of higher taxonomic units as indicators of species richness and found significant correlations between the numbers of families and the number of species for certain groups of organisms that were examined over fairly large areas. Beccaloni and Gaston (1995) made a similar comparison between the number of species of a specific butterfly family *(Nymphalidae: Ithomiinae*) and the total species richness of all other butterflies for Central and South America. Higher-taxon richness as indicator of species richness was found to possess several limitations in tropical areas by Balmford et al (1996). There was little spatial congruence in the distribution and abundance of species of various higher taxa in Britain (Prendergast and Eversham 1997) or in Canada (even negative for mosses and epiphytic lichens, Gould and Walker 1999), while Swiss examinations (Obrist and Duelli 1998) found good correlations between species richness of certain taxa as *Coleoptera*, *Diptera* and *Hymenoptera* and total species richness in the samples. When the effort needed for sorting and species determination was included in the latter analysis then *Heteroptera* and vascular plants appeared as most efficient indicators of species richness.

Such endeavours and observations have recently led to a more general theory for the selection of species indicators for more or less distinct communities (Dufrene and Legendre 1997, see also McGeoch and Chown 1998). Algorithms select species that are both highly specific to a site group and wide-spread within it. The statistical method employed has already found its way into a commercially available software for ordination as ORD (McCune and Mefford 1997). A somewhat related theory relies on the degree of nestedness of more or less fragmented communities (Worthen 1996; Atmar and Patterson 1995 for software); species with high or intermediate level of nestnedness may be useful indicators. Some studies show, however, little congruence in nestedness between taxa (e.g. Hansson 1998).

In spite of all these suggestions, there has been little evaluation in the field of how well one or several suggested indicator species do cover the requirements and occurrence of other species. One exception is Nilsson et al. (1995) who showed that the occurrence of the lichen *Lobaria pulmonaria* coincided with occurrences of several other red-listed lichen species. The agreement with the occurrence of red-listed wood beetles was worse but the number of beetle species dependent on hollow trees were larger in sites with *L. pulmonaria*. Abensperg-Traun et al. (1996) found certain potential indicator species to predict very little of the species richness of a West Australian fauna while the inclusion of structural variables as vegetational structural diversity and patch area as covariates considerably improved the predictions.

Functional indicators

As mentioned earlier, indicator systems have been developed for measuring biotic integrity, particularly in limnic ecosystems. The first approach (Karr 1981), based on fish assemblages, considered mainly environmental (water and stream) quality but, as permitting monitoring of ecosystem features, it was also suggested to be useful in surveying the functional biodiversity and thus generally applicable in conservation (Karr 1991). It has been used for practical monitoring during almost a decade in USA. A locally adapted system is being developed to measure the quality and biodiversity of central American streams (Lyons et al. 1995). As an example, it is not based only on general community composition but on a partitioning of the metrics between various guilds and sensitive species. The authors thus delimit ten measures that are estimated in various streams to indicate biotic integrity. These measures are: Number of native species, percent of benthic species, number of water column species, number of sensitive species, percentage of tolerant species, percentage of exotic species, percentage of omnivores, percentage of native livebearing species, relative abundance and number of diseased or deformed specimens. Each of these measures is thought to be affected by various types of human disturbance and pollution. A related indicator for areas of high conservation value ('hot spots') only (Winston and Angermeier 1995) is based on the relative densities of the various species (in this case fish) that occurs within a region.

This type of biodiversity analysis may be said to be performed with functional indicators. Such an approach was also suggested by Alard et al. (1994) for grasslands in France. They recognized that grassland vegetation consisted of both indigeneous and anthropogenic plant species and that particularly the proportion of competititve species (sensu Grime) indicated changes in general biodiversity. More recently, Angelstam (1998) has proposed a more extensive system of functional indicators for boreal forests. Several plant and animal species, closely dependent on the pristine disturbance regimes of these forests, are supposed to function as indicators of original biodiversity. Similarly, Kuusinen (1996) found that cyanobacterial lichens, including *Lobaria pulmonaria*, indicated old-growth status and long-term continuity of a forest stand. Similar observations were done by Tibell (1992) for crustose lichens in boreal forests. Nilsson and Baranowski (1994) suggested that the number of click beetle species (*Elateridae*), dependent on hollow trees, were good indicators of mega-tree (and woodland) continuity.

Certain authors have remarked about the great diversity among insects and their potential as an indicator group (e.g. Kremen et al. 1993). As an example, tiger beetles have been suggested as a suitable indicator taxon because of good knowledge of habitat affinities and easy sampling (Pearson and Cassola 1992). Other authors have instead suggested vertebrates and butterflies (and possibly vascular plants) as indicators for gap analyses, i.e. for securing important but underrepresented habitat or ecosystem fragments for conservation by GIS analysis. Again these taxa are assumed to be well-known and to have a precise habitat selection (Scott et al. 1993, however, see Flather et al. 1997 for criticism). Kremen (1992) proposed the use of ordination methods (especially CCA = Canonical Correspondance Analysis) for establishing relationships between the occurrence or abundance of indicator species and environmental factors, especially those related to original and disturbed habitats. Functional indicators can also be more specific: Anderson (1994) suggested the height of a preferred plant species to be used as an indicator of deer browsing pressure and deer effects on plant diversity and, inferentially, also on insect pollinators and herbivores. Deer have also been suggested as suitable indicators of both forest management and landscape quality (Hanley 1996).

Functional indicators may not necessarily be determinants of ecosystem functions even if some authors assume that keystone species would perform particularly well as indicators. In view of present problems with the keystone species concept (e.g. Lawton 1994), less emphasis may be put on such possible relationships. However, functional indicators should be closely related to or strongly dependent on important structures or processes in the ecosystems.

Indicators from hierarchy theory

Noss (1990) advocated an application of hierarchy theory in the selection of indicators. Within each level of organisation, from genetics via species, community, ecosystem, landscape and finally to region, he distinguished three features, composition ('taxonomy'), structure (often equal to spatial distribution) and function (ecological processes). He then observed that hierarchy theory e.g. predicts that higher levels incorporate lower levels and constrain the behaviour of dependent entities. The lower levels contain species identities, abundance and many main functions but higher level properties may emerge, and effects at one level may be expressed in unpredictable ways at another level. One main conclusion was that total biodiversity needs many indicators and several of them may profitably be physical ones, e.g. structures or processes. Indicators may thus be derived from the basic factors or premises for community composition or local biodiversity. More generally, there is a need to monitor indicators of compositional, structural and functional biodiversity at multiple levels of organisation. However, all features and levels cannot be utilised in any realistic system; the most important indicators have to be selected for specific systems and problems. Table 1 lists some potential indicator features for common terrestrial system. They may all be considered as functional indicators.

Focal species

Lambeck (1997) outlined a management approach involving 'focal species'. He distinguished the (focal) species in a local community, pristine or not, that were most sensitive with regard to 1) area requirement 2) short dispersal distances or connectivity, 3) critical resources (e.g. food or substrate specialisation), and 4) natural or induced processes (e.g. recurrent fires or grazing). If the landscape was managed with regard to structure and function to retain such species then the vast majority of other species should also be thriving. The focal species complement was also reflected in a specific landscape composition, including particular ecosystem processes.

An indicator system based on focal species may be adjusted for pristine landscapes (emphasising the requirements of very specialised species), managed landscapes (considering requirements of the species we want particularly to retain), to 'metapopulations' (considering the most sensitive subdivided population) and even to 'one-species-systems'. Such indicator systems can be applied at various scales, at larger scales probably by stressing connectivity and possibilities for dispersal. Furthermore, if we want it cost-effective we may use only the physical landscape structure as an indicator of what is or will be retained and how to change the landscape in order to get desirable biodiversity.

Properties of indicator species

The more recent publications have thus often proposed indicator species even if non-living types of indicators have not been completely disregarded (e.g. Faith and Walker 1996). Thus, there are reasons to examine what characteristics are necessary or desirable for species that may serve as (functional) indicators.

Some desirable characteristics, related to general adaptations in ecology and behaviour of the particular species, are:

- being specialised on the ecosystem or landscape to be monitored (habitat specialist)
- sensitive to artificial disturbance in at least one specific factor, over a wide range of natural variability (reactive)
- having fairly large area and resource requirements (spatial coverage)

Table 1. Possible indicator features according to level of organisation and and structural (incl. taxonomical or compositional) and functional properties. Original based on hierachy theory, this list could be considered as a 'smorgasbord' for functional indicators but actual indicators have to depend on characteristics of the specific system to be monitored. Based on Noss (1990).

Levels	Composition	Structure	Process
Region	Geomorphology Endemism	Heterogeneity Fragmentation	Geomorphic processes Economic processes
Landscape	Patch types beta & gamma diversity	Connectivity Juxtaposition	Disturbances Movements Patch dynamics
Local ecosystem/community	Species/guilds alfa-diversity	Biomass Physiognomy	Productivity Herbivory Predation Pollination
Population	Abundance	Dispersion	Natality Mortality Dispersal
Genetic	Allelic diversity	Heterozygosity Effective population size	Inbreeding Drift

- being fairly common and easily and cheaply identified and sampled (economy)

Some authors suggest that use of indicator species should be independent of sample size or scale (Noss 1990, Weaver 1995) but that is probably too much to hope for.

There are also certain requirements on the spatial distribution of such potential indicator species (cf. Harrison 1991):
- they should have continuous and demographically balanced populations, i.e. clumping should not be too severe and particular age classes should not dominate in the system examined
- they should preferably be resident species
- if their populations are characterised by sinks and sources then the monitored habitat should contain source populations
- if they exist as subdivided or fragmented populations then the patches examined should at least at the outset host equilibrium metapopulations

Similarly, there are requirements on the temporal dynamics. Suitable species should
- consist of population with rapid density responses to disturbances or habitat changes (i..e. short-lived species) or
- monitoring should be focused on reproduction, recruitment or individual health, for plants on growth characteristics (long-lived species) and
- the populations examined should not be affected by any conspicuous demographic stochasticity or genetic impoverishment due to long-term marginal population sizes.

It might be noticed that most plant species are long-lived and that short-lived animal species are often naturally characterized by irregular or cyclic fluctuations even in fairly stable environments. A compromise may have to be reached; however, reproduction or physiological condition may often serve as a more reliable indicator than presence or numbers.

Some indicator systems in use

Indicator systems have been developed and used in practical monitoring in limnic environments in U.S.A. and other North American countries (Karr 1981) and e.g. in Sweden (Johnson and Wiederholm, undated) and have been outlined for boreal forests in Canada (McKenney et al. 1994). A system of 'signal' species for delimiting old-growth boreal forests was developed from natural history observations in northern Sweden by the local team 'Steget före' (Karström 1992) and further analysed by Olsson and Gransberg (1993). It relied on occurrences of certain rare cryptogams and fungi. Preliminary results from an extensive Swedish research project on indicators of forest biodiversity is available in Swedish (Anon 1999).

Acknowledgements: I appreciate comments by Lena Gustafsson, Gunnar Jansson, Tor-Björn Larsson and Per Sjögren Gulve

References

Alard, D., Bance, J. F. and Frileux, P. N. 1994. Grassland vegetation as indicator of the main agro-ecological factors in a rural landscape: Consequences for biodiversity and wildlife conservation in central Normandy (France). – J. Environ. Manage. 42: 91–109.

Anderson, R. C. 1994. Height of white-flowered trillium (*Trillium grandiflorum*) as an index of deer browsing intensity. – Ecol. Appl. 4: 104–109.

Anon. 1999. Indikatorer på biologisk mångfald i skogslandskapet. – Skog and Forskning 99: 2: 7–59, in Swedish.

Angelstam, P. 1998. Towards a logic for assessing biodiversity in boreal forests. – In Bachmannn, P., Köhl, M. and Päivinen, R. (eds), Assessment of biodiversity for improved forest planning. Kluwer, pp. 301–313.

Angermeier, P. L. and Karr, J. R. 1994. Biological integrity versus biological diversity as policy directives. – BioScience 44: 690–697.

Abensberg-Traun, M. et al. 1996. Biodiversity indicators in semiarid, agricultural Western Australia. – Pacific Conserv. Biol. 2: 375–389.

Atmar, W. and Patterson, B. D. 1995. The nestedness temperature calculator; a visual basic program. – AICS Research, Chicago.

Balmford, A., Green, M. J. B. and Murray, M. G. 1996. Using higher-taxon richness as a surrogate for species richness. I. Regional tests. – Proc. R. Soc. Lond. B 263: 1267–1274.

Bader P., Jansson, S. and Jonsson, S. G. 1995. Wood-inhabiting fungi and substratum decline in selectively logged forests. – Biol. Conserv. 72: 355–362.

Beccaloni, G. W. 1995. Predicting the species richness of neotropical forest butterflies: Ithomiinae (*Lepidoptera: Nymphalidae*) as indicators. – Biol. Conserv. 71: 77–86.

Cairns Jr, J. 1986. The myth of the most sensitive species. – BioScience 36: 670–672.

DeGraaf, R. M. and Chadwick, N. L. 1984. Habitat classification: a comparison using avian species and guilds. – Environ. Manage. 8: 511–518.

Dufrene, M. and Legendre, P. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. – Ecol. Monogr. 67: 345–366.

Faith, D. P. and Walker, P. A. 1996. How do indicator groups provide information about the relative biodiversity of different sets of areas? On hotspots, complementarity and pattern-based approaches. – Biodiv. Lett. 3: 18–25.

Flather, C. H. et al. 1997. Identifying gaps in conservation networks. Of indicators and uncertainty in geographic-based analyses. – Ecol. Appl. 7: 531–542.

Gould, W. A. and Walker, M. D. 1999. Plant communities and landscape diversity along a Canadian arctic river. – J. Veg. Sci. 10: 537–548.

Grime, J. P. 1997. Biodiversity and ecosystem function. The debate deepens. – Science 277: 1260–1261.

Hanley, T. A. 1996. Potential role of deer (Cervidae) as ecological indicators for forest management. – For. Ecol. Manage. 88: 199–204.

Hansson, L. 1998. Nestedness as a conservation tool: plants and birds of oak-hazel woodland in Sweden. – Ecol. Lett. 1: 142–145.

Hansson, L., Fahrig, L. and Merriam, G. (eds) 1995. Mosaic landscapes and ecological processes. – Chapman and Hall.

Harrison, S. 1991. Local extinction in a metapopulation context: an empirical evaluation. – Biol. J. Linn. Soc. 42: 73–88.

Harrison, S. and Fahrig, L. 1995. Landscape pattern and population conservation. – In Hansson, L., Fahrig, L. and Merriam, G. (eds), Mosaic landscapes and ecological processes. Chapman and Hall, pp. 293–308.

Hawksworth, D. L. and Rose, F. 1976. Lichens as pollution monitors. – Arnold, London.

Järvinen, O. and Väisänen, R. 1979. Changes in bird populations as criteria of environmental change. – Holarct. Ecol. 2: 75–80.

Johnson, R. K. and Wiederholm, T. Undated. State of the environment index – freshwater. – Cent. Environ. Monit., Uppsala.

Jones, S. G., Lawton, J. H. and Schachak, M. 1997. Positive and negative effects of organisms as physical ecosystem engineers. – Ecology 78: 1946–1957.

Karr, J. R. 1981. Assessment of biotic integrity using fish communities. – Fisheries 6: 21–27.

Karr, J. R. 1990. Biological integrity and the goal of environmental legislation: Lessons for conservation biology. – Conserv. Biol. 4: 244–250.

Karström, M. 1992. Steget före – en presentation. – Svensk Bot. Tidskr. 86: 103–114.

Kremen, C. 1992. Assessing the indicator properties of species assemblages for natural areas monitoring. – Ecol. Appl. 2: 203–217.

Kremen, C. et al. 1993. Terrestrial arthropod assemblages: their use in conservation planning. – Conserv. Biol. 7: 796–804.

Kuusinen, M. 1996. Cyanobacterial macrolichens on *Populus tremula* as indicators of forest continuity in Finland. – Biol. Conserv. 75: 43–49.

Lambeck, R. J. 1997 Focal species: a multi-species umbrella for nature conservation. – Conserv. Biol. 11: 849–856.

Landres P. B., Verner, J. and Thomas, J. W. 1988. Ecological use of vertebrate indicator species: a critique. – Conserv. Biol. 2: 316–328.

Lauder, A. E. and Murphy, D. D. 1994. Umbrella species and the conservation of habitat fragments: a case of a threatened butterfly and a vanishing grassland ecosystem. – Biol. Conserv. 69: 145–153.

Lawton, J. H. 1994. What do species do in ecosystems? – Oikos 71: 367–374.

Loiskekoski, M., Halko, P. and Patosaari, P. 1994. Sound forestry – sustainable development. List of criteria and most suitable quantitative indicators. – Ministerial Conference on the protection of forests in Europe, Helsinki.

Lyons, J. et al. 1995. Index of biotic integrity based on fish assemblages for the conservation of streams and rivers in west-central Mexico. – Conserv. Biol. 9: 569–584.

McCune, B. and Mefford, M. 1997. ORD – Multivariate analysis of ecological data. Ver. 3.10. – MJM Software, Gleneden Beach, Oregon.

McGeoch, M. A. and Chown, S. L. 1998. Scaling up the value of bioindicators. – Trends Ecol. Evol. 13: 46–47.

McKenney, D. W. et al. 1994. Towards a set of biodiversity indicators for Canadian forests: proceedings of a forest biodiversity indicators workshop. – Can. For. Serv., Sault St. Marie.

Naeem, S. et al. 1994. Declining biodiversity can alter the performance of ecosystems. – Nature 368: 734–737.
Nilsson, S. G. and Baranowski, R. 1994. Indicators of megatree continuity – Swedish distribution of click beetles (Coleoptera, Elateridae) dependent on holllow trees. – Entomol. Tidskr. 115: 81–97.
Nilsson, S. G. et al. 1995. Tree-dependent lichens and beetles as indicators in conservation forests. – Conserv. Biol. 9: 1208–1215.
Noss, R. F. 1990. Indicators for monitoring biodiversity: a hierarchial approach. – Conserv. Biol. 4: 355–364.
Obrist, M. K. and Duelli, P. 1998. Wanzen und Pflanzen. Auf der Suche nach den besten Korrelaten zur Biodiversitet. – Informationsblatt des Forschungsbereiches Landschaftsökologie 37.
Olsson, G. A. and Gransberg, M. 1993. Indikatorarter för identifiering av naturskogar i Norrbotten. – SNV Report 4276.
Pearson, D. L. and Cassola, F. 1992. World-wide species richness patterns of tiger beetles (*Coleoptera: Cicindelidae*): indicator taxon for biodiversity and conservation studies. – Conserv. Biol. 6: 376–391.
Prendergast, J. R. and Eversham, B. C. 1997. Species richness vovariance in higher taxa: empirical tests of the biodiversity indicator concept. – Ecography 20: 210–216.
Reid, W. V. et al. 1993. Biodiversity indicators for policy-makers. – World Resour. Inst.
Ritchie, M. E. 1999. Biodiversity and reduced extinction risk in spatially isolated rodent populations. – Ecol. Lett. 2: 11–13.
Scott, J. M. et al. 1993. Gap analysis: a geographical approach to protection of biological diversity. – Wildl. Monogr. 123: 1–42.
Severinghaus, W. D. 1981. Guild theory as a mechanism for assessing environmental impact. – Environ. Manage. 5: 187–190.
Skye, E. 1979. Lichens as biological indicators of air pollution. – Annu. Rev. Phytopathol. 17: 325–341.
Tibell, L. 1992. Crustose lichens as indicators of forest continuity in boreal coniferous forests. – Nord. J. Bot. 12: 427–450.
Väisänen, R. and Järvinen, O. 1977. Dynamics of protected bird communities in a Finnish archipelago. – J. Anim. Ecol. 46: 891–908.
Verner, J. 1984. The guild concept applied to management of bird populations. – Environ. Manage. 8: 1–14.
Walker, B. H. 1992. Biodiversity and ecological redundancy. – Conserv. Biol. 6: 18–23.
Weaver, J. C. 1995. Indicator species and scale of observation. – Conserv. Biol. 9: 939–942.
Williams, P. H. and Gaston, K. J. 1994. Measuring more of biodiversity: can higher-taxon richness predict wholesale species richness? – Biol. Conserv. 67: 211–217.
Wilcove, D. S. 1989. Protecting biodiversity in multiple-use lands: lessons from the US Forest Service. – Trends Ecol. Evol. 4: 385–388.
Winston, M. R. and Angermeier, P. L. 1995. Assessing conservation value using centers of population density. – Conserv. Biol. 9: 1518–1527.
Worthen, W. D. 1996. Community composition and nested-subset analyses: basic descriptors for community ecology. – Oikos 76: 417–426.

The BEAR Technical Reports provide scientific and/or methodological information of relevance to the development of indicators of forest biodiversity produced within the project: “Indicators for monitoring and evaluation of forest biodiversity in Europe” financed by the Commission of the European Communities, Agriculture and Fisheries (FAIR) specific RTD programme CT-3575 (Scientific Officer Mme A. Katsada).

Bear homepage http://www.algonet.se/~bear

Coordinator: Tor-Björn Larsson, Swedish Environmental Protection Agency, SE-106 48 Stockholm, Sweden.
E-mail: tor-bjorn.larsson@environ.se