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Abstract: We review the effects of human impact on biodiversity of European forests in the light of recent views on disturbances and succession in ecosystems, and discuss recent ideas on how biodiversity affects ecosystem functions such as productivity and ecosystem stability. With this as a background we discuss how to better manage European forests for both production and biodiversity. We argue that the next generation of forestry practices need to understand and mimic natural disturbance dynamics much better than the present ones. Of particular importance is the fact that most species in European forests have evolved in forests that were to a large extent influenced by large grazers, first by megaherbivores and later, in historic times, by domestic animals. We highlight several areas where new knowledge and management tools are urgently needed: (i) How do species survive and adapt to the natural disturbance regimes in different regions and forest types? (ii) How can new and imaginative forest management practices be devised that take natural disturbance regimes into account? (iii) How does forest biodiversity affect ecosystem function and stability in a changing world, in particular in the light of predicted climate changes? (iv) How are ecological processes at different levels and scales related to diversity, and how do different management practices affect biodiversity? (v) How can efficient agroforestry methods be developed to preserve biodiversity? (vi) What is the role of humans and human behaviour for sustainable management of ecosystems?
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Keywords: Biodiversity; Disturbances; European forests; Natural forest dynamics; Ecosystem function; Forest management; Succession; Renewal cycle; Grazers; Megaherbivores; Stability and insurance hypothesis

1. Introduction

The natural vegetation in most of Europe is forest, from the Mediterranean through the deciduous forests of Central and Western Europe to the boreal forests in Fennoscandia. Many of these forests are now long gone due to human activities, and some European forest types belong to the most endangered ecosystems in the world. For example, it has been estimated that only 0.2% of the Central European deciduous forests remains in a relatively natural state (Hannah et al., 1995), making it and the species living therein as threatened as more recognised endangered ecosystems.
such as tropical rainforest. A long history of human land-use changes has created the European forests that we know today (e.g. Perlin, 1988). The hunting of large herbivores and predators, the grazing of domestic herbivores, the clearing of forests for agriculture, firewood and industrial purposes, extraction of litter for fertilising purposes, and more recently the planting of monocultures and exotic species are examples of such human impacts. The Mediterranean forests have been altered by human activities for a very long time and practically no pristine forest appears to be left in the region. The generally high human population densities have led to intensive cultivation practices like coppice with short rotations. Along with overgrazing and frequent fires this has resulted in severely degraded forests (often given a specific local name) becoming common (Di Castri et al., 1981). This situation makes the remaining pristine or close to pristine forests even more valuable (Stanners and Bourdeau, 1995).

Traditionally, ecosystems left without human intervention and disturbances were supposed to develop towards stable ‘climax’ systems (e.g. Clements, 1936; Odum, 1969). This static view of nature has now given way for a more dynamic one in which change and disturbance are seen as natural features of ecosystems (e.g. White, 1979; Pickett and White, 1985; Botkin, 1990; Holling, 1992; Holling et al., 1995; Ellenberg, 1996). Most species in European forests have evolved under and adapted to past natural disturbance regimes. Therefore, an understanding of former natural disturbance dynamics and how they relate to human disturbances and management practices is essential to preserve and manage biodiversity as well as ecosystem functions in the present human-dominated European forests (Nilsson and Ericson, 1997).

During the last decade, studies and discussions of biological diversity have emerged from the obscurity of basic scientific discourse to become one of the most pressing and relevant subjects in environmental policy. This volte-face has been met with mixed feelings both in the scientific community and in forestry. While many ecologists are happy that ecological issues become part of the political agenda, they also have problems in coming out of academia to become part of the real world of resource management, economy and politics. In forestry, many foresters have had problems accepting that biodiversity, which previously had no economic value, should affect how they manage forests. However, market pressure requiring forestry to manage biodiversity quickly made forestry pay attention to the preservation of diversity.

The concern over declining biological diversity has several roots, and only some of them are part of what is normally regarded as science. One of the main ecological arguments for preserving biodiversity is that the losses of diversity may impair the life-supporting processes that humans need, i.e. ecosystem functions such as primary productivity, carbon storage, water retention and provision of clean water. Diversity may also entail ecological stability. Thus, maintaining diversity may be necessary for long-term sustainability. These are old unsolved questions in ecology, and the recent debates have not resolved them (see below). A major force behind the Biodiversity Convention in Rio 1992 was that many developing countries wanted some degree of control and gains from the largely unexplored biological diversity in the tropics — an economic rather than an ecological argument for preserving biodiversity. Other reasons to preserve biodiversity are ethical, and the pleasure many people experience from a high diversity in their environment.

In the following, we offer a personal perspective on some of the issues that we believe are of major importance for preserving and enhancing biodiversity in European forests. The paper is not intended as a review of the extensive literature on the subject (see e.g. Hansson, 1997; Niemelä, 1997). Rather, it should be seen as part of an ongoing discussion, and many of the issues we raise are subjects of current debate and disagreement. Since biodiversity conservation priorities tend to focus on species diversity, this will be the focus of our paper, but we acknowledge that in the long term the conservation of diversity also involves conservation of genetic diversity.

2. Humans and biodiversity in European forests — a historical perspective

We do not know exactly what the European forests looked like before humans became important agents of landscape change (Rackham, 1998). However, large megaherbivores such as the forest elephant and rhinoceros were probably important in influencing forest structure in many areas. Most trees have adapted and
evolved in response to unselective and fairly intense grazing pressure by megaherbivores (Owen-Smith, 1987). It is likely that grazing resulted in a forest with more openings and gaps, a higher abundance of large trees and less saplings than the present 'virgin forests'. Otherwise it is difficult to understand why a majority of forest species, e.g. among insects and lichens, prefer or require a half-open forest (e.g. Andersson and Appelkvist, 1990; Nilsson and Ericson, 1997). Some pasture woodlands, like the New Forest in England and the Dehesha woodland in Spain, are probably more similar to the forests where most forest organisms evolved than dense ungrazed stands. Fire has also been an important disturbance factor in many forests, especially in the taiga forests of the boreal zone (Zackrisson, 1977) and in the Mediterranean, but not in Central Europe.

In addition to short-term disturbances, long-term changes such as glacial cycles have influenced European forests. The refuge areas in south-eastern, southern and south-western Europe support the highest diversity and contain the species with most restricted continental ranges. This is clearly born out by some well-known organisms such as longhorn beetles, Cerambycidae (Bense, 1995). In addition, as predicted by population genetic theory (Hewit, 1996), high genetic diversity has been found in the refugia from which recolonization waves were started. Good examples of this are oak species in which a higher diversity of cpDNA haplotypes was found in southern refugia in Italy, the Iberian peninsula and the Balkans (Dumolin-Lapegue et al., 1997), and beech which within Italy shows a higher allozyme diversity in the glacial refuge area of Sicily (Leonardi and Menozzi, 1995). These refuge areas are essential for the preservation of the biodiversity of the forests of Europe.

At least during the last 4000–5000 years humans have been important agents affecting landscape composition and dynamics and biological diversity in Europe. Many large predators and herbivores have gone regionally extinct since Roman times. As these large animals disappeared domestic animals took the place of the herbivores. The domestic grazers have affected most forests in Europe for centuries to millennia. Relative to the megaherbivores, smaller grazers seem to be more selective in diet than the extinct ones, resulting in a changed species composition of the forests, although several key structures of the original forests, such as small open glades and large old trees, were retained (Peterken, 1996; Nilsson, 1997). The cover of forest has been fluctuating as human populations have gone down and up, mainly in conjunction with plagues and with industrialism and trade, respectively. The last century has seen the most rapid landscape changes, as technological advances have made agriculture capable to utilise more land, and the remaining marginal areas have gradually been converted to managed forests. During this process, many features of old forest and old agricultural landscapes such as dead wood, old trees, fire and natural grazed areas have declined or been lost over large areas. This has had large negative consequences for biodiversity. We know that a high proportion of red-listed (threatened) species in Scandinavia, Britain and Central Europe are dependent on these structures and processes (e.g. Berg et al., 1994, 1995), but such knowledge is not available for all Europe. In the Mediterranean, applications of the standard proposed for red-listing species are difficult because of the lack of information on the rarity and fragility of local species. This has led to the red-lists containing species that are rare in central European forests but relatively common in the Mediterranean region, and the over-looking of taxa absent at more northern latitudes but threatened in the Mediterranean.

The large-scale changes in landscape structure have influenced diversity both positively and negatively. The opening up of landscapes by human activities has probably led to increased diversity during prehistoric and historical times, although the changes in this century have mainly resulted in diversity losses. For example, many species adapted to open grazed forests have disappeared. However, there are exceptions. Many bird species, primarily those adapted to scrub habitats, have increased temporarily as marginal agricultural land and grazed forests have been abandoned and are undergoing succession towards high forest. Also, many exotic species have become naturalised. In the short term diversity has often increased at the local

\[1\] One of the reviewers questioned our emphasis on the importance of megaherbivores. We regard the evidence for substantial megaherbivore impacts in many pre-historical forests as convincing, but acknowledge that the issue is still partly unsolved.
and national (regional) levels, while over evolutionary time it may result in a lower global diversity.

Unfortunately, neither ecologists nor foresters have had the tools or the knowledge to examine the consequences of large-scale landscape changes on diversity, as most research has been conducted on relatively small scales, e.g. experimental plots. Research from small scale experiments may not be relevant to predict large-scale dynamics of ecosystems. For example, among soil fauna, responses of groups such as springtails and mites which have population dynamics on a smaller spatial scale than the normal size of plots (ca. $10^2$ m$^2$), can probably be extrapolated to larger areas. This may not be the case for more mobile animal groups such as Dipterans, where responses at the spatial scale of the plot reflects individual movements and egg-laying preferences rather than population dynamics (e.g. Bengtsson et al., 1997b). Recently developed research areas such as landscape ecology, metapopulation biology, and analyses of large-scale and long-term patterns in communities may yield better insights into these questions in the future, and are imperative for a better management of forest resources with respect to biodiversity (e.g. Siitonen and Martikainen, 1994; Kareiva and Wennergren, 1995; Angelstam, 1997).

3. Changing views on stability and change in natural ecosystems

For a long time, ecologists and especially people in conservation organisations viewed nature as rather static. Without human intervention and disturbances, ecosystems were supposed to develop towards ‘climax’ systems which were stable and in which biomass and nutrients had accumulated (e.g. Clements, 1936; Odum, 1969). Although there are some examples from boreal forests that this may actually happen, the static view of nature has given way for a more dynamic one in which change and disturbance are regarded as integral features of ecosystems (e.g. White, 1979; Botkin, 1990; Holling, 1992; Holling et al., 1995).

The dynamic view of nature has its roots in discussions in vegetation ecology in the beginning of the 20th century. It is useful to contrast two opposing views. The first one, pioneered by (Clements, 1916, 1936), proposed that the different components of vegetation communities were almost like parts of an organism. The equilibrium point was called climax, and it was mainly the result of climatic factors. Any discrepancy from the supposed climax was viewed as a disturbance. This view was rather static, as climes theoretically might last for a very long time if no disturbance did occur. The other view was that of Gleason (1926), who proposed that individuals within the vegetation were adapting independently to similar conditions, and the vegetation cover should be more or less seen as a collection of non-interacting plants that happened to be adapted to the same site conditions. This view is not very far from a standard Darwinian view of communities, where selection at the individual level (and not the species or community level) is regarded to be the rule. The problem evolved with Tansley’s seminal paper on the ecosystem (Tansley, 1935). After a while, most researchers acknowledged that vegetation is never locally stable, with disturbances and succession as the major triggers of change.

Succession is thus of importance for understanding the dynamics of natural ecosystems. Other important processes are disturbances and factors affecting how organisms survive in temporally changing mosaic landscapes, e.g. dispersal. Holling (e.g. Holling, 1992; Holling et al., 1995) has formulated the modern dynamic ideas on succession and disturbance in a simple conceptual cyclic model of ecosystems (Fig. 1). Several things are important here: According to this view, ecosystems alternate between periods of weak interactions between organisms (phases 1, exploitation, and 4, reorganisation) and periods when species interact strongly (phases 2, conservation, and 3, release). On a small spatial scale, the system is ever-changing, but on a larger scale the shifting mosaic of patches is more stable. Different processes are important to maintain the system during the transitions between the phases: succession during the slow transition from phases 1–2, rapid disturbances such as fire or pests in the transition from 2 to 3, and dispersal during 4 to 1. These ideas were linked to the biodiversity issue by Peterson et al. (1998). Biological diversity is especially important during the succession and reorganisation phases, because a high regional diversity means that there will be an appropriate pool of species to continue the cycle. Some disturbances can carry the ecosystem into different stability domains (Fig. 1), essentially flipping the present...
system to a new one, and the likelihood for this increases as species disappear regionally.

4. Natural forest dynamics

Different natural forests are characterised by different types of natural dynamics, because the scale of disturbances vary much between forest types. Taiga forests in northern Europe were often disturbed by large-scale fires (Zackrisson, 1977), while nemoral deciduous forests, the natural vegetation of most of central and western Europe, are mostly disturbed by small-scaled windthrows (Falinski, 1986). In the wide transition zone both large-scale and small-scale disturbances occur in different types of forests (Nilsson, 1997). These different types of disturbances have major implications for conservation of diversity and for sustainable forestry (Nilsson and Ericson, 1997). Recent studies in boreal forest (Wardle et al., 1997) indicates that fire frequency can have important effects on the forest ecosystem, influencing vegetation dynamics, diversity patterns and ecosystem processes. Fire is also a particularly relevant ecological factor for Mediterranean forests. It has been estimated that 0.5–1% of Mediterranean forests are affected by fire every year (Di Castri et al., 1981).

It is reasonable to assume that organisms in natural forests are adapted to the characteristic disturbance regimes of these forests. In addition, there are forest species with adaptations that happen to make them favoured by the human-induced landscape changes in historical times — for example, open glades created by small-scaled forestry and domestic herbivores. As discussed above, it is likely that over evolutionary time large herbivores have been an important factor in forests. Therefore, the continuation of some traditional use of self-regeneration forests may be important to maintain their biodiversity, because it to some degree mimics the megaherbivore grazing that the species were originally adapted to. The megaherbivores contributed to several structures that nowadays are becoming rare and need to be retained in managed forests. An example may be that they created wounds on large branches and trunks resulting in barkfree wood on living trees. Many insects are dependent on such trees with sun exposure (Nilsson and Ericson, 1997). Also, standing dead
or dying trees were much more common than they are now.

5. Forest management practices and natural forest dynamics

Since most forestry practices involve disturbances to forest ecosystems, sometimes severe ones, forestry will inevitably have effects on both diversity and on ecosystem function. The preservation of biodiversity in managed forests requires a consideration of how forestry practices such as clearcutting or selective cutting correspond to natural disturbances and natural forest dynamics (e.g. Haila et al., 1994; Angelstam, 1997; Niemelä, 1997). It is sometimes argued by the forest sector that, for example, clearcutting is almost equivalent to fire or windthrows and thus not very ‘unnatural’. This is misleading, if not completely wrong (Essen et al., 1997). The similarities between fire or windthrows and clearcutting are superficial. Many features that are present after fire and other natural disturbances are lost when clearcutting. An important task for a sustainable forest management will be to approach natural forest dynamics (Niemelä, 1997). Comparisons with the few large natural forest areas in Europe, such as eastern Poland or northeastern Russia, have led to important insights, and will continue to do so.

Such comparisons have revealed that several features and structures of natural forests decline or disappear in managed forests. Old-growth forest features with old and large trees, both standing, living, dying and laying are especially prone to disappear (e.g. Peterken, 1996). Some such structures are obvious, such as old logs, while some are often overlooked. For example, in old-growth forests strong winds and megaherbivores often broke branches leading to wounds on large branches and trunks of living trees. Recent studies indicate that several species are dependent such hollow trees (e.g. Martin, 1989; Nilsson and Baranowski, 1997). Other features of most natural forests often lacking in managed forests is burned wood, open glades created by grazers, deciduous trees — in particular old ones — and a mixture of tree species and of tree ages.

In many areas, the continuation of some traditional use of self-regeneration forests, such as grazing and selective cutting, may be important in maintaining their diversity, although it does not automatically follow that all traditional practices favour biodiversity. Activities similar to the effects of natural disturbances and grazing by large herbivores could (and should) be simulated by forestry, while other traditional practices such as litter-raking may be destructive. It should also be pointed out that in Mediterranean forests overgrazing is still a problem at many places. This use of forests is different from the northern ones which suffer from excessive spatial homogeneity. In these Mediterranean cases grazing should be reduced to allow a recovery of degraded forests already threatened by other disturbances such as fires and water stress.

Not all species are equally affected by forestry. Some species, primarily generalists, are often little or even positively affected. Many of these species disperse easily and are less sensitive to fragmentation as long as their habitat requirements are fulfilled. Such species are often found in the formerly glaciated areas in Russia, Finland and Scandinavia. Other species are severely affected by fragmentation and habitat loss, for example specialist species requiring old-growth forest or old trees. These are often poor dispersers and very sensitive to forestry disturbances, fragmentation and isolation of habitat patches. Among such species is a rich flora and fauna connected to ancient trees of nemoral deciduous species (e.g. Rose, 1976; Speight, 1989). The most extreme of these are a number of insect species found only in small refuges in human-dominated landscapes in SW and SE Europe (e.g. Dajoz, 1966). For such species as well as for old-growth forest species with particular habitat requirements it is imperative to identify and preserve forest areas with long continuity over time (Peterken, 1996; Nilsson and Ericson, 1997). Thus, many species may require species- or group-specific management practices to be preserved in today’s forests. Some species may need large areas of long continuity, while for others only small unmanaged patches or even single trees in managed forests may be required. Simplified forestry practices that are good for some species may not be appropriate for others. In order to protect diversity in the long perspective, the spatio-temporal dynamics of both species and disturbance regimes at several scales in forest landscapes need to be understood.
6. Effects of biodiversity on ecosystem function

The projected decline in biodiversity has concerned ecologists for several reasons: species diversity may have direct positive effects on important ecosystem processes such as productivity and nutrient cycling (e.g. Tilman et al., 1996). A high diversity may also entail ecosystem stability, for example, resistance to perturbations, resilience after disturbances and more stable and reliable ecosystem functions over time (e.g. Peterson et al., 1998; Naeem, 1998). The major long-term importance of diversity may be as a source of species capable of performing desired ecosystem functions if the present species should disappear, for example because of climate change (the ‘insurance’ hypothesis; Folke et al., 1996).

6.1. Diversity and ecosystem stability

The idea that diversity is related to ecosystem stability has a long history in ecology (see, e.g. Pimm, 1991). Until the early 1970s, this relationship was usually regarded as positive, the argument being that more diverse and complex ecosystems have more possible pathways for energy and nutrient flows than species-poor ones. Note that this argument is essentially one about stability in ecosystem processes, not in population numbers or species composition. May (1973) argued the opposite. Based on the stability properties of multi-species model communities with strong species interactions, he argued that diverse communities were less stable than simple ones. May’s argument was about species abundances, not ecosystem processes. After hot discussions, the tide seems to have turned once again. Polis (1994) put this succinctly when he wrote “... recent analyses of food webs pound yet another nail (hopefully the final one) into the coffin of May’s paradox. ... I am attracted to the position that complexity promotes stability and conclusions from dynamic models are simply wrong.”

Thus, more diverse systems may be more resistant to perturbations and more resilient than species-poor ones, as suggested for plant communities by Tilman and Downing (1994), although this study has been heavily criticised. Nonetheless, although there are some exceptions, recent research has largely supported this view (McNaughton, 1993; McGrady-Steed et al., 1997; Naeem and Li, 1997; see below), restating the ‘ecological intuition’ of the times before the 1970s that diverse ecosystems are more stable.

6.2. Diversity and ecosystem processes

Although many ecologists agree that diversity often is important for the rate of ecosystem processes such as productivity or decomposition rate, this has until recently mainly been based on informed guesses and common sense arguments. The few experiments on these issues are ambiguous. For example, Tilman et al. (1996) showed positive effects of diversity on productivity, while e.g. Rusch and Oesterheld (1997) claimed the opposite. Sometimes, species diversity per se is not be as important as the presence of several functional groups (Hooper and Vitousek, 1997; Tilman et al., 1997; Laakso and Setälä, 1999). It is unclear if these results can be extrapolated from the relatively species-poor experimental systems to natural species-rich ecosystems.

However, there are some general patterns worth noticing. Often, it seems that there are advantages with more diverse ecosystems, at least compared to the monocultures found in forestry and agriculture. For example, species mixtures may provide a higher yield than monocultures (e.g. spruce and birch, Burkhart and Tham, 1992) and several experiments in grasslands show that average productivity increases as species richness increases from 1 to ca. 10 species. However, often it is possible to find some single species that under some circumstances do as well as mixtures, as witnessed by the widespread use of monocultures in forestry and agriculture. Other interesting observations are that species mixtures appear to have lower levels of pest damage and higher resistance to invaders and weeds (McGrady-Steed et al., 1997; S. Naeem in Bengtsson et al., 1997a). In forests, a lower frequency of insect damage and stem rot have been found in mixed forests compared to monocultures (Su et al., 1996; Gerlach et al., 1997).

In agroecosystems, populations with a low genetic diversity (monocultures) have sometimes — but not always — been associated with higher levels of damage from pests (e.g. Power and Kareiva, 1990). Yields of monocultures are also more susceptible to environmental vagaries. Such effects may on a longer time-scale be important also in forestry and deserve more attention.
However, the direct positive effects of diversity on ecosystem functions such as productivity may only be relevant at the low end of a diversity gradient, i.e. when we go from monocultures to few-species mixtures, and sometimes not even there (see e.g. Bengtsson et al., 1997a). A more generally relevant and important advantage of retaining diverse ecosystems is the so-called ‘insurance hypothesis’, which suggests that high diversity leads to more reliable ecosystem functions over time when environmental conditions vary (Naeem, 1998), e.g. because of climate change. This hypothesis is extremely difficult to test in the field, but there is some support from studies of zooplankton in lakes (Frost et al., 1995). Recently, two laboratory studies using unicellular protists have supported the insurance hypothesis (McGrady-Steed et al., 1997; Naeem and Li, 1997), although these still concern the low end of the diversity gradient. The insurance hypothesis may thus provide one of the most convincing arguments for preserving biodiversity, as suggested by e.g. Bengtsson et al. (1997a).

If the goal is to maintain and create sustainable forest ecosystems, the most crucial role for diversity is as a supplier of species performing functions and conferring stability (Bengtsson, 1998). Declines in diversity means losses of species including key species, which in turn may have a number of undesirable consequences: Changes in food webs, loss of specialist functions, and loss of ecosystem engineers, keystone species and other species or functional groups. Present ecological theory is not ready to address the effects of these changes on ecosystem function, although recent theoretical advances may swiftly lead to applications in forestry. For example, Bengtsson’s research has focused on the impact of intensive harvesting on soil food webs, and how this affects carbon and nitrogen cycling in theory and practice (Zheng et al., 1997, 1999; Bengtsson et al., 1997b). Extensions of such analyses incorporating diversity changes may be directly relevant to forest management. Another example is the suggestion from food web theory that consumers sometimes can speed up nutrient cycling and thus be positive for ecosystem productivity (Loreau, 1995). If these types of analyses proceed to incorporate changes in diversity as well as changes in species identities they may become useful tools in forest management.

Developments in the analysis of the role of diversity in species-rich and complex communities may shed further light on the importance of biodiversity for ecosystem function. It has been suggested that focus on the number of species, being taxonomic entities, may not be the most efficient way of examining this problem. Instead, it could be more fruitful to concentrate on the distribution of ecological traits in a community, for example the distributions of resource acquisition efficiencies or tolerances to environmental stress across species. Of course, to some degree these distributions are likely to be related to species diversity. More importantly, different distributions probably reflect differences between communities in ecosystem function or species complementarity. Focus on trait distributions rather than species numbers is potentially more relevant for understanding ecosystem function and its relation to biodiversity.

7. Implications for forest management

Although expanded nature reserve systems will be essential in managing forests for sustainability at the landscape level, reserves alone are not sufficient to preserve the biodiversity and dynamics of European forests. It will always be necessary to manage most forest land for both production and biodiversity, even with an expanded reserve system. Although some minor part of the forest area could possibly be used for very intensive production, it is naive to argue that splitting forests into reserves and high-intensity forestry areas will preserve even a fraction of the biodiversity of European forests. The area of existing and potential reserves is simply too small. For example, in Scandinavia forest reserves constitute only 1–3% of the productive forest area (Essen et al., 1997), and there are much too few large stands >100 years old that could become part of larger reserve systems. Therefore, we strongly argue that the only way to achieve sustainability of European forests will require that the major part of forest land is managed by methods that are acceptable from the point of view of the environment and of biodiversity, as well as timber yield (e.g. Niemelä, 1997). This means that there will be a strong need and incentive for new forestry methods and innovative technology.
To retain biodiversity during forestry operations, it is first necessary to identify stands with a long continuity. Such forests are the dispersal sources to the surrounding forests for many slowly dispersing organisms, e.g. many snails, insects and lichens. These refuge forests make up a decreasing and very small proportion of the forests in Europe, but they are essential for restoring biodiversity in the surrounding landscape. In most cases they should be left unmanaged, while in others non-native species invading from planted forests must be removed. In all cases suitable habitat should be present in the near surroundings for maintaining viable populations in the long run. Furthermore, old trees and coarse woody debris must be allowed to develop in managed forest. Such trees may also be useful for forestry as wind breaks along edges to open habitats.

The next generation of forestry practices need to more thoroughly understand and mimic natural disturbance processes and dynamics than the present ones. For example, present methods of large-scale clearcutting need to be reconsidered in the light of recent advances in succession theory and conservation biology. The recognition of the importance of large herbivores for diversity in many forests requires attention during forestry operations. Recent studies showing the problems with monocultures in forestry imply that we have to reconsider the present dominating forestry methods in Europe. This is in fact already happening in, for example, Germany where mixed-species forestry is often practised nowadays. We have to develop practices and techniques that are adapted to more diverse forests. Locally, there have always been such methods in Europe, but few have been scientifically evaluated and improved. The development of new technology is unlikely to be a big problem in forestry. Rather, the most crucial gaps in ecological knowledge need to be identified and made the subject of research (see below), and the results communicated to the forest sector.

However, some species, such as those dependent on old-growth forest, will not be able to survive in managed forests. For these species nature reserves are necessary, and forestry will have to accept that reserves or other set-aside areas are an integral part of land management. In some parts of Europe, such as in the high-diversity glacial refuge areas, large reserves are especially important. Besides preserving rare and threatened species, reserves may be useful because they have more natural forest dynamics and thus act as source areas for managed forests, increasing landscape resilience (Folke et al., 1996).

8. Identification of key areas for future research

1. How does what we know and may learn about natural forest dynamics and ecosystem processes affect management practices? An understanding of natural forest dynamics is a prerequisite for sustainable forest management. For example, most natural forests in Europe are composed of several or many tree species and with varying structure and ages of trees, but forest management is too often focused on even-aged monocultures. How can this be changed?

   Firstly, it is crucial to understand the natural disturbance regimes in different regions and forest types, and how species survive and adapt to these regimes. Secondly, imaginative and innovative new forest management practices that take these regimes into account need to be devised. For instance, recent research on mycorrhizal fungi (Kärén, 1997) suggests that with appropriate management practices, more species survive the harvesting phases and the mycorrhizal communities in middle-aged stands become more similar to old-growth stands. These species may be required for efficient ecosystem function (although this is not yet established). If forestry practices can be changed to incorporate knowledge on these issues, there will be a great potential for a more sustainable forest management for both production and biodiversity.

2. How does biodiversity affect ecosystem function and stability in a changing world, in particular in the light of predicted changes in climate? This is a key issue that involves (i) establishing which are the present key species and functional groups, and (ii) an understanding of the possible roles of rare species in ecosystems. The issues must be addressed in long-term experiments — the present funding on a 3-year basis does not provide the incentives or facilities for such long-term research. In particular, a concerted action to establish field tests of the insurance hypothesis in forests would be appropriate.
3. How are ecological processes at different levels and scales related to diversity? The classical questions in ecology concerning the mechanisms behind different levels of diversity have not yet received satisfactory answers. In this sense, different management practices can be regarded as ongoing ecological experiments that are useful to elucidate diversity patterns and suggest mechanisms that could be examined in more detail. This potential is clearly under-utilised. However, a major problem with this approach is that proper controls in extensive natural forests must be established. In view of this it is tragic that the largest area of Central European mixed deciduous forest in Bialowieza in Poland is still diminishing in area.

4. There is also a clear need to develop efficient agroforestry methods. As argued above, pasture woodlands may simulate structures and processes that have been important when megaherbivores dominated European forests, when most present forest organisms acquired their adaptations. Therefore, we suggest that production of wood, meat and other products in a half-open forest could be the most sustainable use of forests in many parts of Europe. By tradition, forestry and agricultural research have been different branches and this has clearly hindered research efforts in agroforestry. Organisational changes are necessary to rectify this.

5. An issue that recently has been discussed is the role of humans and human behaviour for sustainable management of ecosystems. Previous views that economy rules over ecological and environmental considerations have now been challenged. It has been shown that environmental costs have seldomly been taken into account, but if they were this would change the rationality of many decisions in, e.g., forestry. Interactions between ecologists, foresters, economist and social scientists may be of great value, in particular as it becoming important to estimate the economic and societal values of ecosystem functions and biodiversity (e.g. Perrings et al., 1995; Folke et al., 1996; Bengtsson et al., 1997a).

To examine questions such as these, it is clear that we need to use a variety of approaches from studies of population dynamics of different key species, mechanisms for diversity patterns, and studies of ecosystem processes affecting forest functioning for humans. Also, the previous small-scale studies in forestry need to be complemented with studies at the landscape level, something that is already done in several European countries (e.g. Angelstam, 1997). However, an appropriate understanding of biodiversity in forest ecosystems, and how to use biodiversity for the sustainable use of forest resources, requires linkages between all these approaches.

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