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Dominance reduction of species through disturbance—a proposed management principle for central European forests

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Abstract

Forest management must take into account in its management schemes very different goals such as timber production, protection from natural hazards, and biological conservation. In this paper we propose a new management principle based on the basic ecological characteristics of forests that could help the integration of these goals. We discuss the factors influencing species richness in forests and relate changes in species richness to the history of forest management. A closer look at hypotheses about possible links between disturbances and species richness reveals that dominance reduction is considered to be the main effect of disturbance events on species richness. We therefore propose dominance reduction as a management principle for forests in central Europe that are actively managed. This, we claim, is a way to maintain biodiversity in an integrative management approach. Three types of disturbances are distinguished: endogenous, exogenous, and human-induced disturbances. This distinction allows a connection to be made between natural and anthropogenic impacts on forests, thus overcoming the negative connotation disturbance events have. Planning forest management according to the principle of dominance reduction will facilitate the search for new ways to integrate the different needs society wants to have fulfilled by forests.

Keywords: Species richness; Central Europe; Disturbance; Dominance reduction; Forest management; Switzerland

1. Introduction

Maintaining biodiversity is a declared aim in most modern societies. Forest management should take into account such a demand. This means, ways have to be found to maintain biodiversity in forests without putting traditional tasks, such as timber production and protection from natural hazards, at risk. In order to thoroughly understanding the requirements of biodiversity protection, the factors determining biodiversity have to be understood. Biodiversity has a multitude of different meanings, but it almost always refers to the number of different biological entities. This number is mostly understood as the number of species, i.e. species richness (Simberloff, 1999). Although species richness gives a rather limited estimate of biodiversity, we use it in what follows as it is the measurable and understandable term.

Determinants of species richness may be roughly classified into two groups, static and dynamic, although the distinction between the two categories is not rigid. Static determinants include latitude, altitude, area, and to some extent habitat heterogeneity. Dynamic determinants comprise disturbance, fertilization, and short-term seasonal changes, e.g. phenology. Whereas, in a given landscape, the static

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influences on species richness remain constant over long periods of time, dynamic influences may change species richness in a landscape fairly quickly as the result of the impact of natural hazards, pathogens or decay as well as of human impact. Among all the possible dynamic influences, we consider disturbance to be the single most important factor affecting changes in species richness in most of landscapes from the time of early human settlement until the present.

In central Europe, human activities began thousands of years ago. The growing population influenced the previously untouched vegetation in different ways, especially by reducing the original forest area and by introducing agricultural activities. These resulted in the steady introduction of new alien species. Compared with the species richness in the vegetation before human settlement, species richness in today's landscapes is believed to be higher (e.g. Korneck et al., 1998). Here we focus on the forests in central Europe, where the vegetation has been changed by a multitude of management approaches affecting both species structure and species composition. The frequency of disturbances is generally higher than it was in pre-settlement, natural disturbance regimes. The intensity of disturbances in forests culminated 300–100 years ago as the result of the growing demand for energy (wood for fuel), fooder (woodland pastures), construction supplies, and other specific purposes, e.g. litter for indoor feeding or oak bark for tanning (Bürgi, 1998b). As a consequence of the ongoing deforestation in the Swiss Alps and galvanized by the frequent occurrence of floods in lower regions of the central Plateau, the federal Forest Police Law of 1876 and its revision in 1902 prescribed that the shape and area of existing forests should remain unchanged in the future (Flury, 1925; Pfister and Brändli, 1999; Mather and Fairbairn, 2000). The law also prohibited clear-cutting. Almost 100 years later, the total forested area in Switzerland has increased by at least 40% (BUWAL, 1997). According to the results of the Second National Forest Inventory (Brassel and Brändli, 1999), Swiss forests generally have become older and denser, and as a consequence, darker over the past 80 years (Schiess and Schiess-Bühler, 1997; Bürgi, 1998b). In order to sustain α-, β-, and γ-diversity (Groombridge, 1992), this development needs to be examined carefully.

In this paper, we discuss the development of species richness from early settlement until today and the impact of different types of disturbances on this development. Up to now, disturbance—especially in its German translation, "Störung"—has had a negative connotation in forest management in central Europe. We show in our paper that, in fact, many natural and anthropogenic processes in forests can be seen as disturbances and we illustrate how the effects of many disturbance events are actually beneficial for species richness. A closer look at current hypotheses about the link between disturbances and species richness reveals that dominance reduction has been the main effect of disturbance events on species richness. We therefore propose dominance reduction as a management principle for central European forests with the goal of maintaining biodiversity in an integrative management approach.

2. Driving forces influencing species richness

2.1. Spatio-temporal development of species richness

Human impact has changed species composition as well as species richness. This impact will undoubtedly continue in the future as long as humans have an influence on forests. Whereas the dramatic human impact on wild animals in the holocene resulted in the local or global extinction of many large mammals and birds in Australia, Europe and North America (Primack, 1993; Diamond, 1997), the human impact on plant species seems to have been quite different. According several publications, a steady increase in species richness until about 1850 probably took place on the regional scale, followed by a dramatic decrease up to today (Fukarek, 1980; Landolt, 1991; Korneck et al., 1996). In a comprehensive analysis of the Red Book data for pteridophytes and phanerogams (Korneck et al., 1996), Korneck et al. (1998) showed that there has been no such distinct peak in total species richness in Germany since 2000 B.C. (Fig. 1). Rather, the development of three species groups is distinguished: (1) indigenous species, which immigrated after glaciation in a natural process; (2) archaeophytes, which immigrated before 1500 with human help, particularly from east and south-east Europe; and (3) neophytes, which have immigrated since 1500 with human help, to a considerable extent from the New World (Birks and Birks, 1980; Huntley and Birks,

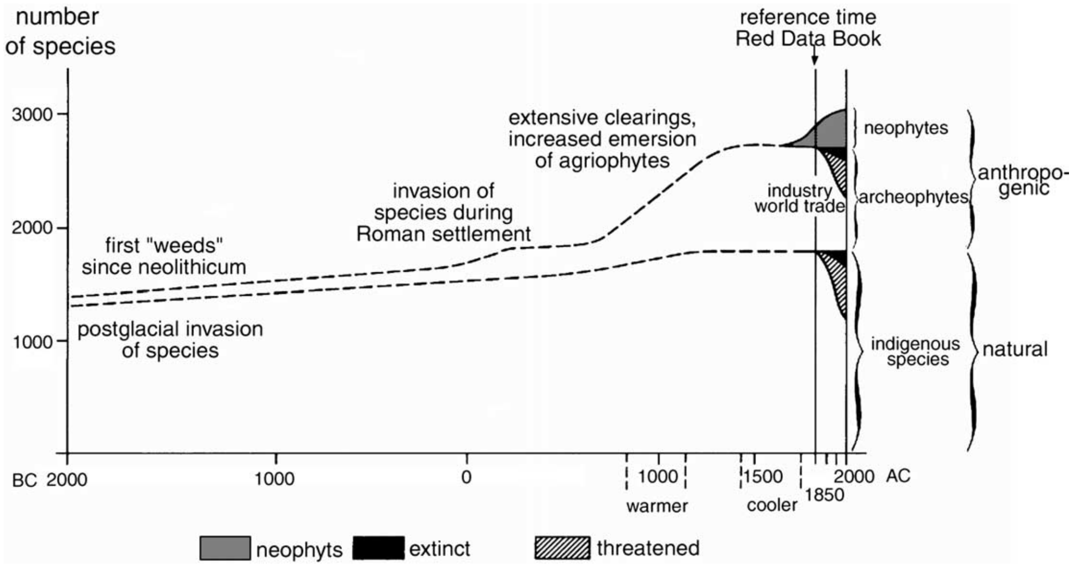

Fig. 1. Presumed development of regional species richness of vascular plants in Germany during the past 4000 years. Post-glacial immigration of plants predominantly caused the increase in species. Archeophytes: plants that immigrated before 1500 due to human activities; neophytes: plants that immigrated after 1500 due to human activities (from Korneck et al., 1998).

1983; Ellenberg, 1988; Lohmeyer and Sukopp, 1992; Lang, 1994; Burga, 1998).

Indigenous species richness began to increase as a consequence of re-immigration after the last glaciation and continued to increase until the beginning of industrialization in Germany. Then it began to decrease, particularly as a result of habitat loss and the abandonment of traditional land use (Küster, 1995). A considerable number of archaeophytes, in particular agriophytes, i.e. species which immigrated because of agricultural activities, began to invade around 1000 A.D., when extensive clearings probably started. Since the beginning of industrialization, however, the number of agriophytes has decreased. Total species richness also increased after the introduction of neophytes in 1500, resulting now-a-days in the highest species number ever. Lohmeyer and Sukopp (1992) estimate that 420 plant species had invaded Germany by 1990; 164 species before 1500 A.D. and 256 species during the past 500 years.

Ellenberg (1963, 1988) claims that most of the landscape in central Europe would, if it had been left undisturbed by humans, be today covered by dense forests. The phanerogamic species richness in such a pristine landscape would clearly be lower than it is today due to the lack of cultural influences. The question to what extent and how dense central Europe used to be covered by forests has been the subject of lively debate (Geiser, 1992; Zoller and Haas, 1995). However, if we focus on presumed changes in the number of indigenous plants and archaeophytes, then the scale needs to be taken into account. On the scale of continents or countries, an extinction rate is a number that is difficult to interpret. This is demonstrated in Fig. 2, which shows scale-dependent extinction rates in Europe as a whole, Germany, Switzerland and a region within Switzerland. In Europe, only 25 out of 12,500 plant species (0.2%) have become extinct since the year 1600 (WWF and IUCN, 1994). The numbers for Germany and Switzerland are 47 and 79 (1.5 and 3%, respectively). The really alarming extinction rate of 20% occurs on a more local scale, though, namely, in a 1400 km^2 region in the Swiss central Plateau (Keller and Hartmann, 1986). On the scale of 1 km^2, Jäger (1977) even reported an extinction rate of 50%. We maintain that such extinction rates are, on a local scale, representative for many other regions in central Europe. It is the development on this more local scale that has generated the recent debate about species loss.

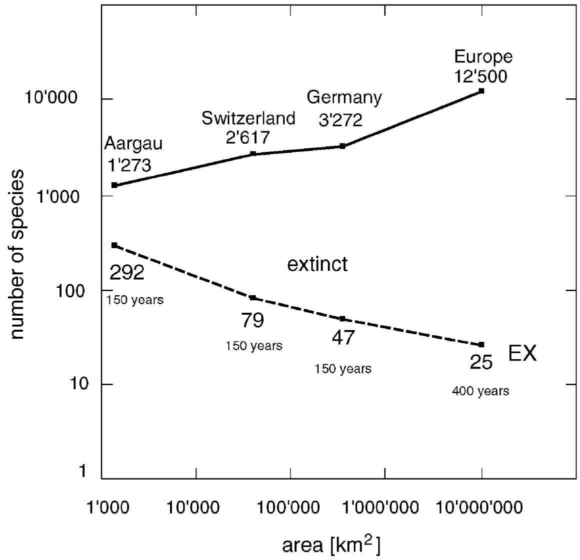

Fig. 2. Species numbers of present and extinct species on different scales with indication of time period. Data are retrieved from WWF and IUCN (1994, for Europe), Korneck et al. (1998, for Germany), Landolt (1991, for Switzerland) and Keller and Hartmann (1986, for the canton Aargau, Switzerland).

2.2. Light conditions

Reliable information on species richness in the former woodlands of central Europe is hard to find (Schuler, 1998). Pollen records show that thousands of years ago, woodland clearance for settlement purposes increased tree species richness (Tipping et al., 1999). Zoller and Haas (1995) suggested inductive reasoning to reconstruct forest's conditions before settlement. They drew on pollen data, notes from former travelers in different regions, and personal impressions of the remnants of pristine forest, in concluding that pristine forests in central Europe must have been dense and dark. When vegetation began to be recorded scientifically in the last century, information on species richness became more accurate, but was still rare. What scant data there are support the widespread assumption that the structure of forests in the 18th or 19th century was generally more diverse than it is today (Egloff, 1991; Duelli, 1994; Bürgi, 1999). The main reason for this is that forest management at that time differed from today's management with respect to both intensity and variety (Schuler, 1998).

Schiess and Schiess-Bühler (1997) documented a decrease in the number of butterfly species in a formerly intensively disturbed woodland area in Switzerland due to the abandonment of traditional forest management practices such as low coppice, coppice-with-standards, forest pasture and removal of grass and litter. During the last 70 years, up to 40% of the butterfly species traditionally occurring in these forest stands have disappeared due to continuous forest regeneration and the resulting darkening of the woodlands. This figure is even 59% if the adjacent open country is taken into account. For the same region, Bürgi (1999) mentioned a multitude of different forest uses in the 19th century, so-called minor forest uses, such as forest-pasture, litter-collecting, short-term agricultural use and the collection of tanbarks.

The past flora of the wooded region of the Lägern (Switzerland) was reconstructed by studying old herbarium specimens, excursion notes and publications, with the aim to compare the results with the present day flora (Egloff, 1991). A total of 74 plant species have become extinct locally during the past 100 years (extinction rate of about 10%). Corresponding with the gradual change in light conditions, 13 light-demanding plant species typical of forests or forest edges have disappeared and another 10 species were reported to be reduced in population size or numbers of sightings. The increase in shade was considered to be the predominant cause of species loss. As a remedy, Egloff suggests that forest management should be more intensive. For a similar time period, Keller and Hartmann (1986) reported extinction rates ranging from 4 to 8% for various forests in canton Aargau (Switzerland).

Many authors have reported that the species richness of different taxa increases after disturbance impacts on forest ecosystems. Palmer et al. (2000) demonstrated species richness of vascular plants increasing in a pine and in an oak forest over the course of 14 years after a catastrophic windthrow. In a comparison of windthrown forests and adjacent undisturbed forests, Duelli and Obrist (1999) found insect species increased in richness on windthrow areas. Niemelä et al. (1996) showed that the small-scale heterogeneity arising from different forest succession states increased invertebrate diversity on the forest floor. Disturbed forest structure was considered an important factor in influencing bird diversity (Easton and Martin, 1998; Fuller and Green, 1998). Annand and Thompson (1997) highlighted the correspondence between a wide variety of forest management practices and greater bird species richness. At the same time, there are many publications demonstrating a decrease in species richness in undisturbed forests where succession has caused a decline in the light available within the stands. The abandonment of management has resulted in a decrease in light-demanding vascular plants. Trautmann (1976) and Wilmanns et al. (1986) have shown the consequences of changes in light conditions for tree and shrub species in Germany. In Switzerland, many locations of rare forest plants documented in old sample plots have been re-visited after 30–50 years. Results show that many light-demanding species have disappeared during this period due to the increased darkening of forests that have not been managed for a long time (Känzig-Schoch, 1996). More generally, the average light indicator values of monitored Swiss forest plots have decreased in almost all plots considered (Kuhn et al., 1987; Kuhn, 1993). In summary, disturbances in forests tend to positively influence the number of species of many taxa, whereas undisturbed forest succession can limit many plant and insect species.

There are, however, forest species that need long-term succession to become established. Indeed, numerous epiphytic lichens, especially late-stage colonizers such as foliose lichens of the genera *Lobaria*, *Sticta* and selected species of *Arthonia* are well known as indicators of ecological continuity over centuries (Rose, 1992; Goward, 1994), i.e. of an undisturbed lichen habitat during the past tree generation. Recent investigations have shown that the dispersal of species with relatively large symbiotic diaspores is limited. Such species are therefore inevitably lost in a habitat with even lower rates of disturbance (Scheidegger et al., 1998). In central Europe and Scandinavia, dead wood fauna (Niemelä, 1997; Bakke, 1999; Schiegg, 2000) and cryptogamic species (Rose, 1992; Ohlson et al., 1997) are most effectively conserved in old-growth forests where dead wood and bark substrate are continuously available. Vast reserves are needed to protect viable populations of several large mammals (Shafer, 1990). Habitat requirements of continuity-demanding species therefore have also to be considered in an ecology-based management approach.

2.3. Human impacts

The development of forests in central Europe is closely linked with the history of human impact. Humans have had a wide range of impacts on forests (e.g. Radkau and Schäfer, 1987). Forests were cleared as agriculture spread and trees cut down to satisfy the need for fuel, construction, fencing, and all sorts of tools. Later, forests also had to fulfill wood requirements of many early industrial activities. Furthermore, forests were used for a whole range of other uses, e.g. for wood pasture, collecting litter, bark, berries, mushrooms, and many other forest products. Taken together, these human-induced disturbances had profound, complex, and long-lasting consequences on the forests as ecosystems (e.g. Salbitano, 1988; Glatzel, 1991; Teller et al., 1992).

Since the 16th century, the increase in forest use has given rise to voices predicting timber shortages. However, prophetic warnings seem to have been much more widespread than timber shortages have actually ever been (Radkau and Schäfer, 1987). Nevertheless, these warnings fostered the emergence of scientific forestry with corresponding legal tools during the 18th century first in Germany and later in other central European countries as well. In order to ensure that timber production continued to be sustainable, forests were organized by well-trained foresters, who classified and surveyed the stands. The more diverse the forests were, the harder it was to survey the area or even to quantify the standing timber volume. Therefore, Lowood (1990) states that forest science originally was aimed at the reduction of stand diversity. During the 19th century, various traditional non-timber forest uses, now disqualified as “minor forest uses”, were banned from the forest area (Schiess and Schiess-Bühler, 1997; Schuler, 1998). Changes in the agricultural system favored the abandonment of such agroforestry practices. Thus, the period of “traditional multiple use” of the forests was followed by a period of “primacy of timber production” (Bürgi, 1999). Together with the so-called minor forest uses, a great variety of locally adapted legal forms eventually disappeared (Schuler, 1998). The loss of legal diversity was paralleled by a loss of diversity in anthropogenic disturbance, causing a loss of habitat diversity, which contributed to changes in species composition.

In the second half of the 19th century, the spread of new ideas in forestry was enhanced by the growing availability of new sources of energy. In around 1850, the Swiss economy was still largely based on fuelwood energy (Pfister, 1990), but by around 1910 coal had become the most important source of primary energy (Marek, 1994). This shift in the energy supply explains why erosion control, and not the fear of timber shortage, was the main concern fostering the creation of the federal Forest Police Law in 1876 (Schuler, 1996). The decline in demand for timber and other forest products made it easier to protect the forests from exploitation and to apply legal restrictions to forest use and management. Moreover, this decline in demand was paralleled by a shift from erratic forest use to more strictly organized forest management. These changes led to a significant decline in the anthropogenic disturbance of forests, beginning in the 19th century and lasting until the present day. Less tree cutting meant that the quantity of timber in the forests increased not only in Switzerland but in almost all European countries (Kuusela, 1994). Today, annual felling amounts to only 65–77% of the annual growth. Proposals have been made to increase wood usage in both central Europe and Scandinavia (BUWAL, 1999; Parviainen, 1999). In addition, recent studies in many European countries on forest growth have revealed that forest stands today are growing faster, at least in central Europe, than previously (Spiecker et al., 1996). This raises questions about a potential increase in the risk of windthrow due to increases in tree age and tree size (König, 1995; Gardiner and Quine, 2000).

3. Disturbances and their effects on species richness

3.1. Causes of disturbances

Disturbances have been defined in various ways, such as limitation of plant biomass (Grime, 1979), cause of mortality (Huston, 1979), disruption of an ecosystem, community or population structure (Pickett and White, 1985) or discrete events causing unusual mortality and changing resource availability in ecological communities (Davis and Moritz, 2001). We adopt the latter definition in this article and see disturbances as promoting environmental heterogeneity and preventing ecosystems from reaching equilibrium. They are caused by a wide variety of factors (see e.g. White, 1979; Attiwill, 1994; White and Jentsch, 2001) and have been categorized in various ways, e.g. according to whether they have endogenous and exogenous causes (White, 1979; Scherzinger, 1996) or are of natural or human origin (Attiwill, 1994). White (1979) suggests that exogenous and endogenous causes are actually in continuum and claims that it is impossible to clearly distinguish between these two categories. With respect to the distinction between natural and human-induced disturbance, Oliver and Larson (1990) commented "that there are probably only few human disturbances for which a counterpart cannot be found in nature". In the context of forest ecosystems in central Europe, we nevertheless suggest that it is useful to try to distinguish between (a) endogenous; (b) exogenous; and (c) human-induced disturbances (Table 1), where the causes are (a) biological events such as gap-dynamics or insect outbreaks (endogenous disturbances); (b) natural hazards such as windthrow, fire, floods, avalanches and landslides (exogenous disturbances); and (c) forest use and management (human-induced disturbance).

The frequency and intensity of disturbances in endogenously disturbed communities is low. Forests evolve more or less undisturbed and in a long-term succession if natural gap dynamics only occur rarely, pressure from game is low and there is no exogenous disturbance. Whereas there are hardly any natural forests in Switzerland, 13% of the forest area in Switzerland have not been managed for more than 50 years (Brassel and Brändli, 1999), i.e. in these areas human-induced disturbance has been absent for a long time.

In central Europe, wind is clearly the most important exogenous disturbance factor. About two-thirds of all unplanned felling in Switzerland is caused by storm winds. Insect calamities which cause mortality account for an additional 13% of unplanned felling (BUWAL, 1997). In comparison, the impact of avalanches or landslides on forests is relatively small. The catastrophic avalanches of 1999 in Switzerland felled 160,000 m^3 of timber, compared to 5 million m^3 timber thrown by the storm 'Vivian' in 1990 or 12.5 million m^3 by the storm 'Lothar' in 1999 (WSL, 2000). Fire may be of importance only in the southern

Table 1
Categories of disturbance and their effects on forest ecosystems in Central Europe

Disturbance types	Cause	Examples	Disturbance regime			Effects on species			
			Spatial extent	Intensity	Frequency	Dominance	Ecological groups	α-Diversity	γ-Diversity
Endogenous (≈gradual)	Forces inside a stand	Aging and decay resulting in gaps, moderate game pressure	Small	Low	High	Reduction or increase depending on gap size	Maintains continuity demanding species	Small contribution	Large contribution
Exogenous (≈episodic)	Forces outside a stand	Wind, fire, avalanches, flooding, landslides, pests	Potentially large	High	Low	Often reduces dominance	Maintains light-demanding species	Large contribution	Small contribution
Human-induced (≈periodic)	Human activities	Forest management (cutting, planting), pasture, collecting of firewood, litter and other forest products	Highly variable	Highly variable	Highly variable	Highly variable	Highly variable	Highly variable	Highly variable

parts of Switzerland where most forest fires are considered to be of anthropogenic origin (Tinner et al., 1999).

Human-induced disturbances in central European forests arise predominantly through management practices. According to the Swiss National Forest Inventory, tree cutting is predominantly selective. Sanitation cutting is of equal importance in forests that have been damaged by natural hazards as well as by insect calamities (Brassel and Brändli, 1999). In mountain forests on steep slopes, regeneration felling is increasingly being applied (Ott et al., 1997; Brang, 1998).

The effects of disturbances are as diverse and complex as the causes. However, in the ecological literature we find several hypotheses regarding the link between disturbance and species richness which suggests that a major effect of many disturbances is characteristically dominance reduction.

3.2. Effects of disturbances on species richness

Among the many hypotheses proposed to explain variations in species (Palmer, 1994), we focus on those which refer to dynamic influences and which are hence based on or related to disturbance as an initiating process. For this theoretical discussion, we evaluate two hypotheses and one principle with respect to the role of disturbance intensity.

3.2.1. Intermediate disturbance hypothesis

The hypothesis is usually associated with the paper of Connell (1978), containing a hump-back graph showing how diversity peaks at intermediate disturbance levels. Wilkinson (1999) argued that it was Grime (1973) who first published a similar graph that links intermediate disturbance to high levels of species richness. However, what Connell actually said was: "high diversity is maintained only when the species composition is continually changing. Diversity is higher when disturbances are intermediate on the scales of frequency and intensity". Disturbance causes the mortality of dominant organisms. Intermediate levels of disturbance is defined with respect to the intensity, the frequency, and the size or time since the last disturbance. The hypothesis is based on the assumption that equilibrium in nature is hardly ever reached. Connell assumes that non-equilibrium is normal, because species assemblages change as a result of frequent disturbances or as a result of more gradual climatic changes. He refers to studies of the ecological succession of tropical rain forests as well as of coral reefs. Soon after a severe disturbance, new species arrive in the cleared space. Repeated disturbances cause diversity to remain low because there are only few species capable of reaching maturity and eventually reproducing. As the intervals between disturbances lengthen, more species will invade and more species will reach maturity resulting in higher species richness. As disturbance frequencies decline further, competitive species will become dominant over inferior, often ruderal species, eventually resulting in the competitive exclusion of the latter species.

3.2.2. Dynamic equilibrium hypothesis

Huston (1979) also argued that "equilibrium must occur rarely, if at all". He assumes that: (a) competition would reduce diversity at or near equilibrium; (b) different species have different population growth rates; (c) changes in environmental variables (caused by disturbance) affect all competing populations. Taken together this means that mortality-causing disturbances are not independent of the rate of competitive displacement. On this basis, the dynamic equilibrium model of species diversity consists of two opposing forces: the competitive interactions that lead to competitive exclusion and the disturbances that give rise to mortality. Species diversity can be affected by either of the two processes. It is high if the disturbance frequency equals the rate of population growth and of competitive displacement (Huston, 1979, 1994).

3.2.3. Competitive exclusion principle

In a synopsis of existing hypotheses related to species variation, Palmer (1994) listed 120 hypotheses published in 81 different papers. In order to aggregate most of the listed hypotheses, he proposed reformulating the competitive exclusion principle following the structure of the Hardy–Weinberg principle of genetic equilibrium (Hardy, 1908). In a "given suite of species, interspecific competition will result in the exclusion of all but one species". Palmer lists seven conditions under which the principle holds (Table 2). The greater the degree to which the conditions are broken, the greater is the number of species that can coexist. Disturbance processes potentially break all of these conditions (Table 2).

Table 2
Conditions of the reformulated competitive exclusion principle according to Palmer (1994), and the role of disturbance processes

No.	Condition that favor competitive exclusion	The role of disturbance as a process to break the condition
1	Time has been sufficient to allow extinction	Disturbance disrupts the succession
2	The environment is temporally constant	Disturbance stops the constancy
3	The environment has no spatial variation	Disturbance changes (and generally enhances) environmental variation
4	Growth is limited by one resource	Disturbance causes new arrays of resources. In forests, the growth of many herbs under the tree canopy is limited by light. If a dead tree falls down, there is no longer a local light limitation for such plants so that their growth accelerates. Depending on the size of the gap, shade-tolerant species or shade-intolerant species will temporarily dominate
5	Rarer species are not disproportionately favored in terms of survivorship, reproduction, or growth	If a disturbance damages or kills some dominant tree species disproportionately, also the reproduction and growth of some species other than the canopy trees, e.g. shade-intolerant herbs, will also be disproportionate
6	Species have the opportunity to compete	Disturbance events are frequently isolated in space and time. Early successional species in a patch disturbed, e.g. by catastrophic windthrow cannot compete with those in another windthrow patch, resulting in the coexistence of these plants in a larger landscape
7	There is no immigration	Disturbance fosters the temporal establishment of species from adjacent communities (mass effect or vicinism; Shmida and Whittaker, 1981; Zooneveld, 1995). In special cases, such as large-scale disturbance, species may even immigrate further afield

3.3. Dominance reduction

The hypotheses mentioned above refer explicitly to the process of disturbance. Implicitly, however, they also describe the effect of the disturbance on one or more species that eventually causes changes in diversity. The relation between disturbance rate, species dominance and species richness is hypothetically illustrated in Fig. 3. The dominance of a few species may be high with low disturbance rates, e.g. prevailing in forests that are managed by selective thinning, in unmanaged mature and old-growth forests with undisturbed succession or in forests where disturbance only affects the less common species. Only one species also tends to dominate if disturbance rates are high, e.g. if there is agricultural production. Most of the forest ecosystems in Central Europe are more or less dominated by only a few tree species (Ellenberg, 1988). The low tree species richness in the temperate flora of Europe accounts to a considerable extent for the development of such an obvious dominance hierarchy (Latham and Ricklefs, 1993). Additionally, extensive afforestation during the second half of the last century leveled the stand age and reduced local tree species diversity (Salbitano, 1988; Schuler, 1988). Some specific management practices have led to a monotonous forest structure as well. Therefore, disturbance to canopy trees in central European forest ecosystems frequently causes the limitation or reduction of dominant species.

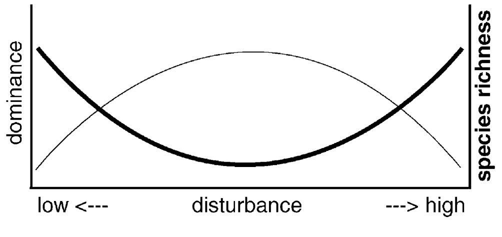

Fig. 3. Relationship between disturbance rate, dominance of species and species diversity. Low and high disturbance rates correspond to timber and agricultural production. The dominance of species is marked as a bold curve, the species diversity as standard curve (from Schiess and Schiess-Bühler, 1997).

Many of the features that are generally related to disturbance can be addressed as dominance reduction. Windthrow often reduces the dominance of all trees resulting in a tree-regeneration accompanied by a rapid spread of vegetation that favors clearings with a considerable amount of random colonization (Connell, 1978; Gilgen, 1994; Wohlgemuth et al., 1995; Palmer et al., 2000). Fire causes the mortality of most of the species in the herbaceous layer, regardless of whether it is in forests or in grasslands. In many regions of the world, fire has proved to play an essential part in the life cycle of an ecosystem (e.g. Oliver and Larson, 1990). Floods cover the ground with sediments causing the mortality of most of the species in the herbaceous layer. Landslides create new sites. Both floods and landslides enable ruderal species to seed and spread until other species begin to competitively exclude them.

The death of a canopy tree can have different effects: if the canopy tree has dominated other species for decades, these species and new ones will benefit from the improved light conditions and react with improved growth. In contrast, if the canopy tree itself has been dominated by larger trees for decades, either the dominance conditions will not dramatically change, or the already dominating species will even increase their dominance.

Insect calamities bring about a reduction in dominance of a population. In central Europe, Norway spruce (*Picea abies* (L.) H. Karst) is the tree species most affected by such calamities (Stenseth and Kirkendall, 1989). Because foresters have been promoting this fast-growing tree species for centuries, its actual representation in stands far exceeds its natural occurrence. In combination with unfavorable growth proportions, Norway spruce is prone to windthrow. In forest stands that are dominated by Norway spruce, spruce bark beetles (*Ips typographus* L.) can considerably reduce dominance resulting, again, in improved light conditions. In contrast, if a disease affects a less common tree such as the Wych elm (*Ulmus glabra* Huds.) in central Europe (elm disease; Brasier, 1988), the dominance of adjacent canopy trees may be increased. Forest management can lead to both a reduction or an increase in dominance.

A multitude of traditional management practices affect the mortality of dominant species leading to dominance reduction, e.g. clearcut, group felling, strip system, coppice system, coppice-with-standards forest and to some degree, forest pasture. In contrast, if forest management is aimed at promoting rare species in a mixed forest or promoting preferred individuals in a forest that is dominated by only one or two species, the effect of such a disturbance on single trees is an increase in dominance of the preferred tree species. Selective thinning, a widely applied technique in Swiss forestry ("Swiss selective thinning") may best maintain the ecological continuity of forest communities under management regimes (Frey, 1958; Schütz, 1998), but it presumably has a negative influence on the species richness of trees and vascular plants.

In order to distinguish between disturbance effects with respect to species richness, we believe that a dominance reduction enhances species richness and a dominance increase reduces species richness. We define dominance reduction as the direct effect of any disturbance process that (a) causes the mortality of one or several of the dominating species in an ecosystem; and (b) thus alters the dominance hierarchy in this ecosystem. Our definition is based on a recent publication on the ecological principle of "Dominanzminderung" (Schiess and Schiess-Bühler, 1997). "Dominance reduction" is the normal translation of "Dominanzminderung", but differs slightly in meaning from what Schiess and Schiess-Bühler (1997) intended. They were particularly concerned to translate "disturbance" adequately. In our definition we stress the distinction between process, i.e. alterations in resource availability and system structure (Pickett and White, 1985), and effect, i.e. parameters that respond to disturbance, to clarify the difference between disturbance and dominance reduction.

4. Dominance reduction as a management principle outside forest reserves

Bunnell and Huggard (1999) recommended being wary of any rule, policy or guideline that prescribes the same management approach everywhere. In other words, if we want to generate heterogeneity, we have to address a wide range of conditions to which no single management scheme can be applied. Homogeneous management practices would reduce diversity, including biodiversity (Bürgi, 1998a; Bunnell and Huggard, 1999). If we understand forest management as providing guidance in the short-term while keeping long-term goals in mind (Alpert, 1995; Bengtsson et al., 2000), the long-term goals have to be specified before management principles and site-specific management schemes can be developed.

During the 20th century, forest management has undergone a shift from a period of "primacy of timber production" to a period of "multi-impact management" (Bürgi, 1999), as new demands from society have led to the incorporation of recreational needs and of nature conservation into traditional forest management. Today, the goals of forest management often include sustaining or promoting biodiversity. Thus, they rely heavily on scale-related management networks where strictly preserved forests reserves are linked with forests managed according to close-to-nature silvicultural practices (Angelstam and Petterson, 1997; Parviainen et al., 2000). The diversity of schemes necessary to achieve the long-term goal of sustaining biodiversity is well-illustrated by attempts to combine forest reserves and actively managed forests. Considerable scientific effort has been put into network design and into long-lasting monitoring programs aimed at surveying the ecological continuity of these networks (Indermühle et al., 1998; Diaci, 1999). But how much forest area does actually fall into the reserve category? The percentage of protected forests compared to the total forest area in European countries ranges from 0.1 (Belgium) to 24.0% (Spain), or 7.1% on average in the countries mentioned in Diaci (1999). Even if the total area of forest reserves may increase in future, a considerable part of the biodiversity has to be protected outside of forest reserves. In other words: ‘‘reserves alone are not adequate for nature conservation but they are the cornerstone on which regional strategies are built’’ (Margules and Pressey, 2000).

In forest reserves, endogenous and exogenous disturbance types (Table 1) are the driving forces behind forest development. For the remaining 75–99% of the total forest area, we have to identify the appropriate management approaches—interpreted as human-induced disturbances—to achieve the long-term goal. A wide variety of legal, economic, ecological, and social factors have to be considered in developing forest management schemes. An integration of many of the different, and sometimes conflicting, needs and demands was achieved in the Swiss federal Law on Forests in 1991. According to this law, the main legal constraint on silviculture in Switzerland is that it should serve to fulfill the three forest functions that are given by the law: (1) the protective function, i.e. forests have to protect people and property against natural hazards; (2) the social function, which covers the importance of the forest for recreation, tourism and biodiversity; and (3) the economic function, aimed at safeguarding and developing the commercial aspects of forestry.

Even if forest managers find ways of taking all these different needs and demands into account, they will repeatedly have to face the widespread effects of major exogenous disturbance events, which severely hamper long-term management plans. If we take dominance reduction as a management principle, as we propose in this paper, then these unexpected disturbances can be incorporated within the long-term goal of biodiversity protection. Instead of trying to include an increasing number of needs and demands, forest management should be guided by the core ecological characteristics of forests. They include not only all potential anthropogenic impacts on forests (i.e. human-induced disturbance), but also the exogenous and endogenous disturbance regime to which forest are naturally subject.

Given that (a) forests in Central Europe are becoming older, denser and darker; and (b) biodiversity may be enhanced by generally improving light conditions, we propose that forest management outside forest reserves should be directed towards the controlled reduction of dominance. What are the implications of this theoretical approach for forest management in practice? One is that a diversity of traditional and alternative timber harvesting methods should be encouraged. For example, several authors have recently suggested promoting the small-scale species richness by applying controlled forest management practices that mimick the effects of natural disturbances (Haila et al., 1996; Niemelä et al., 1996; Vetaas, 1997; Niemelä, 1999). Identifying those management practices which lead to dominance reduction may be helped by considering past agricultural and silvicultural forest use and management practices. For example, controlled grazing by sheep or goats in abandoned forest pastures can bring back a moderate disturbance rate (Valderrábano and Torrano, 2000). Even the clear-cutting of certain forest stands may, in some cases, be both economically and ecologically appropriate, although this harvesting method is prohibited by law in Switzerland.

The past cannot give us all the answers we need for the future, but it is one source. In seeking of new ways of managing central European forests, the principle of dominance reduction may well be seminal, because it captures certain ecological and historical aspects of the relation between species richness and the three types of disturbance we defined (endogenous, exogenous, and human-induced disturbance). We believe that by applying dominance reduction as a management principle within a network of forest reserves, it will become possible for the forests of Central Europe to better fulfill the ecological functions necessary for a healthy environment as well as the economic functions required of them by society.

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