DISSERTATIONES BIOLOGICAE UNIVERSITATIS TARTUENSIS

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THREATENED VASCULAR PLANT SPECIES IN ESTONIA: CAUSES OF RARITY AND CONSERVATION

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CONTENTS

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I Pärtel, M., Kalamees, R., Reier, Ü., Tuvi, E.-L., Roosaluste, E., Vellak, A., Zobel, M., 2005. Grouping and prioritization of vascular plant species for conservation: combining natural rarity and management need. Biological Conservation, 123, 271–278.

II Reier, Ü., Tuvi, E.-L., Pärtel, M., Kalamees, R., Zobel, M., 2005. Threatened herbaceous species dependent on moderate forest disturbances: A neglected target for ecosystem-based forest management. Scandinavian Journal of Forest Research, 20 (Suppl 6), 145–152.

III Pärtel, M., Helm, A., Ingerpuu, N., Reier, Ü., Tuvi, E.-L., 2004. Conservation of Northern European plant diversity: the correspondence with soil pH. Biological Conservation, 120, 525–531.

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INTRODUCTION

There is growing worldwide concern about the status of biodiversity. The IUCN Red List is being developed as a tool that helps to organize biodiversity conservation (Lamoreux et al., 2003). In recent years, Red Lists have enjoyed an increasingly prominent role in guiding national conservation activities (Gärdenfors, 2001). In Europe, there are also species that deserve attention across all European countries and are listed in the annexes of the European Commission Habitats Directive (1992; 92/43).

Species listed in Red Data Books, lists of species protected by national laws, and species in EC Directives are all accorded certain “conservation status”, i.e. they are considered to be endangered by some kind of factor on a certain scale, and active or passive means need to be taken to stabilize or improve their status. Red Lists describe how threatened a species is (low number of localities found or low number of individuals), and the major likely reasons for its decline (Hilton-Taylor, 2000). Habitat loss, direct exploitation, indirect human influence through changing local ecological interactions, natural disasters, pollution and intrinsic factors (unfavorable species traits) have been listed among the main threats. This attribution is frequently based on only the personal experience of a few conservation biologists; exact knowledge is often limited. Conservation legislation, however, also includes other types of arguments, such as commercial importance and aesthetics. In addition, the conservation assessment of different taxonomic groups is unequal.

Biodiversity conservation requires careful planning (e.g. Younge and Fowkes, 2003). An example is a scientifically reasoned action plan for a particular species (Palmer, 1996). The number of species with conservation needs has increased, however, to a level where we no longer have the time and resources to elaborate action plans for each individual taxon. When focusing on some subjectively selected “hot” species, the status of overall diversity may worsen. Instead, one might collect a kind of general information about the possible factors and mechanisms behind the real or potential decrease of the local or global abundance and distribution area of these species. On the basis of such information, one could prioritize species conservation needs and establish groups of species that could be subjected to similar action plans.

In addition to being important for practical nature conservation, study of the causes of plant species rarity has been of fundamental importance for understanding the distribution and dynamics of plant species (Kunin and Gaston, 1997; Rosenzweig, 1997). There are two dominant approaches to the study of possible causes of plant rarity. The first, “inductive approach”, focuses on the comparative study of the traits of rare and common plant species. Despite optimistic expectations, the results of such studies have not always resulted in much conceptual advance, because no clear differences have emerged between the traits of rare and common plant species (Bevill and Louda, 1999; Murray et al., 2002) and relationships between traits and rarity are evidently context-dependent (e.g. Pilgrim et al., 2004).

Several studies have shown that rare plant species are concentrated on high pH soils, for example in the Sheffield region (Hodgson, 1986), Estonia (Kull et al., 2002), Swedish forests (Gustafsson, 1994), and grasslands in the Netherlands (Roem and Berendse, 2000). Plant diversity in Europe is generally strongly positively related to soil pH (Grime, 1979; Grubb, 1987; Ewald, 2003). In a global-scale study, it has been shown earlier that the soil pH/plant diversity relationship depends on soil type in regional evolutionary centers (Pärtel, 2002). An additional aspect is the broadness of species soil pH requirement. According to Rabinowitz (1981), habitat specificity is one criteria of rarity. For example, rare species had a narrow ecological range in the region of Sheffield (Hodgson, 1986) and Finland (Lahti et al., 1991).

Biodiversity is a relatively new indicator of nature conservation value (Haila and Kouki, 1994). In contrast, the presence of threatened species has been used in reserve selection for a long time. Threatened species can serve as indicators of overall diversity if they share similar requirements with non-threatened species, e.g., they do not have higher soil pH requirements than non-threatened species. Comparison of soil pH preferences of threatened and non-threatened species using raw lists of species gives information about the current trait patterns, but, due to phylogenetical relationships between species, is biased to reveal causality. Grytnes et al. (1999) showed that rare and common species of Fennoscandia are not taxonomically equally distributed. Moreover, species soil pH preference showed significant phylogenetic conservatism: it depends on the legacy from species' ancestry, not only on species' own adaptations (Prinzing et al., 2001). Causal relationships between rarity and soil pH preference or its broadness can be revealed correctly with methods which consider phylogenetical relations of species (Silvertown and Dodd, 1996; Eriksson and Jakobsson, 1998; Tofts and Silvertown, 2000; Pärtel et al., 2001).

The "deductive approach" of species rarity studies is based on classifying plant species into so-called rarity categories according to the nature of their distribution and habitat requirements. Rabinowitz (1981) proposed a general scheme by which species are classified into categories according to their geographic range, habitat specificity and local population size. These categories offer a general hypothetical explanation for species rarity. Species with narrow geographic range may be rare for historical reasons. In the case of habitat specificity, the basic reasons for rarity are of evolutionary origin, but habitat destruction may also play a role. If local populations are small, local factors, such as biotic interactions and human impact are probable causes of rarity. There are rather few studies that have attempted to use Rabinowitz's scheme in regard to the flora of particular regions, e.g. British Isles (Rabinowitz et al., 1986), France (Médail and Verlaque, 1997), Spain (Blanca et al., 1998) and Amazonia (Pitman et al., 1999). Until now, such an approach has been mostly theoretical and the link to practical conservation has been weak. In particular, one must note that human impact is not specifically considered in Rabinowitz's system.

There is, however, also a "synthetic approach" on species rarity, which tries to combine the use of traits and rarity categories (Lahti et al., 1991; Saetersdal, 1994; Gustafsson, 1994; Kull et al., 2002; Rogers and Walker, 2002). Though most of these trials have evidently not yet reached the stage by which the results could be useful for practical conservation, this approach clearly has higher application potential than the previous two, since it indicates the main threats for species and the main habitats for rare species. Successful examples in which the link to practical conservation already exists include priority analysis for Central European plants, where threat status was combined within formation about world-wide distribution (Schnittler and Günther, 1999), and a statistical study on rarity and threat factor relations in Iberian flora (Lozano et al., 2003).

From our synthetic approach (I) it become evident that a special category is often neglected in nature conservation: species dependent on moderate forest disturbances (II). Nature conservation in forestry has mostly concerned old-growth stands (Linder, 1998; Trass et al., 1999). Several components of biodiversity are exclusively associated with late-successional natural forests (Bossuyt et al., 1999; Graae and Sunde, 2000). Consequently, a part of plant diversity may be lost "between" strict protection and conventional forestry.

Most plant communities in the world have been influenced by human activities (Pickett and White, 1985). In some cases, coevolution with humans has made them richer in species, as exemplified by semi-natural grasslands (Marttila et al., 1999; Pärtel et al., 1999; Critchley et al., 2003). Recent findings show that forest has also developed together with human influence, even in the Amazonian region (Willis et al., 2004). Most forests in Europe and the USA have been continuously influenced by humans (Meikar et al., 1999; Bellemare et al., 2002; Wulf, 2003). A forest considered primeval according to many features, may in fact have a long domestic grazing history (van der Maarel, 1996). Nature conservation has gradually expanded its goals, now encompassing both human-influenced as well as pristine plant communities (Palmer et al., 2004). Nowadays, forest management means not only timber production, but also biodiversity, rare species conservation and social benefits (Roberts and Gilliam, 1995; Simberloff, 2001, Jõgiste et al., 2002). In an ideal case, biodiversity conservation can also be incorporated into ecosystem-based forest management (Kuuluvainen, 2002; Wulf, 2003).

In forest ecosystems, any impact that removes organisms and opens up space can be considered a disturbance (Pickett and White, 1985). In addition to natural forest disturbances such as windthrows and animal-created gaps, forest cutting and fires ignited by people are the most frequently considered forest disturbances of human origin. In most cases, human disturbances in forest ecology have been considered in relation to the tree layer: partial or total exclusion of trees (Crow and Perera, 2004). Much less information has been available on moderate human disturbances influencing mainly the understorey: grazing of domestic animals, leaf harvesting, moss gathering, forest paths, etc. Many such activities were formerly common forest utilization practices in addition to tree cutting (Berg et al., 2002). In addition, human-induced fire can sometimes be less intensive, not affecting grown trees but creating gaps in the understorey (Ryan, 2002).

As biodiversity is a major target for nature conservation, attempts are made to maintain biodiversity in forest management practices. Species diversity is one of the criteria in the restoration of natural forests (Jõgiste et al., 2002). In theory, an intermediate level of disturbances is associated with the highest diversity (Connell, 1978; Shea et al., 2004). In temperate and boreal regions, the forest understorey is typically much more diverse than the woody layers. There are, however, very few examples in which the intermediate disturbance hypothesis has been validated for the forest herbaceous layer. In Canadian boreal forests, species diversity generally peaks at intermediate site treatments (Haeussler et al., 2002). In Japanese beech forests, the locations that sustained an intermediate frequency of disturbance had the highest species diversity (Hiura, 1995). Similarly, the highest plant diversity in Himalayan oak forest was observed at the intermediate level of disturbances, not in undisturbed sites (Vetaas, 1997).

Contrary to the intermediate disturbance hypothesis, there are several examples in which clear-cut sites have higher richness than less disturbed forests (Zobel, 1993; Peltzer et al., 2000; Pykälä, 2004). This high plant richness, however, typically consists of several ruderal or even exotic species, or just species that have their main habitat outside forests. This means that counting the number of species without filtering out the forest species pool is not a reasonable basis for planning biodiversity conservation (Pärtel et al., 1996; Ingerpuu et al., 2001). Similarly, it has been recommended that exotic species must be excluded when calculating biodiversity (Watkins et al., 2003). Consequently, the focus should be on a set of species that occurs mainly in forests, since ruderal and grassland species are much better protected in their main habitats. There are successful examples from Belgium (Honnay et al., 1999; Godefroid and Koedam, 2003) and Finland (Pykälä, 2004) where biodiversity studies have focused namely on forest species groups. Among forest species, most attention has still been paid to the human-avoiding taxa typically occurring in old-growth stands (Bossuyt et al., 1999; Graae and Sunde, 2000). Having worked with the national list of plant species with conservation need (I), we note that there is a number of species of nature conservation interest that actually require moderate forest disturbances for regeneration. These species are in reality not protected by strict nature conservation (human disturbances prohibited), and they are also suffering in conventionally managed forests (clear-cutting and the creation of uniform stands). Since most of these species are actually characterized by relatively similar ecological requirements, they could be treated as a coherent target group for nature conservation in forests. To the author’s knowledge, disturbance-dependent forest understorey species have not been considered in the context of biodiversity conservation before. The number of such species present can be an indicator to measure forest conservation values or the adequacy of conservation management.

Disturbance-dependent forest understorey species are listed and their traits characterized for Estonia (II). Estonia is a small country in northern Europe that may as well serve as a good model for such a survey owing to its long history of nature conservation on the one hand (Sepp et al., 1999) and long-term active forestry on the other (Örd, 2000; Meikar, 2002).

The general objective of this thesis was to study the causes of rarity of Estonian vascular plants and to propose a new synthetic approach for plant species conservation. To solve this task we undertook the following:

– Paper I analyzed the national list of vascular plant species with conservation need in order to understand the main possible causes of plant rarity, to suggest new priority categorization within the list and to group plant species according to different conservational aspects. We tested whether our conservation characteristics are related to each other, and how our conservation characteristics are related to the present conservation legislation and national Red Data Book criteria.
– Paper II provided a national list of herbaceous species that depend on moderate forest disturbances, and tested whether these species share some specific traits with other species with conservation need, to propose sustainable forest management and conservation practices to preserve these species for the future.
– Paper III tested whether threatened plant species in Northern Europe have higher soil pH requirements than non-threatened species and whether threatened species have more restricted soil pH preference than non-threatened species.

MATERIAL AND METHODS

The national list of vascular plant species with conservation need (I, II) was compiled on the basis of the lists of legally protected vascular plant species of Estonia (Ü. Kukk, 1999), plant species in the Red Data Book of Estonia (Lilleleht, 1998) and species from Annexes of the EC Habitats Directive (1992; 92/43) that are found in Estonia.

The vascular plant flora of Estonia contains 1441 species (T. Kukk, 1999). There are 185 legally protected vascular plant species in Estonia and these are divided into three priority categories. The Red Data Book of Estonia lists 309 vascular plant species and subspecies in five categories. Annexes of the Habitats Directive list 21 vascular plants species that also occur in Estonia. In order to make the lists comparable, we excluded all infraspecific taxa and microspecies with no clear taxonomic status (e.g. species from the genera *Alchemilla, Crataegus, Euphrasia, Hieracium, Pilosella, Rosa, Taraxacum*) as suggested by Schnittler and Günther (1999). The lists largely overlapped, and the final summarized national list of plant species with conservation need was found to consist of 301 species.

The assessment was based mostly on information from Ü. Kukk (1999) and the Estonian Red Data Book (Lilleleht, 1998). In addition, available long-term unpublished records were used: herbarium collections (TU, TAA) and expert opinions on the distribution of endangered species. Published information on a few particular species in Estonia is also available (Kull, 1999; Pilt and Ü. Kukk, 2002). Nomenclature follows T. Kukk (1999).

In order to analyze the entire list of plants species of conservation status in Estonia (I), each species was assessed on the basis of the following eight qualitative conservation characteristics: four reflecting natural causes of rarity (restricted global distribution; restricted local distribution within Estonia; always small population size; very rare habitat type), and four related to nature management (species depending on the management of semi-natural grasslands; dependence on local natural and human-induced disturbances; needing traditional extensive agriculture; species which may be threatened due to collecting).

According to these qualitative features we classified species into groups threatened by the same major factors. In order to rank the studied species by the associated number of conservation characteristics we analyzed the co-occurrences of different conservation characteristics by principal component analysis (PCA) with eight characteristics as factors and 301 species as cases. A similar approach has been used successfully in other regions (Given & Norton, 1993; Lozano et al., 2003). In addition, the Fisher Exact Test was used to discover associations between factor pairs. The interrelation of different conservation characteristics with the species categorization according to legislation and according to the Red Data Book was studied with the help of Spearman rank correlation. Existing species categorization was coded so that a higher number was given to the most threatened or rare species.

Since the second study assessed herbaceous species, all trees and shrubs were excluded from the list. The target list of herbaceous species with conservation need was found to consist of 247 species. Species whose regeneration takes place mostly either in small gaps or in disturbed forest areas were extracted (II). Species that grow mainly on grasslands or ruderal habitats, but that may occur in forests very occasionally were excluded (II).

To compare disturbance-dependent species with other species of conservation interest, different traits in their conservation, biogeography and ecology were considered:

- belonging to one of the three conservation categories according to Estonian legislation (Ü. Kukk, 1999)
- belonging to one of the five Estonian Red Data Book categories: endangered, vulnerable, rare, care demanding, indeterminate (Lilleleht, 1998)
- global distribution type: Europe, Eurasia or circumpolar (T. Kukk, 1999)
- whether a species is at the border of its distribution area (T. Kukk, 1999)
- commonness within Estonia: six ordinal classes (T. Kukk, 1999)
- life form: therophyte, geophyte, hemicryptophyte, chamaephyte, hydrophyte (Ellenberg et al., 1991)
- requirements for habitat light conditions, according to the Ellenberg ecological indicator values: ordinal nine-scale classes (Ellenberg et al., 1991)
- requirements for soil moisture (Ellenberg et al., 1991)
- requirements for soil pH (Ellenberg et al., 1991)
- requirements for soil nitrogen content (Ellenberg, et al., 1991).

Since the aim was to describe the group of disturbance dependent species in forests, not to reveal evolutionary or ecological causalities, cross-species analyses were performed using species as independent replicates (II).

To find differences between forest disturbance-dependent species and other species of conservation interest, the χ^2-test was used for nominal variables (Red Data Book, global distribution, distribution border, life form) and the Mann-Whitney *U*-test for ordinal values (legal protection categories, commonness within Estonia, Ellenberg ecological indicator values).

For the third paper we determined threatened vascular plant species from the Red Data Books for twelve Northern Europe countries or Russian administrative districts: Denmark, Estonia, Finland, Karelia, Latvia, Lithuania, Murmansk, Norway, Novgorod, Pskov, St. Petersburg, Sweden. Soil pH preferences were taken from Ellenberg et al. (1991). We compared species soil pH preferences among congeneric threatened and non-threatened species pairs to eliminate the effect of phylogeny (for methods, see Pärtel et al., 2001). Wilcoxon-matched pairs test was used to check whether threatened species require higher soil pH than non-threatened species. Using the same species pairs we also checked whether threatened plant species were more likely to prefer narrowly defined soil pH and non-threatened species a wider range. We compiled 2 x 2 tables (threatened/nonthreatened and specified pH preference/ indifferent) and used one-tailed Fischer Exact Test. Additionally, we performed Wilcoxon-matched pairs test to check if this pattern is significant over all countries (comparing the number of indifferent species among threatened and non-threatened taxa). Since repeated tests were made with species pairs for each country ($n = 12$), Bonferroni correction was used for *P*-levels and a result was considered significant at $P < 0.004$.

RESULTS

Grouping and prioritization of vascular plant species for conservation (I)

The distribution of the conservation characteristics among the species of conservation need varied greatly. *Restricted global distribution* was the most common conservation characteristic, associated with 38% of species of conservation need. Other common conservation characteristics included *restricted local distribution* (28%)*, dependence of grassland management* (32%)*, threat due to collecting* (31%)*, always having small populations* (21%). The last common conservation characteristic was *very rare habitat* (7%). Other less frequent characteristics were *dependence on forest disturbances* and *dependence on traditional extensive agriculture*.

PCA on conservation characteristics revealed that the first axis described 17.2 % and the second 16.9 % of the total variation (Fig. 1). On the ordination diagram, all characteristics show very little overlap. There was only one significant positive association between conservation characteristics: *restricted local distribution* and *small population size* (Fisher exact test, two-tail, $P = 0.026$). Significant negative associations were between *restricted global distribution* and *threat due to collecting* ($P = 0.020$), *restricted local distribution* and *threat due to collecting* ($P = 0.007$), *restricted local distribution* and *dependence of grassland management* ($P = 0.037$), *threat due to collecting* and *dependence on traditional extensive agriculture* ($P < 0.001$).

Most species were associated with one or two characteristics (31% and 37% respectively), 15% were associated with three, 5% with four, and 1% with five characteristics. For 11% of the species, none of the eight conservation characteristics were considered to be important.

The relation of different conservation characteristics to conservation categories according to Estonian legislation and the national Red Data Book is presented in paper I Table 1. Categories in the present laws for species protection were related to *restricted local distribution, small population size* and *very rare habitat.* There was a negative correlation between *threat due to collecting* and the legislation. In the case of the Red Data Book, there was only a single significant positive correlation: species with *restricted local distribution* had mostly been placed in a high category. Species with *dependence on traditional extensive agriculture* were mostly in a low category. The sum of characteristics was correlated with the protection categories according to legislation ($n = 179$, $r = 0.28$, $P < 0.001$), but not with the categories of the Red Data Book ($n = 270$, $r = 0.08$, $P < 0.191$).

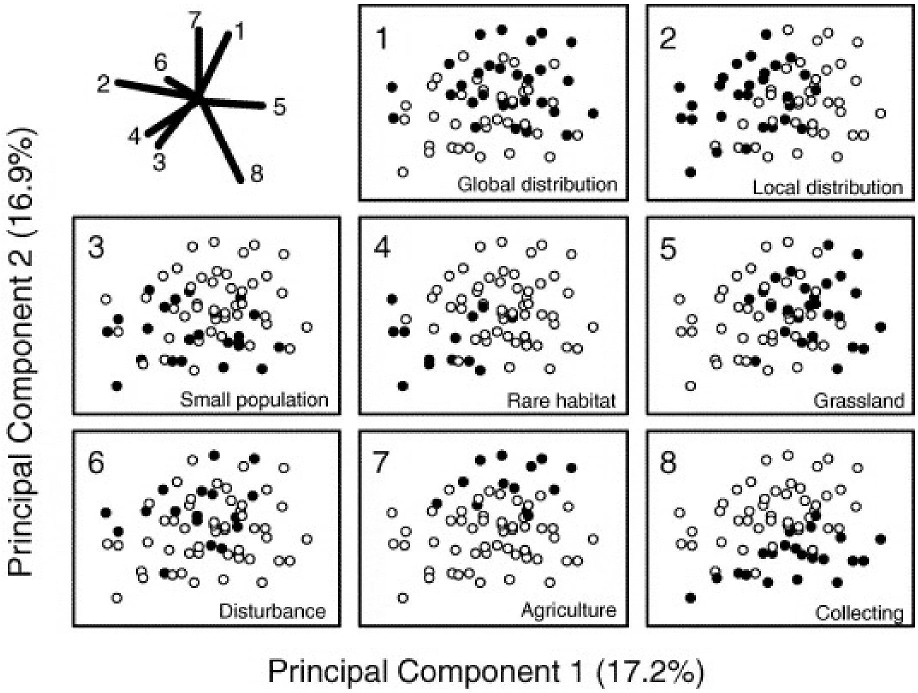

Fig. 1. Principal component analysis of eight conservation characteristics for 301 vascular plant species with conservation need in Estonia. Projection of the conservation characteristics (top left) and species for each characteristic (filled circles) on the factor-plane. Conservation characteristics include: (1) restricted global distribution; (2) restricted local distribution within Estonia; (3) small populations; (4) very rare habitat type; (5) species needing management of semi-natural grasslands; (6) species needing small-scale forest disturbances (e.g. fires); (7) species needing traditional extensive agriculture; (8) species threatened by collecting.

Threatened herbaceous species dependent on moderate forest disturbances (II)

Sixty-seven herbaceous species of conservation interest are dependent on moderate forest disturbances (II, Table 1). This is 28% of all the herbaceous species of conservation interest in Estonia.

Most of the disturbance-dependent species inhabit dry forests, either in boreal forests on sandy soils or in alvar forests on thin calcareous soils. Species characteristic to fresh boreo-nemoral forests and even to some moist forest types were also represented. The growth of virtually all these species is facilitated by small-scale gaps, created by partial tree harvesting or as a result of natural tree-fall gaps. Many species are benefited by soil disturbances. A smaller number of species require mechanical clearing of undergrowth, grazing by domestic animals or prescribed fire.

There were no differences among disturbance-dependent forest species and other species of conservation interest regarding representation of the conservation categories of the national legislation (U = 3535, Z = –0.37, P = 0.711). At the same time, a significant difference appeared in the representation of the Red Data Book categories (II, Fig.1): disturbance-dependent forest species more often belonged to the endangered category and less frequently to the indeterminate category.

No differences were found between disturbance-dependent and other species with respect to global distribution, proximity to distribution boundary or commonness in Estonia.

Life-form distribution was significantly different between the two species groups (II, Fig. 2). Ecological requirements differed between the two species groups in regard to light (disturbance-dependent species require less light, U = 2133, Z = –5.5, P <0.001) and moisture requirements (disturbance-dependent species prefer drier soils, U = 2464, Z = –4.7, P < 0.001).

Northern European vascular plant diversity in relation to soil pH (III)

The number of congeneric species pairs for each 12 countries/districts ranged from 14 to 78 (III, Table 1). Soil pH preference differed between threatened and non-threatened species only in Norway, where threatened species required higher pH than non-threatened. This result, however, became non-significant after Bonferroni correction.

Broad pH requirements were consistently less common among threatened species than among non-threatened (III, Table 2). After Bonferroni correction most of the tests remained significant. Wilcoxon-matched pairs test revealed that this pattern is significant within the region (n = 12, T = 0.00, Z = 3.1, P = 0.002).

DISCUSSION

The possible causes of rarity may be classified into two broad categories: "natural rarity" and rarity due to human activity. We showed that these categories do not overlap and should be used in combination (I). The existing conservation system, however, focuses on the former. Each particular cause of rarity can describe a group of species that require similar conservation measures. Thus, same strategies can be applied to several species, not just to individual species.

Quite a large number of rare species show a small distribution area on a global scale, i.e. their rarity may have "biogeographic reasons". In addition, as is the case in Finland (Lahti et al., 1991), the great majority of rare plant species in Estonia are at the northern margin of their distribution area, i.e. their distribution and local abundance are restricted by climatic constraints (Kukk, 1999). Comparative studies of the ecology of rare and common species have shown that "biogeographic reasons" may have an important role in determining the local abundance of species (Witkowski and Lamont, 1997; Walck et al., 2001), although particular processes and mechanisms are not easy to identify. In such cases, "active" conservation is scarcely possible and nature conservation usually entails simply the preservation of particular ecosystems in which the particular species already occurs. There are several studies that claim that most rare species in Europe require high pH soils (Hodgson, 1986; Nilsson and Götmark, 1992; Gustafsson, 1994; Roem and Berendse, 2000). However, we had to reject our initial hypothesis that a shortage of high pH soils in Northern Europe causes rarity and is a threat to plant species (III). The most European threatened species do require high pH soils, but this is also true for non-threatened species. We have shown that the requirement of threatened species in Northern Europe was not more biased towards high pH soils than non-threatened species. Consequently, the number of threatened species can be successfully used as an indicator of overall biodiversity level. Our second study showed that biogeographical parameters did not differ between forest disturbance-dependent and other species, indicating that the target group consists of species of different origin (II).

In addition, there are species whose rarity is directly or indirectly dependent on human activity. Cessation of management in seminatural grasslands is an important reason for the decrease of the distribution area and local abundance of many plants species (Linusson et al., 1998; Austrheim et al., 1999; Cousins and Eriksson, 2001). Contemporary forestry, which inhibits wildfires and results in uniform dense stands without natural gaps, may suppress the regeneration of species whose regeneration is favored by the suppression of competition due to local disturbances (Uotila, 1996; Pilt and Ü. Kukk, 2002; Korpilahti and Kuuluvainen, 2003). We have shown that almost one-third of threatened herbaceous species in Estonia were deemed dependent on moderate forest disturbances (II). There is, however, little information from other countries in which endangered forest disturbance-dependent species are considered specifically for conservation. Similarly, the most important threats for forest biodiversity in Finland are considered to be the changes in forests induced by modern silviculture (Rassi et al., 2000). Consequently, introducing moderate forest disturbances into forestry and forest conservation practices can support a large number of species.

Species with low dispersal ability suffer from fragmentation of habitats – this has been studied, for example, for many ecosystems in Europe (Graae and Sunde, 2000; Butaye et al., 2002; Graae et al., 2004; Bossuyt et al., 2004). In the case of such species, "active" conservation measures are possible and reasonable. These measures may include not only the restoration of former management or disturbance regimes in specially protected areas, but also the restoration of local populations by introducing diaspores or transplanting plant individuals into habitats from which the species has vanished.

Conservation priority categorization of vascular plants frequently relies on the experience and intuition of conservation biologists (Sutherland et al., 2004). The current approach may give a more objective basis for prioritization, since one may assume that the more conservation characteristics a species has been assigned, the higher the overall risk that the species will become extinct in the particular region under consideration. Therefore, one can assign different status to species in the conservation lists. Analysis of conservation characteristics over the whole list of species with conservation need would furnish conservationists with a powerful objective tool with which to confirm or challenge subjective decisions. For example we can put the following species in the order of conservation priority in Estonia: (1) *Hypericum montanum*: found just in Europe, low number of localities in Estonia, small populations, needs grassland management and forest disturbances; (2) *Dianthus arenarius* subsp. *arenarius*: low number of localities in Estonia, threat due to collecting, needs grassland management and forest disturbances; (3) *Filago minima*: found just in Europe, low number of localities in Estonia, needs traditional agriculture; (4) *Asplenium ruta-muraria*: very rare habitat type, threat due to collecting; (5) *Viola elatior*: needs grassland management.

The analysis of categories in the Red List of Estonia (Lilleleht, 1998) revealed no correspondence between the categories and the number of associated conservation characteristics. The Estonian Red Data Book describes solely restricted distribution in Estonia. Weeds associated with traditional agriculture have been given low priority, probably for psychological reasons. Such a mismatch indicates that additional analysis is needed of the categories in the Red Data Book of Estonia. The match was much better when species categories in Estonian legislation were considered. The legislation covers all aspects of rarity according to Rabinowitz (1981). A negative association with species threatened by collecting is due evidently to a tradition of including rather common yet esthetical species (e.g., several *Orchidaceae* species) in the lowest category. The results of our second study (II) showed that disturbance-dependent forest species in Estonia are equally represented in all three legal protection categories, but significantly overrepresented in the highest Red Data Book threat category, ‘‘endangered’’. Thus, practical nature conservationists have evaluated these species as being more endangered than the rest of the herbaceous species of conservation interest in Estonia (Lilleleht, 1998; Ü. Kukk, 1999).

Traditionally, the starting point in plant conservation has been the identification of rare species (scarcity of localities), followed by the identification of possible threats. In reality, the rarity of most species is the outcome of multiple and frequently either unknown (or overlooked) processes. The traditional approach is certainly justified in most cases, but it can be complemented by the additional approach proposed below. We suggest that the planning of conservation measures should start with cases where active conservation is possible, i.e. those in which human influence is the most probable cause of rarity, and then consider the remaining species in the order of most probable cause of rarity (Fig. 2).

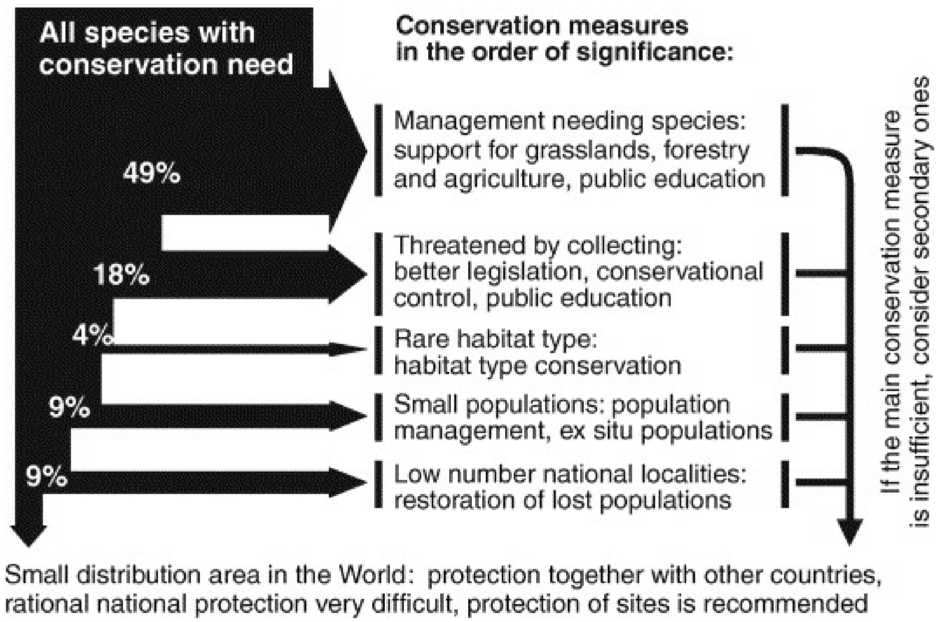

Fig. 2. Suggested order of vascular plant species conservation planning for Estonia, starting with human-induced causes and progressing through to natural causes of rarity. The situation for most species can be improved with modified human influence and better legislation.

The status of almost half (49%) of species with conservation need can be improved by proper management. Conservation actions entail support for conservation management, such as traditional grassland management and agriculture, and prescribed forest disturbances. As was shown previously, almost one-third of threatened herbaceous species in Estonian were estimated to be dependent on moderate forest disturbances (II). Public education is an important aspect as well.

An additional 18% of species are threatened by collecting, and better legal regulation and public education can help. Since the cause–effect relationship is relatively evident in management and threat due to collecting, one may expect that either supported management or restrictive regulation will result in a relatively rapid positive effect on local biodiversity.

A smaller share of species with conservation need (4%) depends on the presence of particular rare habitat types. Some of these types, such as rocky habitats, oligotrophic lakes or flood plain and escarpment-associated forests, may be rare in a particular region for natural reasons (cf. Paal, 1998).

Other habitat types may be rather common, but their late successional stages may be rare due to overwhelming management activities. Old-growth forests and undrained mires serve as examples in Estonia (Paal et al., 1999; Viilma et al., 2001). We have shown that threatened vascular plant species in Northern Europe require more restricted soil pH, whereas non-threatened species tolerate a broader range of soil pH (III, Table2). In a comparison of threatened and non-threatened vascular plant species in Finland, the threatened species had more specialized edaphic requirements (Lahti et al., 1991). Likewise, habitat specificity was the most frequent form of plant rarity in Norway (Sætersdal, 1994). Habitat specificity is a widely used criterion for defining rare species (Rabinowitz, 1981). Restricted habitat specificity is characteristic of 59% of British vascular plants (Rabinowitz et al., 1986) and 67% of vascular plants in Estonian grasslands (Ingerpuu, 2002). Consequently, in order to protect a wide array of threatened species, it is important to have reserves not only on high pH soils but also on low pH soils.

In both cases, the persistence of specific natural habitat types depends mostly on restrictive regulations. Consequently, these habitat types should be strongly protected in situ.

The subsequent 9% of species with conservation need have very low populations, evidently for evolutionary and historical reasons. For instance, a species may be outside its optimal geographical distribution, it may be a climatic relict, etc. In such cases, there are expensive conservation mechanisms available, such as artificial regeneration of local populations (sowing of seeds, planting individuals) or ex situ conservation, based on population viability analyses (Menges, 2000). In order to avoid extinction due to chance events, the average population size should be much larger than needed for a viable population in general.

There are 9% of species with conservation need that have healthy populations but very limited distribution. Such species may be rare due to inadequate dispersal. For these species, the same measures as mentioned above may be applicable. In particular, restoration of historical locations may be justified (Heywood and Iriondo, 2003).

There are 11% of species with conservation need that are considered to be threatened mainly due to a small global distribution area, although national dispersal and population sizes are large. These species require international protection, though continuous monitoring of these species is requested. Schnittler and Günther (1999) used the term "conservation responsibility" for species that can successfully be protected by the authorities of one region, since the species is mainly restricted to those regions.

In addition, if the leading conservation measure is insufficient, subsequent measures should be considered in proper sequence (see Fig.2). It is not wise to apply population management or population restoration for species that actually need grassland management or are suffering due to collecting. Similarly, restoration of abiotic conditions of a plant community should be followed by the introduction of diaspores and proper future management of this site (van Diggelen and Marrs, 2003).

One possibility to include scientific knowledge into conservation strategies is to collect more evidence-based information (Sutherland et al., 2004). We have shown that another important possibility is a synthetic approach, combining different conservation characteristics and measures in regard to lists of species with conservation need. It allows one to work with species groups with similar conservation needs instead of individual species, and to set priorities by assuming that a high number of different conservation characteristics associated with a species indicates its vulnerability. Such an approach has a potential to improve strategies for national plant diversity conservation.

We have tried to implement this synthetic approach in selecting and analysing threatened herbaceous species dependent on moderate forest disturbances (II). In this study some principles for sustainable management of forest biodiversity were proposed with the emphasis on disturbance-dependent herbaceous species as a group that comprises almost one-third of threatened herbaceous species in Estonia. The growth of virtually all these species was facilitated by small-scale gaps, created by partial tree harvesting or as a result of natural tree-fall gaps. Many species were favoured by soil disturbances. Fewer species need mechanical clearing of undergrowth, grazing of domestic animals or prescribed fire.

It may be suggested that a certain type of human disturbance has to be accepted for conservation purposes. Until now, many such disturbances have been totally prohibited by conservation authorities. There is also an example from Belgium in which some rare forest species occurred more commonly close to the city border than in less disturbed forest (Godefroid and Koedam, 2003). Similarly, 25% of all species in a hardwood landscape in Wisconsin were associated with forest roads and just 12% with the forest interior (Watkins et al., 2003).

Some disturbances may have serious negative effects as well. There are several examples in which some type of human disturbance has decreased plant diversity in forests. For example, waste deposits in the boreo-nemoral zone decreased both vascular and bryophyte diversity (Ingerpuu et al., 2003). Controversial effects of forest disturbances are reported in Belgium, where disturbances increased the number of rare forest species, at the same time causing the appearance of competitive non-forest species (Bossuyt et al., 2002). Therefore, it is important that any artificial disturbance regimen has the correct intensity and linkage to traditional forest use practices (Verkaik and Nabuurs, 2000). Since this work is based on scarce literature data and personal observations, more research on the biology of forest disturbance-dependent species is needed. Experiments on different forest disturbance regimens and their impact on biodiversity are urgently required since only the first steps have so far been taken (Jõgiste et al., 2002).

CONCLUSIONS

Many earlier decisions on conservation status and possible threats rely on tradition, not on analysis of scientific information. The number of species with conservation needs has increased, however, to a level where we no longer have the time and resources to elaborate action plans for each individual taxon. Species grouping by different conservation characteristics allows one to focus on species groups with similar conservation needs instead of individual species. We propose a new combined approach by which species are grouped according to the similar activities needed for their conservation. We used the national list of vascular plant species with conservation need for Estonia (301 species), and linked these species to eight qualitative conservation characteristics, four reflecting natural causes of rarity (restricted global distribution; restricted local distribution within a country; always small populations; very rare habitat type), and four connected with nature management (species needing the management of semi-natural grasslands; species needing local disturbances such as forest fires; species needing traditional extensive agriculture; species which may be threatened by collecting). It was shown that natural causes of rarity and management aspects do not overlap, and both should be used in conservation activities. Prioritization of species with conservation needs can be based on the number of conservation characteristics that are associated with a particular species. Our prioritization did not correlate with the categories of the national Red Data Book, but a positive association was found with legal protection categories. The legislation, however, covers only the natural causes of rarity. We propose a new combined approach for conservation planning of plant species that starts by considering human-induced rarity and progresses through to natural rarity causes.

Intensive forest management is an example of human-induced rarity of moderate disturbance-dependent herbaceous plants. Most forests have a long history of moderate human disturbances. In the temperate region this coevolution has resulted in high species diversity because many threatened herbaceous species depend on moderate forest disturbances. We applied our new approach to identify this group of species and the similar activities needed for conservation in Estonia. One-third of threatened herbaceous species were estimated to be dependent on moderate forest disturbances (mainly small-scale gaps through partial cutting or natural uprooting of trees, and moderate soil disturbances). Disturbance-dependent species ranked high in the national Red Data Book and were particularly common to dry forests. Disturbance-dependent herbaceous species should be considered as a target group for ecosystem-based forest management. Moderate disturbances are required in both managed and protected forests to conserve forest biodiversity.

Effective biodiversity conservation requires analysis of the existing system. Since biodiversity data are never complete for all taxa, biodiversity indicators, e.g., threatened species, should be used. In temperate and boreal regions, plant diversity has a strong positive association with soil pH. We tested whether soil pH requirement differs between threatened and non-threatened vascular plant species and found that threatened and non-threatened species in Northern Europe do not differ in their soil pH requirements, but threatened species required a narrower soil pH range than non-threatened species. Consequently, threatened species diversity can be used to indicate overall plant diversity.

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SUMMARY IN ESTONIAN

EESTI OHUSTATUD SOONTAIMELIIKIDE HARULDUSE PÕHJUSED JA KAITSE

Praeguseks on kaitset vajavate liikide (k.a. liigisised taksonid) arv tõusnud sedavõrd suureks, et ei jätku enam ei aega ega vahendeid neile kõigile eraldi kaitsekorralduskavade koostamiseks. Seetõttu põhinevad otsused kaitsekategooriate ja võimalike ohtude osas endiselt rohkem traditsioonidele kui teaduslikule analüüsile. Selline olukord ei taga ohustatud liikide ja bioloogilise mitmekesisuse edukat säilitamist. Väljapääs oleks liikide rühmitamises vastavalt nende looduskaitselisele väärtusele (tunnustele), mis annab võimaluse rakendada sarnaseid kaitsemeetmeid tervele grupile sarnaste tunnustega liikidele, selle asemel, et tegeleda iga ühega eraldi. Oma uurimuse tulemusena esitasime uue kombineeritud lähenemisviisi, mille puhul ohustatud soontaimeliigid on rühmitatud vastavalt sarnastele kaitsemeetmetele. Analüüsi aluseks olid kaitstavate soontaimede ja Punasse Raamatusse kuuluvate soontaimede koondnimestik (301 taksonit), sest Eesti tingimustes kattuvad need nimestikud osaliselt. Koondnimestiku taksonid seostati kaheksa looduskaitseliseliselt olulise tunnusega, millest neli peegeldasid looduslikke harulduse põhjuseid (piiratud levikuga kogu maailmas, piiratud levikuga Eestis, alati väikesearvuliste populatsioonidena, väga haruldastes kasvukohtades kasvavad) ja neli olid seotud majandustegevusega looduses (poollooduslike rohumaade majandusviise vajavad liigid, häiringuid nagu metsatulekahjud jms vajavad liigid, traditsioonilise ekstensiivse põllumajandusega seotud liigid ja liigid, mida võiks ohustada korjamine). Analüüsi tulemused näitasid, et looduslikud harulduse põhjused ja erineva majandamise mõju harulduse põhjusena ei kattu ja kaitse edukaks korraldamiseks tuleks arvestada mõlemaid. Iga liigiga seotud looduskaitseliste tunnuste arv võiks edaspidi saada kaitse korraldamise vajaduse pingerea koostamise (liikide kaitsekategooriatesse rühmitamise) aluseks. Analüüsi tulemusena selgus, et meie rühmitamise alusel saadud liikide grupid ei korreleerunud praegu kehtiva Punase Raamatu kategooriatega, kuid olid positiivselt seotud riiklike kaitsekategooriatega. Riiklikult kaitstavate taimeliikide nimestike koostamise puhul on peamistena võetud arvesse looduslikke harulduse põhjuseid. Käesoleva analüüsi tulemuste alusel meie poolt koostatud uus kombineeritud rühmitamine võtab arvesse nii inimtegevusest põhjustatud kui looduslikke harulduse põhjuseid ja oleks kaitsealuste taimede rühmitamise alusena objektiivsem ja ilmselt kaitse korraldamise alusena tulemuslikum.

Üheks inimtekkeliseks harulduse põhjuseks on kaasaegne intensiivne metsamajandus, mis puudutab peamiselt mõõdukat häiringut vajavaid rohttaimi. Meie metsade traditsiooniline majandamine on sajandeid olnud teistsugune kui viimased pool sajandit. Kogu parasvöötmes on toimunud pikaaegne koosareng mõõduka inimtegevuse ja seda vajavate soontaimeliikide vahel, mille tulemusena on Eestis kujunenud liigirikkaid metsakooslusi, kus esineb hulgaliselt ka haruldasi liike. Viimasel ajal on teadvustatud puisniitude traditsioonilise majandamisega seotud liigirikkuse püsimist, traditsioonilise metsade majandamisega seotud häiringuliikidele on seni vähe tähelepanu pööratud. Mõistetavalt on sellistele liikidele kahjulik intensiivne metsa majandamine, vähem on teadvustatud, et sama saatuslikuks võib osutuda ka range reservaadi režiim. Meie eesmärgiks oli eristada kaitse aluste taimede ja Punase Raamatu rohttaimede hulgast metsa häiringuliigid. Rakendades nende liikide analüüsimisel meie poolt varem väljatöötatud uudset kaitsealuste taimede rühmitamise metoodikat, selgitasime välja võimalikke sarnaste häiringuvajadustega liigid, mille kaitse korraldamine nõuaks sarnaseid majandamise viise. Analüüsi tulemusena selgus, et peaaegu üks kolmandik ohustatud rohtaimeliikidest osutus mõõdukaid metsaga seotud häiringuid vajavateks (peamiselt väikeste häilude tekitamisega üksikute puude langetamise tulemusena või ka tuuleheidet soodustavate tingimuste tekkimisel erivanuselistes metsades, aga ka metsa majandamisel kaasneva mõõduka mullahäiringuga). Häiringuliigid klassifitseerusid Punase Raamatu analüüsi tulemusena ohustatumatesse kategooriatesse ja peamiselt oli tegemist liikidega, mis esinevad kuivadel mineraalmuldadel kasvavates metsades. Seega tuleks edaspidi üha rohkem metsade ökosüsteemsel majandamisel arvestada häiringuliikidega. Mõõdukate häiringutega majandamine on metsa alustaimestiku liigirikkuse ja haruldaste liikide säilitamiseks vajalik nii kaitstavates kui ka aktiivselt majandatavates metsades.

Selleks, et eluslooduse mitmekesisust ka tulevikus edukalt säilitada ja kaitsta on vajalik praegu kehtivat korraldust analüüsida. Me ei saavuta kunagi ideaalset olukorda, kus me valdame täielikku andmestikku kogu mitmekesisuse kohta ja seda isegi mitte sellises väikeses ja botaaniliselt üldiselt hästi läbi uuritud riigis nagu Eesti. Rohkem on andmeid ohustatud liikide kohta. Sellest lähtuvalt püstitasime ülesande uurida, kas ohustatud liike võiks kasutada teatud juhtudel bioloogilise mitmekesisuse indikaatoritena ja saadud tulemusi kasutada kogu bioloogilise mitmekesisuse kaitse korraldamisel. Nagu on varem kindlaks tehtud, kehtib parasvöötmes tugev positiivne seos mulla lubjarikkuse ja soontaimede liigirikkuse vahel. Sellest lähtuvalt kontrollisime, kas mulla pH vajaduste osas on statistilisi erinevusi ohustatud ja tavaliste liikide vahel. Meie poolt uuritud kaheteiskümne Põhja-Euroopa riigi ja (Venemaa) muu võrreldava administratiivse üksuse puhul sellist üldist erinevust tuvastada ei õnnestunud, küll aga vajasid ohustatud liigid kitsamat pH vahemikku. Eelnevast võib järeldada, et ohustatud liike võib kasutada üldise liigirikkuse hindamiseks.

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PUBLICATIONS

I

Pärtel, M., Kalamees, R., Reier, Ü., Tuvi, E.-L., Roosaluste, E., Vellak, A., Zobel, M., 2005. Grouping and prioritization of vascular plant species for conservation: combining natural rarity and management need. Biological Conservation, 123, 271–278.

II

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III

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3. Conference thesis:

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Participation in the inventory of semi-natural grasslands and Natura 2000 habitats. Inventory of species listed in annexes of the nature directives of the EU and selection of relevant protected areas (*Dianthus arenarius* subsp. *arenarius*), compilation of management plans for protected species (*Rubus arcticus*, *Saussurea esthonica*). Participation in the expert groups at Ministry of the Environment (biodiversity *ex situ* conservation, legislation for protection of genetic resources, protected plant species list for nature conservation legislation, Red Data Book). Supervision of *BSc* and *MSc* student research concerning protected species or areas (*Dianthus arenarius, Dianthus superbus, Potentilla fruticosa, Hypericum montanum, Daphne mezereum, Rhinanthus osiliensis*, Haanja Nature Reserve, Otepää Nature Reserve).

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Pihu, S., Kook, Öpik, M. & Reier, Ü. 2005. Molecular and morphological variatiomn in *Myosotis laxa* Lehm. in the Baltic Sea region and the status of *M.laxa* ssp. *baltica*. – In: XVII International Botanical Congress. 17–23 July Vienna. Abstracts. Vienna, p. 444. (www.ibc2005.ac.at)
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